

Visions of Evolution: Self-organization proposes what natural selection disposes

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*“I am convinced that natural selection
has been the most important,
but not the exclusive,
means of modification.”
Charles Darwin*

SUMMARY

This paper reviews the seven “visions” of evolution proposed by Depew and Weber (1995), concluding that each possible relationship between natural selection and self-organization may have suited different aims and approaches. In the second section of the paper, we show that these seven viewpoints can be conveniently collapsed into three fundamentally different ones: (1) natural selection drives evolution; (2) self-organization drives evolution, or (3) natural selection and self-organization are complementary aspects of the evolutionary process. We then argue that these three approaches are not mutually exclusive, since each may apply for different stages of development of different systems. What emerges from our discussion is a more encompassing view: *That self-organization proposes what natural selection disposes.*

Keywords: Complex systems; Evolutionary biology; Natural selection; Self-organization

1. INTRODUCTION

In the final chapter of their book *Darwinism Evolving: System Dynamics and the Genealogy of Natural Selection*, David Depew and Bruce Weber suggest that evolutionary theory will remain incomplete as long as self-organizational and dissipative phenomena are kept at a distance from the current synthesis of evolutionary theory among biologists (see Depew and Weber, 1995). They raise important questions relevant to the debate about the relationship between natural selection and self-organization, providing a glimpse of the future of Darwinism. For example:

- (1) Can the self-organization of dissipative structures be brought into the present evolutionary synthesis or some expanded version of it?
- (2) Alternatively, will such assimilation be so challenging that it will require a change of background assumptions in the Darwinian tradition comparable to that which produced acknowledgment of the importance of developmental constraints (Brakefield, 2006).

- (3) Will self-organization and dissipative structures acquire such prominence in evolutionary thought that Darwinism's core concept – natural selection – will become merely a part of the background theoretical framework of evolution discourse, as a final step in the evolutionary process?

Other biologists share similar concerns. For example, while agreeing that natural selection is fundamentally important, Stuart Kauffman claims that it has not labored alone to craft the architectures of the biosphere, from cell to organism to ecosystem. Instead, self-organization is suggested to be the root source of order in the biological world. This order is not merely tinkered, but arises spontaneously because of the physico-chemical principles of self-organization – dynamical rules of complex processes that we are just beginning to uncover and understand (see Kauffman, 1993 & 1995). Although most biologists are now aware of the existence of self-organization, many have chosen to ignore its potential implications.

In their book, Depew and Weber tackled this problem philosophically, by posing a set of logically possible relationships between natural selection and self-organization, then surmising how the Darwinian tradition would be affected in each case. Later, they used this discussion to show why the way they elect to look at this relationship is preferable to others. Without wishing to prejudice the reader for or against any of the seven visions of evolution that they proposed, we repeat them below:¹

1. Natural selection and self-organization *are unrelated* (our emphasis).
2. Self-organization *is auxiliary to* natural selection.
3. Self-organization *constrains* natural selection, which drives evolution.
4. Natural selection *constrains* self-organization, which drives evolution.
5. Natural selection *instantiates* self-organization.
6. Natural selection *generates* self-organization.
7. Natural selection and self-organization *are aspects of a single process*.

Depew and Weber stress that early explorers of this terrain have occupied one or more of these perspectives, but each view has proved spacious enough to accommodate several, seemingly different, possibly competitive theoretical stances. In the first part of this paper, we review each of the seven visions briefly and dispassionately, identify some advocates, explain the context and discuss some issues associated with it. This leads us to the conclusion that these different perspectives may have suited different aims and approaches.

In the second section of the paper, we show that these seven viewpoints can be conveniently collapsed into three seemingly different ones: (1) natural selection drives evolution; (2) self-organization drives evolution; (3) natural selection and self-organization are complementary aspects of the evolutionary process. We then argue that these three approaches are not mutually exclusive, since each may apply for different stages of development of different systems. What emerges from our discussion is a more encompassing view: ***That self-organization proposes what natural selection disposes.***

2. SEVEN VISIONS OF EVOLUTION

¹ These seven positions alter slightly in a later paper by the same authors (Weber and Depew, 1996), but the differences are not significant for our overall purpose.

