

Conditions for Major Transitions in Biological and Cultural Evolution

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Abstract

Evolution by natural selection can be seen as an algorithm for generating creative solutions to difficult problems. More precisely, evolution by natural selection is a *class* of algorithms that share a set of properties. The question we address here is, what are the conditions that define this class of algorithms? There is a standard answer to this question: Briefly, the conditions are variation, heredity, and selection. We agree that these three conditions are sufficient for a limited type of evolution, but they are not sufficient for open-ended evolution. By *open-ended evolution*, we mean evolution that generates a continuous stream of creative solutions, without stagnating. We propose a set of conditions for open-ended evolution. The new conditions build on the standard conditions by adding fission, fusion, and cooperation. We test the proposed conditions by applying them to major transitions in the evolution of life and culture. We find that the proposed conditions are able to account for the major transitions.

Introduction

In biology, *evolution* generally means change in the gene pool of a population over time, which can be caused by genetic drift, gene flow, natural selection, and other processes. In this paper, when we use the term *evolution*, we specifically mean *evolution by natural selection*.

Brandon (1996, pp. 5-6) states the following three components are crucial to evolution by natural selection:

1. Variation: There is (significant) variation in morphological, physiological and behavioural traits among members of a species.
2. Heredity: Some traits are heritable so that individuals resemble their relations more than they resemble unrelated individuals and, in particular, offspring resemble their parents.
3. Differential Fitness: Different variants (or different types of organisms) leave different numbers of offspring in immediate or remote generations.

In the literature, *differential fitness* is often called *selection*. Godfrey-Smith (2007) lists the same three components, calling them *conditions for evolution by natural selection*.

Taylor et al. (2016, p. 409) define an *open-ended evolutionary system* as “one that is capable of producing a continual stream of novel organisms rather than settling on some quasi-stable state beyond which nothing fundamentally new occurs,” where *organisms* include “both biological organisms and individuals in artificial evolutionary systems in software, hardware, or wetware.” There is a growing consensus (Taylor et al., 2016) that the standard three conditions (variation, heredity, and selection) are sufficient for a limited type of evolution, but they are not sufficient for open-ended evolution (OEE).

Dennett (1995) and Boden (2015) have argued that evolution by natural selection is an algorithm for generating creative solutions to difficult problems. The promise of this view is that simulated evolution can be a source of solutions to human problems, in addition to providing us with a better understanding of evolution in nature. The problem is that current simulations are not open-ended; they reach a point where further processing yields diminishing returns.

Our goal in this paper is to discover the conditions that enable open-ended evolutionary systems. Taylor et al. (2016, pp. 415-416) provide a comprehensive list of the *behavioural hallmarks* of OEE. To evaluate our proposed conditions, we use their hallmark 1(c), *major transitions in evolution*. The tests for our proposed conditions are seven major transitions in biological evolution from Maynard Smith and Szathmary (1995), seven major transitions in human cultural evolution from Nolan and Lenski (2010), and one super transition (the evolution of human language) that bridges biological and cultural evolution (Deacon, 1998; Richerson and Boyd, 2005).

We selected the major transitions in biological and cultural evolution as our hallmark for several reasons. First, the very idea of OEE comes from observing evolution in biology and culture (that is, evolution *in vivo*, as opposed to *in vitro* or *in silico*); therefore it seems plausible that we can learn what OEE requires by studying major transitions in biology and culture. Second, the major transitions are relatively clear, whereas other hallmarks involve concepts, such as *novelty* and *complexity*, that lack consensus defini-

tions and measures. Third, focusing on abstract measures of complexity and novelty may yield conditions that have theoretical interest but are irrelevant for understanding biological and cultural (*in vivo*) evolution.

In the next section, we will present our proposed conditions for major transitions. The following section will examine related work. The next three sections will test the conditions by applying them to seven major transitions in biological evolution (Maynard Smith and Szathmáry, 1995), one super transition in biocultural coevolution (Deacon, 1998; Richerson and Boyd, 2005), and seven major transitions in human cultural evolution (Nolan and Lenski, 2010). We will then summarize our results, discuss future work, and conclude.