Until recently, the conventional wisdom has been that self-organization and natural selection have little or nothing to do with each other. Natural selection is presumed to shoulder most of the evolutionary burden, with some help from associated forces like genetic drift and mutation pressure. Such an attitude is hardly surprising if we recall that classical theories of evolution via natural selection were confined to living systems, whereas early theories of self-organization were formulated for non-living systems. The current ascendancy of population genetics in evolution discourse enhances the view that natural selection is the principal architect of evolution, and that this principle can be parlayed into a Universal Darwinism that would govern evolutionary processes in any field.

A very strong version of this view, held by genocentric biologists, portrays replicating genes as the evolving entities. Some writers even claim that genes function as selfish agents (Dawkins, 1976). Dawkins has suggested that an analogous replicator is at work among human populations, namely the *meme*. Memes are ideas that get copied, and thus can survive and get passed down through generations of human cultures. They may be susceptible to similar rules of natural selection as are genes. For example, they can spread, mutate, reproduce or die.

Maynard Smith and Szathmary (1995) have posited that the biological order observed around us, and the inferred emergence of new levels of biological organization and new phenomena, are due solely to the power of natural selection. They believe that the major transitions in living systems result from the emergence of new levels of selection. Replicators that were initially self-sufficient become associated with others, eventually being coordinated into larger units in a reorganizing environment. In turn, these larger units become subject to selection pressures on larger scale phenotypic properties. They document what they presume to be the organismic results of this process in early evolution.

Evolutionary economists frequently adopt an explanatory scheme that is borrowed from Darwinian evolutionary biology. In a seminal contribution, Nelson and Winter (1982) admit to borrowing the idea of economic natural selection to support their analytical view of “organizational genetics” – a process by which certain traits of organizations are transmitted through time. Defined as regular and predictable behavioural patterns of firms, organizational *routines* are the economic analogs of genes in organisms. Just as the genome stores information that governs the setup, development and behaviour of organisms, routines condition the competitive performance of firms.

Other evolutionary economists claim that general principles of Universal Darwinism are appropriate for economics (Hodgson and Knudsen, 2002). In their theories, selection does not refer to the natural selection mechanism found in biology, but is defined generally as any process in which the interaction of a set of entities with its environment modifies the frequency with which the different entities occur in the set. An implication of this broad definition is that the Lamarckian inheritance of acquired traits is not excluded from their definition of Darwinism – which is in accordance with the historical record, since Darwin himself did not reject the possibility that acquired traits may be inherited. This view is being championed currently by Eva Jablonka (Jablonka and Lamb, 1995; and forthcoming).

Cosmic natural selection has been suggested as an answer to the puzzle of why the universe is complex (Smolin, 1997). A black hole is suggested to be the means by which a universe reproduces – that is, spawns another. As such, Smolin thinks that daughter universes may be born of black holes. Universes with more black holes will have more daughter universes. Given minor variations in the constants of the laws of the daughter universes, cosmic natural selection will select for universes whose constants support the formation of a near-maximum number of black holes. Smolin felt that the only principle powerful enough to explain the high degree of organization of our universe – compared to a universe with the particles and forces chosen randomly – is natural selection. If only complex, organized universes are stable enough to last for a long time, this is why ours is manifest. Yet Smolin also acknowledges that the galaxy could be a self-organized system, and that a successful theory that merges relativity and cosmology with quantum theory will be a theory of self-organization.

Despite the strong emphasis on natural selection in these theories, there is growing evidence that selection is accompanied, to a greater or lesser extent, by processes of self-organization in living and non-living systems (Mittenthal and Baskin, 1993; Salthe, 1993; Camazine et al, 2003). As there is insufficient space to elaborate on biological examples of self-organization in this paper, the reader is directed to the above-mentioned references for further discussion. Once we acknowledge that self-organization is a force to be reckoned with, however, a series of other potential niches come into view.