Conditions for Major Transitions

Before we present our conditions for major transitions, we need to discuss the kinds of conditions that we are seeking. First, for the sake of simplicity, we are seeking conditions that make the transitions *possible*, not the conditions that make them *probable*. We assume that the conditions for possible open-endedness are a subset of the conditions for likely (highly probable) open-endedness. For example, a given transition might be likely given a very large population, but merely possible given a population of arbitrary size. Second, we are seeking *declarative* conditions (general, abstract requirements), not *procedural* conditions (step-by-step recipes), because we are interested in a general class of algorithms, not a specific algorithm. We assume that there are many different systems that can manifest OEE, and we wish to characterize the general class, not a special case.

Simon (1962), in his well-known parable of two watchmakers, argued that we should expect a complex system to be composed of relatively stable intermediate components, because a system without such components would be fragile and unlikely to evolve. Living organisms, human-built machines, social organizations, and human languages are composed of stable parts, forming a connected whole. In complex systems, parts can be decomposed into sub-parts, forming a nested hierarchy.

Koestler (1967) coined the word *holon* for a thing that can be seen as either a whole or a part, depending on the level in the hierarchy that is the focus of our attention. In the following description of the conditions for major transitions, our basic unit is the holon. Examples of holons in biology are cells, animals, plants, organs (parts in plants and animals), and organelles (parts in cells). Examples of holons in culture are tools (languages, machines), social organizations (families, governments, companies), individuals (parts in societies), and components (parts in machines).

1. **Reproduction:** There are two types of reproduction, which we may think of as asexual and sexual, although we generalize these concepts so that they apply to both

biology and culture. Reproduction does not change the number of levels in the part-whole hierarchy of a holon. (A) A new holon is created from a single parent holon (as in asexual reproduction in biology). The child holon has the same parts and sub-parts as the parent (typically with some heritable variation; see 5). (B) A new holon is created from multiple, similar parent holons (as in sexual reproduction in biology, but cultural reproduction may involve more than two parents). Each part in the child holon has traits that are a blend of the traits of the corresponding parts in any or all of the parents (typically with some heritable variation; see 5).

2. **Fission-Fusion:** Unlike reproduction, fission and fusion may change the number of levels in the part-whole hierarchy of a holon. (Fission or fusion may occur during reproduction, but we think of them as distinct from reproduction.) (A) With fission, a holon divides into component parts. Depending on the details of the fission process, the resulting holons may have fewer levels in their part-whole hierarchy than the original holon, which no longer exists after fission. (B) With fusion, two or more holons combine to form a new holon, in which the original holons become parts (as in symbiosis in biology). Depending on the details of the fusion process, the resulting holon may have more levels in its part-whole hierarchy than the original holons, which do not exist independently after fusion.
3. **Differential Fitness:** Heritable variation in holons results in different numbers of offspring in immediate or remote generations.
4. **Cooperation:** Open-ended evolution requires the ongoing emergence of mechanisms that cause parts of a holon to sacrifice (some of) their own differential fitness to support the differential fitness of the whole. For example, when fusion combines holons, the fusion will generally require a mechanism that enforces cooperation among the new parts; otherwise the new holon will have relatively low differential fitness.
5. **Heritable Variation:** Variation that can be passed on to future generations includes (A) change to the traits of holons or to the traits of parts of holons, (B) deletion of parts in a holon, (C) duplication of parts in holons, (D) changes in reproductive mechanisms (see 1), (E) changes in fission or fusion mechanisms (see 2), and (F) changes in the mechanisms by which cooperation is enforced (see 4). (G) When a new holon is formed by fusion, the fusion of these specific parts can be a heritable variation (see 2). (H) When a new holon is formed by fission, the existence of this holon as a separate individual can be a heritable variation (see 2).

Comparing Brandon's three conditions for evolution by natural selection (Brandon, 1996, see above) with our five

conditions for open-ended evolution (OEE), we see that Brandon's first condition implies sexual reproduction, since it mentions *members of a species*. Thus his conditions relate to ours as follows:

1. Brandon's Variation → Turney's Reproduction (1B) and Heritable Variation (5A, 5B, and 5C)
2. Brandon's Heredity → Turney's Reproduction (1B) and Heritable Variation (5A, 5B, and 5C)
3. Brandon's Differential Fitness → Turney's Differential Fitness (3)

Brandon's conditions omit asexual reproduction (1A), fission (2A), fusion (2B), cooperation (4), and some types of heritable variation (5D, 5E, 5F, 5G, and 5H).

Brandon (1996) assumes a fixed, two-level, part-whole hierarchy, consisting of *individuals* that are members of a *species*. Therefore his conditions cannot account for an evolutionary transition that involves a change in levels, such as the transition from single-celled creatures to multi-celled organisms. We shall see that several of the major transitions require fusion and cooperation, which enable a shift in the selection unit (a shift in the level of selection).

Related Work

Related work falls into four categories: various proposals for conditions for evolution, arguments for the importance of part-whole hierarchies in understanding evolution, the role of fission and fusion in evolution, and work on the evolution of cooperation.

Conditions for evolution: Godfrey-Smith (2007, 2011) surveys several different sets of conditions for biological evolution and discusses their problems. His own suggested conditions are similar to those of Brandon (1996). Sterelny (2011) proposes eight conditions for biological evolution. It seems to us that his conditions lack generality, due to their focus on specific biological mechanisms.

Taylor (2015) and Soros and Stanley (2014) present conditions for open-ended evolution in natural and artificial systems. Nolan and Lenski (2010) present seven conditions for innovation in human societies. None of these conditions discuss the necessity of part-whole hierarchies and cooperation. Maynard Smith and Szathmáry (1995) discuss part-whole hierarchies and cooperation, but they do not attempt to formulate the conditions required for major transitions.

Part-whole hierarchies: Simon (1962) argued for part-whole hierarchies in complex systems in the social, biological, and physical sciences. Turney (1989) formalized the argument with graph theory. McShea and Brandon (2011) assert that the increase in complexity of organisms over time is largely due to heritable variation in part-whole hierarchies. Banzhaf et al. (2016) define an architecture for building artificial life simulations, in which part-whole hierarchies play a central role.

Fission and fusion: Fusion (2B), forming a new holon by combining two existing holons, enables part-whole hierarchies to add new levels to the hierarchy. Symbiosis, a kind of fusion, is a core element of the major transitions in biology (Maynard Smith and Szathmáry, 1995). Margulis (1970, 1981) played a major role in recognizing the importance of symbiosis. Fission and fusion (2AB) are also major features of cultural evolution (Nolan and Lenski, 2010).

Cooperation: It is widely recognized that cooperation plays an important role in both biological and cultural evolution (Axelrod and Hamilton, 1981; Hammerstein, 2003). Maynard Smith and Szathmáry (1995) spend much effort on explaining the various mechanisms by which cooperation is enforced in biological organisms. The parts in a holon often have conflicting interests, which require organisms to evolve ways to subordinate the differential fitnesses of the parts to the differential fitness of the whole.

Major Transitions in Biological Evolution

In their highly influential work, Maynard Smith and Szathmáry (1995, pp. 3-14) argue that the increase in complexity of biological organisms over time is mostly due to a small number of major transitions in evolution. They state that the theme unifying these transitions is changes in the way genetic information is passed on from one generation to the next. We present their major transitions and discuss how our five conditions apply to them.

Szathmáry (2015) later revised the list of transitions, dropping sex from the list, because it did not fit his model of major transitions. We use the original list, including sex, as it seems to us that the more transitions our proposed conditions can handle, the better.

Molecular compartments: In the right chemical environment, some molecules can make copies of themselves by a sequence of chemical reactions with other molecules; such molecules are said to be *autocatalytic*, since they catalyze their own production. A slight change to an autocatalytic molecule could increase the efficiency of its chemical reaction, which would result in a kind of evolution, since we would have variation, heredity, and differential fitness in favour of the more efficient reaction. However, this change would be a limited form of evolution, because only a small number of variants will be able to support the autocatalytic reaction; almost all changes would end the reaction. Maynard Smith and Szathmáry (1995) call this *limited heredity*, since only a small number of variations are heritable.