D&W Vision 2: Self-organization <i>is auxiliary to</i> natural selection
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Vision 2 portrays self-organizational properties of biological entities as “add-ons” to natural selection among acknowledged causes of evolution. By this argument, self-organization is appended to a list of approved “forces” that accompany natural selection, like genetic drift, mutation pressure and gene flow. Some or all of these forces play their part in particular evolutionary situations. Here is the first recognition that natural selection alone cannot craft all the wonders of the biosphere single-handedly. Although it is an admirably pluralistic view, natural selection is rarely assumed to be the “explanation of last resort” (Dyke and Depew, 1988). The general idea is: *Look for selection first, and search for other forces only if and when selection fails to yield a persuasive explanation.* Proponents of this view are attributing to self-organization a subservient role to natural selection, similar to that accorded to genetic drift, mutation pressure or whatever.

This is a conservative vision from the self-organizational viewpoint. It could be interpreted as a defensive stance by neoDarwinians when forced to confront a more complex world than is tackled by those relying purely on selection theory. Such a deficiency becomes glaring when some of these other forces are found to be more important than originally conceived. For example, natural selection itself can only reduce the representation of less favourable alleles in a population. To get rid of them completely requires drift, which emerges even in large populations when an allele frequency becomes very low. On this realization, drift becomes a major player in the Darwinian understanding of organic evolution.

Along similar lines, Depew and Weber noted: *“It is, of course, possible to elevate a force other than selection to a heuristically central position within the same conceptual rationale. It is even possible to reduce natural selection to an explanation of last resort.”* (Depew and Weber, 1995, p.481). Kimura’s neutral theory of protein evolution is a familiar example. According to Kimura (1983), when one compares the gene products of existing species, the

vast majority of molecular differences are selectively “neutral.” That is, these differences do not influence the fitness of either the population or the individuals making up the species. Thus his theory regards these molecular features as neither subject to, nor explicable by, natural selection.

A key assertion of the neutral theory is that most evolutionary change is the result of genetic drift acting on neutral alleles. A new allele arises typically through the spontaneous mutation of a single nucleotide within the sequence of a gene. Neutral substitutions create new, selectively neutral alleles. Although some view the neutral theory as an argument against Darwin’s theory of evolution by natural selection, Kimura and most modern evolutionary biologists maintain that the two theories are compatible. Neutral theory is non-Darwinian rather than anti-Darwinian. Neutral theory simply attributes a more central role to genetic drift. Also, it highlights that fact that not all evolutionary change is adaptive, but does not deny that some of it will be adaptive. As such, it has become the foundation of the molecular clock technique, which evolutionary molecular biologists use to measure how much time has passed since species diverged from a common ancestor.

Other non-Darwinian phenomena have been identified that need not be conceived as evolutionary *forces* in the usual sense of the word. For example, evolutionary convergence (Wille, 1911; Conway Morris, 2003) is non-Darwinian in the sense that the Darwinian model – descent with modification – envisions only a continued divergence of lineages, and thus is formally incapable of dealing with increasing similarity. This could be construed as an evolutionary force if viewed from a structuralist perspective, with structural attractors exerting an influence on evolutionary change.

A theory in which self-organization plays a similar heuristic role to genetic drift in Kimura’s theory of protein evolution is logically possible. Self-organization is a process where the selective effects of the environment are less fundamental than the emergence of new macroscopic phenomena. Nevertheless, such a process might be understood on the basis of the same variation and natural selection processes as the other, environmentally entrained forces of evolution. By this route, Depew and Weber reach their third vision. In this conceptual niche, self-organization is no longer just an auxiliary evolutionary force, but is a substantial and expectable constraint on the freedom of action of other evolutionary forces – including natural selection.

D&W Vision 3: Self-organization <i>constrains</i> natural selection

Mechanisms considered to be constraints on evolution have been a subject of considerable discussion. Such constraints can be genetic, developmental, biomechanical-chemical or functional. These constraints place qualitative and quantitative limits on adaptation (Gould and Lewontin 1979; Maynard Smith et al. 1985; Arnold 1992, Brakefield, 2006). Empirical studies of adaptation in natural populations suggest that the interplay between selection and such constraints is a common feature of evolution by natural selection, partly because adaptations involve trade-offs or compromises between competing functions (see, e.g., Reznick and Travis 1996).