A way around this limitation is a *hypercycle*, consisting of a cycle of self-replicating molecules, each of which catalyzes the creation of the next molecule in the cycle. Although each molecule has limited heredity, there is the possibility of adding more molecules to the hypercycle.

A difficulty with hypercycles is that they are vulnerable to parasitic replicators. *Molecular compartments*, by limiting the number of molecules within a compartment, can

penalize parasitic replicators in a hypercycle and force cooperation. Maynard Smith and Szathmáry (1995) argue that molecular compartments are the key development that allowed the transition from limited heredity replicators to *unlimited heredity* replicators.

An autocatalytic molecule is capable of a kind of asexual reproduction (see 1A), although it has limited heritable variation (5A). A hypercycle is a fusion of separate autocatalytic reactions (2B and 5G). Molecular compartments are a mechanism for enforcing cooperation among the autocatalytic molecules (4 and 5F). If an artificial evolutionary system can model autocatalytic molecules and it satisfies our five conditions, then it seems possible for hypercycles to evolve from autocatalytic molecules. The five conditions allow this major transition.

Chromosomes: In modern cells, genes are linked in chromosomes, but it is believed that genes were not linked in the earliest protocells. From the *selfish gene* perspective (Dawkins, 1976), it is necessary to explain why one gene would bind its fate to that of another gene. It takes longer to replicate two linked genes than to replicate either of the genes separately, which puts the linked genes at a disadvantage. Maynard Smith and Szathmáry (1995) contend that two linked genes can out-compete the separate genes when both genes are required for efficient reproduction of the protocell and the number of molecules in the protocell is small.

Linking genes is a kind of fusion (2B and 5G). Limiting the number of molecules in the protocell is a mechanism for cooperation (4 and 5F). Thus chromosomes can evolve in a system that satisfies the five conditions.

DNA and protein: All living cells today use DNA as a replicator and proteins as enzymes. It is generally accepted that early life was based on RNA, which can function as both a replicator and an enzyme for catalyzing chemical reactions. This is called the *RNA world* hypothesis.

One theory is that modern cells evolved from RNA world in two steps: First, cells with RNA alone evolved into cells with RNA and protein; later, cells evolved with RNA, protein, and DNA (Forte, 2005). In the first step, a cell with an RNA genome would benefit from the ability to generate protein enzymes, which are more efficient than RNA enzymes. In the second step, switching to a DNA genome would enable cells to generate a greater variety of proteins. The first step would facilitate the switch, because DNA can be created from the action of protein enzymes on RNA.

A challenge with this theory is to explain how a DNA genome could replace an RNA genome. One possibility is that a cell with an RNA genome was infected by a DNA virus. Over many generations, the viral DNA genome took over the functions of the RNA genome (Forte, 2005).

When a cell with an RNA genome was infected by a DNA virus, the result was a kind of fusion (2B and 5G). Initially cooperation was enforced because the DNA virus relied on the host cell for reproduction (4). Eventually the

RNA genome was eliminated as it became redundant (5B).

Eukaryotes: *Prokaryotes* are single-celled organisms, including bacteria and archaea. *Eukaryotes* may be single-celled or multi-celled organisms, including protists, fungi, plants, and animals. Eukaryotic cells have more complex internal structures than prokaryotic cells, including various *organelles* (little organs) that are wrapped in membranes.

Every eukaryotic cell has a *nucleus*, which is the organelle that contains the main genetic material of the cell. Most eukaryotic cells contain many *mitochondria*, organelles that provide energy to the cell. Many plant cells contain *chloroplasts*, organelles that perform photosynthesis. Mitochondria and chloroplasts were once independent prokaryotes that were taken inside host prokaryotes to eventually become organelles (Maynard Smith and Szathmáry, 1995).

The merging of prokaryotes to form eukaryotes is a kind of fusion (2B and 5G), called *endosymbiosis*. The fusion is mutually beneficial (4): The mitochondria and chloroplasts provide energy to their hosts and the hosts provide key proteins in return. Some of the genes of mitochondria and chloroplasts have migrated into their host's genome, which enforces the fusion (4 and 5F).

Sex: Asexual cloning has many advantages over sexual reproduction: If an organism is better adapted to its environment than other organisms of its kind, then its clone will be equally well adapted, whereas its child by sexual reproduction is likely to be less well adapted. Sexual reproduction brings with it the risks of sexually transmitted diseases. Finding a sexual partner takes time and effort that can be avoided by parthenogenesis. Sexual reproduction leads to wasteful displays, such as the peacocks tail. In plants, sexual reproduction leads to reliance on insect pollinators.

Of the various theories about sex, the evidence appears to support the hypothesis that sexual reproduction allows a beneficial new mutation to spread in a population while also maintaining the variation of genes in the population (Keightley and Otto, 2006). In a population with asexual reproduction, a beneficial mutation might not be favoured by selection if it happens to be combined with a harmful mutation. Sexual recombination can bring together beneficial mutations and split apart harmful mutations.

Our conditions allow sex as an option (1B) without specifying the mechanism. Whether an organism is sexual or asexual is a heritable variation (5D) that can change to adapt to changes in the environment.

Multicellularity: Multicellularity allows organisms with greater complexity and adaptability. Three kinds of eukaryotes have independently evolved multicellularity: animals, plants, and fungi. An animal has many types of cells with varied functions and specializations, such as blood cells, nerve cells, and muscle cells. Maynard Smith and Szathmáry (1995) argue that multicellularity required three key developments: gene regulation, cell heredity, and the evolution of form. The first two of these three developments are

present in prokaryotes, but only eukaryotes are multi-celled, so it seems that the evolution of form was a crucial step.

The *form* of a multi-celled organism is the spatial distribution of the various specialized cells: the shape and structure of the organism. Form is controlled by releasing various chemical signals during the development of an embryo. A chemical signal is released at a specific point and diffuses outwards from that point, resulting in a concentration gradient. The local concentration around a cell determines which genes will be active in that cell. A carefully timed sequence of chemical releases determines how the embryo develops. The initial chemical releases determine the general form of the organism and later releases determine the details.

Multicellularity is an instance of fusion (2B and 5G) in which chemical gradients control the growth and development of the organism (4 and 5F). Cancerous cells escape the control systems of an organism and reproduce at the cost of the health of the organism, although the differential fitness (the number of offspring) of a cancerous cell increases in the short term (until the organism dies). The immune system helps to eliminate cancerous cells (Corthay, 2014), further enforcing cooperation (4 and 5F).

Eusociality: Three characteristics define eusocial animal societies (Maynard Smith and Szathmáry, 1995): (1) There is a division of labour into reproductive and non-reproductive castes. (2) There are overlapping generations within a mature colony. (3) There is co-operative care for the young; some individuals care for the offspring of other individuals. Organisms that have these characteristics include insects (ants, bees, wasps, and termites), mammals (naked mole-rats), and crustaceans (snapping shrimp).

From the selfish gene perspective (Dawkins, 1976), the puzzle is how non-reproductive castes could evolve. This is explained by the concept of *inclusive fitness* (Hamilton, 1964). An individual's child carries half of the individual's genes, whereas the individual's niece or nephew carries one quarter of the individual's genes. Therefore, from the selfish gene perspective, two nieces or nephews have the same value as a single child of one's own. In a colony with one queen, where all individuals are closely related, an individual can spread more copies of its genes by caring for the young of others than it could by raising children of its own.

Another puzzle is that there are some colonies with as many as 100 queens per nest, where individuals might be only distantly related. In multi-queen colonies, it turns out that the workers are sterile, whereas workers in single-queen colonies are typically fertile.

Eusocial societies are a kind of fusion (2B and 5G). In colonies with one queen, the mechanism for cooperation is a set of cooperative behaviours. With multiple queens, cooperation is reinforced by making workers sterile (4 and 5F).

A Super Transition in Biocultural Coevolution

Human language may be seen as a *super transition*, since language is the evolutionary link between biology and culture (Deacon, 1998; Richerson and Boyd, 2005). Cultural inheritance can take place without language; for example, young chimps learn to use sticks to pull ants out of their nests by imitating adults. However, imitation only allows *limited heredity*, compared to the *unlimited heredity* of language. Maynard Smith and Szathmáry (1995) note the analogy between the genetic code and human language: They both enable unlimited heredity by using a linear sequence of a small set of discrete units.

Given that language enabled the transition from biological evolution to cultural evolution, it is natural to ask, how much of language is determined by biology and how much is determined by culture? The answer is that the biological and cultural aspects of language co-evolved; hence they cannot be cleanly divided. Our vocabulary is learned, but certain aspects of our grammar seem to be genetically determined.

The role of genes in grammar raises the question, if a mutation gives an individual a new grammatical ability, what use is that new ability given that nobody else in the population has it? Maynard Smith and Szathmáry (1995) address this problem by appealing to the *Baldwin effect* (Hinton and Nowlan, 1987), which explains how behaviours that are originally learned can become innate, a process known as *genetic assimilation*. A new grammatical ability is at first learned, with some cost in terms of time and effort spent learning. If a new mutation reduces or eliminates the learning effort, that new mutation can spread through the population, and the learned grammatical skill can become innate.

Chimps and humans both form social groups, but language allows greater cooperation among the members of human social groups: Language is a mechanism for strengthening cooperation in a social group (4). It enhances the fusion of the group (2B), enabling more complex group behaviours. The human brain has evolved a variety of mechanisms for supporting language (5F). Some aspects of language are inherited by genetic mechanisms and other aspects are inherited socioculturally (5G).

The evolution of language appears to have been related to the shift to an omnivorous diet, especially big-game hunting. Big-game hunting requires planning, cooperation, and communication, all of which benefit from improvements in language. Chimpanzees in the wild communicate most frequently during meat distribution, which suggests that negotiation of meat distribution may have contributed significantly to the evolution of language in hunter-gatherer societies (Nolan and Lenski, 2010).

Language is the primary technology that characterizes hunter-gatherer societies. Language provided a mechanism for planning, cooperation, and communication that enabled a more effective and efficient fusion of individuals into a society (2B and 4). New social structures in hunter-gatherer

societies (Nolan and Lenski, 2010) provided an environment that encouraged the cultural inheritance of language and knowledge transmitted by language (5F and 5G).

Major Transitions in Cultural Evolution

Human cultural evolution can be viewed in terms of the evolution of social organizations (such as families, governments, and corporations) or in terms of the evolution of human creations (such as technologies, sciences, arts, and languages). Nolan and Lenski (2010) integrate these two views of culture in a principled way. They argue that each major type of social organization is characterized by its *subsistence technology*; that is, the primary technology by which it maintains its way of life. For example, simple horticultural societies are characterized by the domestication of plants.

There are other well-known views of human history, such as the work of Diamond (1997) and Harari (2015), but they do not attempt to systematically divide cultural developments into periods that could be described as major transitions in cultural evolution. We believe that Nolan and Lenski (2010) best define the major transitions in human cultural evolution; therefore the following transitions are based on their work. We present seven major transitions in cultural evolution and apply our five conditions to them.

Domestication of plants: *Simple horticultural societies* emerged around 10,000 to 8,000 BC. Horticultural societies clear land by cutting and burning wild trees and shrubs. The ash provides fertilizer for the crops that they plant. After a few seasons of farming, the ash is depleted and the land must be abandoned until the trees and shrubs grow back.

People in horticultural societies work harder and have less freedom than people in hunter-gatherer societies, so it is not obvious why people would switch from hunting and gathering to horticulture. Nolan and Lenski (2010) argue that three factors led to the transition: (1) environmental change and excessive hunting altered the distribution and reduced the population of large game animals, (2) human population growth resulted in increased demand for food and horticulture was better able to meet the demand than hunting and gathering, and (3) improvements in domestication made horticulture increasingly effective.

Horticulture increased the permanence of human settlements, allowing people to accumulate more tools, weapons, and material goods. Horticulture allowed larger settlements and denser populations, which resulted in growth in trade and commerce. A reliable surplus of food and larger populations allowed specialized occupations (e.g., butcher, bead maker, tool maker) and increased the rate of innovation.

Domestication of plants allowed larger societies (2B), which in turn allowed specialized occupations, analogous to organs in a multi-celled organism. A specialist can acquire a degree of expertise that is not possible for a generalist, which increases the differential fitness of the society. Specialization also enforces cooperation (4), because a spe-

cialist must rely on the skills of other specialists, whereas a generalist is more self-reliant. From a biological perspective, horticulture is a symbiotic fusion of plants and humans (2B), based on the technology of stone tools for cutting and fire for burning wild trees and shrubs (4).

Domestication of animals: *Herding societies* emerged around the same time as simple horticultural societies (Nolan and Lenski, 2010). Many societies practiced both horticulture and herding, but, in some areas, crop cultivation was limited due to lack of rain, short growing seasons, or mountainous land. Herding usually involves a nomadic lifestyle, as the herd exhausts the local pasture. Herding people began riding camels or horses around 2000 BC, which allowed relatively large societies to form in the open grasslands. Horses, camels, and human population size gave herders a military advantage over other societies of the time.

Domestication of animals allowed larger societies (2B), in comparison with the hunter-gatherer societies that they replaced. Larger societies enabled specialization, which enforces cooperation (4). From a biological perspective, herding is a symbiotic fusion of animals and humans (2B), based on the skills and tools of shepherding (4).

Nonferrous metallurgy: *Advanced horticultural societies* are characterized by their use of nonferrous metals for the manufacture of weapons and tools (Nolan and Lenski, 2010). Around 7000 BC, copper nuggets were hammered, without heating, into small tools and ornaments. The earliest advanced horticultural societies appeared around 4000 BC, when annealing copper with heat allowed the creation of less brittle tools for a wide range of purposes.

Further developments were smelting copper ore, casting, and making bronze (alloys of copper with tin or other metals, harder and more durable than pure copper). Bronze weapons made warfare highly profitable and resulted in large, stratified societies, with an aristocratic ruling class, a common class, and often a large number of captive slaves, taken in wars. Large societies (2B) allowed specialized occupations and required an administrative class (4), which resulted in further innovations, such as writing, money, and irrigation.

Plowing: *Simple agrarian societies* use plows to turn over soil, instead of the hoes used by horticultural societies (Latin *horti cultura*: the cultivation of a garden; *agri cultura*: the cultivation of a field) (Nolan and Lenski, 2010). Plows reach a greater depth than hoes, which brings nutrients to the surface where plants can reach them, and also buries weeds, converting them to humus and aiding plant growth. Hoed gardens must be abandoned after a few years, when the nutrients are depleted, whereas plowed fields last longer.

The earliest plows appeared around 3000 BC. At first, plows were pulled by people, but eventually oxen were used, making it possible for a farmer to cultivate a much larger area. The increased productivity resulted in a large economic surplus, enabling more complex forms of social organization (2B and 4).

Iron metallurgy: *Advanced agrarian societies* use iron for tools and weapons (Nolan and Lenski, 2010). Iron is stronger than bronze and the scarcity of tin limits the supply of bronze, but the technology for smelting iron ore is relatively complex and it did not become common until about 1200 BC. Later it was discovered that iron could be hardened by adding carbon and by quenching the hot metal in water. With these developments, iron replaced bronze as the preferred material for tools and weapons. This accelerated the trend to larger and more stratified societies (2B and 4).

Fossil fuel energy: *Industrial societies* derive the majority of their income from goods produced with fossil fuel energy. Around 1800 AD, England became the first industrial society when industry powered by coal became more economically important than agriculture (Nolan and Lenski, 2010). The dominant industries in England at that time were textiles and iron making. Beginning around 1760, the textile industry became increasingly mechanized. Human-powered machines were replaced by larger, faster, more complex machines, powered by steam engines burning coal.

Between 1770 and 1845, the contribution of the textile industry to the national economy increased by a factor of five. The iron industry switched from wood to coal for smelting and refining iron ore. Iron production in England went from 68 thousand tons in 1788 to 1.6 million tons in 1845.

In England before 1760, spinning and weaving were cottage industries. A family with a spinning wheel and a loom could make cloth in their own home. With the introduction of steam engines (burning coal for power) made with iron (smelted and refined with coal), large factories could make cloth much more efficiently, but the manufacturing process became significantly more complex, involving at least three new industries (coal mining, steam engine manufacturing, and iron mining and processing) and a much larger scale of organization (2B and 4).

Information and communication technology: *Information societies* generate more wealth from the service sector of the economy than the manufacturing sector; knowledge, information, and communication surpass energy in importance (Nolan and Lenski, 2010). In the period from 1986 to 2007, world computation capacity (in MIPS per capita) increased 58% annually, telecommunications capacity (in MB per capita per day) increased 28% annually, and storage capacity (in MB per capita) increased 23% annually (Hilbert and López, 2011). Population growth over the same period was 1% to 1.5% per year and economic growth was about 6% to 8.5% per year (Hilbert, 2012).

Hilbert (2012) estimates that 2002 was the year the worldwide quantity of stored digital information exceeded the quantity of stored analog information. In 2007, 97% of all stored information was digital (Hilbert, 2012). Transforming information to digital makes it more accessible and useful by enabling computers to search, index, transmit, and analyze the information. With computation, stored informa-

tion becomes a dynamic resource instead of a static record.

If we view cultural transitions from the perspective of the organization of human societies, each transition has resulted in a significant increase in population size and societal complexity (2B). The number of specialized crafts and occupations also increases with each transition (4). Each transition adds new levels of social organization. If we view cultural transitions from the perspective of technology, we also see increasing complexity and new levels of organization. With written and spoken language and visual representations (architectural drawings, circuit diagrams, chemical formulae, mathematical formulae, and so on), these changes are heritable and open to variations (5A-H).

Discussion

From our analysis of major transitions in biological and cultural evolution, it seems that our five conditions are sufficient to account for the transitions. On the other hand, Brandon's three conditions seem insufficient (Brandon, 1996, see above). In our analysis of the major transitions, most of them involve fusion (2B and 5G) and cooperation (4 and 5F), which are not covered by Brandon.

A core argument of Maynard Smith and Szathmáry (1995) is that much of evolutionary theory has focused on the evolution of plants and animals with sexual reproduction; before their work, evolutionary theory tended to ignore major transitions. Therefore it is not surprising that Brandon (1996) does not account for the major transitions of Maynard Smith and Szathmáry (1995). The recent surge of interest in open-ended evolution (Taylor et al., 2016) has brought more attention to the need for understanding the conditions for major transitions.

In the transitions above, fusion and cooperation play key roles, but fission does not play a large role in the transitions we have discussed here. However, fission plays an important role in cultural evolution, such as in the human migrations out of Africa, to Oceania, Europe, Asia, the Americas, the Pacific, and the Arctic. Fission also plays an important role in the evolution of human social organizations, such as the formation of new religious organizations from existing organizations and the formation of new companies from subsidiaries of existing companies.

Future Work

A natural next step in this research would be to develop a software simulation that satisfies our five conditions and then run various experiments to see how the simulation behaves. As far as we know, there is no existing simulation that satisfies all of our conditions.

One type of experiment would be to simulate a specific major transition by initializing the simulation with a simplified model of the situation before the transition, and then see whether the simulation is able to evolve into a simplified model of the situation after the transition.

Conclusion

Our goal was to find conditions that define a class of algorithms capable of open-ended evolution. As our behavioural hallmark of OEE (Taylor et al., 2016), we chose major transitions in evolution. Our analyses of major transitions in biological evolution, cultural evolution, and biocultural co-evolution suggest that the five conditions presented here are sufficient to account for the transitions. We expect that these five conditions (viewed as cultural products) will themselves evolve over time, just as these conditions have evolved from the work of other researchers (Axelrod and Hamilton, 1981; Brandon, 1996; Maynard Smith and Szathmary, 1995).

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