An unusual grouping of co-authors has provided a widely-quoted definition of developmental constraints, defining them as biases in the production of variant phenotypes, or limitations on phenotypic variability caused by the structure, character, composition or dynamics of the

developmental system (Maynard Smith et al., 1985, p. 265). This group of contemporary thinkers on evolution – John Maynard Smith, Richard Burian, Stuart Kauffman, Pere Alberch, John Campbell, Brian Goodwin, Russell Lande, David Raup and Lewis Wolpert – spans a broad possibility space, since they often hold conflicting views when it comes to general theoretical approaches. The fact that they all seem to agree on the importance of developmental constraints could be interpreted as an acknowledgment by natural scientists of the existence of material limitations on organic evolution.

Subsequent authors (e.g. Fusco, 2001) have narrowed their definition, introducing the term *reproductive constraint* as a bias on the production of altered ontogenetic trajectories caused by mechanisms of transmission of hereditary factors and dynamical propensities during epigenetic interaction. In this interpretation of constraint, only phenomena that directly bias the organization of ontogenetic trajectories are included. Phenomena that are supposed to be acted upon by natural selection during development are excluded. Similarly, Richardson and Chipman (2003) draw a distinction between *generative* and *selective* constraints. In this classification, generative constraints limit the production of certain phenotypes during ontogeny and result in non-random production or nonproduction of certain variants. Selective constraints are supposed to arise by natural selection acting during embryonic development, and remain approximately constant through a broad range of environments.

The evolutionary stasis frequently recorded in the fossil record has been seen by paleontologists as plausible evidence of structural or developmental constraints that limit the effectiveness of natural selection and bias its direction (Gould, 1982). However, it has been suggested that stasis may also be explained by *stabilizing selection* (Charlesworth, Lande and Slatkin, 1982). Although these authors argued that such long-term stasis must be a consequence of stabilizing selection, there is no evidence for this viewpoint. Instead, mechanisms such as constraint-imposed evolutionary inertia may be responsible for short-term stasis.

Nowadays, the consensus seems to be shifting in favour of the widespread occurrence of constraints on selection. Maynard Smith et al (1985) have distinguished between *local* and *universal* constraints. They argue that developmental constraints responsible for the persistence and stability of particular features of particular taxa are local. Writers like Stephen Gould have placed high value on constraints of this sort as sources of narrative explanation. Since organisms are complex systems, among the most interesting group of universal constraints are those that are imposed by the inherent formal or mathematical properties of complex systems architecture. For example, many systems – living and non-living – display *limit cycle behaviour*, with characteristic phase-setting and phase-locking properties (Winfree, 1980). As well, all material systems are organized hierarchically, giving rise to necessary relationships between dynamics at different levels (Haken, 1983; Salthe, 1985, 2002).

Stuart Kauffman has persistently championed this general view, arguing that universal constraints are expectable consequences of interconnections among large genetic ensembles. When he suggests that self-organizational properties of sufficiently complex genetic regulatory networks can be affected by selective forces to (at best) a limited extent, Kauffman (1993) is assigning a different role to self-organization than Maynard Smith and his other co-authors would advocate. Self-organization constrains selection, as well as other evolutionary forces, in the sense that it provides a richer set of spontaneously ordered properties that selection can then sift through and refine.

We might already venture here that *self-organization proposes what selection subsequently disposes*. In order to impose itself upon self-organization when both are operating simultaneously, Kauffman argues that selection must be strong enough, and fast enough, to offset the rate of exploration of emergent novelty arising in the “adjacent possible” by way of self-organization (Kauffman, 2000). One example of self-organization proposing what selection subsequently disposes at the organism level may be the role of the Baldwin effect in mental evolution (Hinton and Nowlan, 1996; Weber and Deacon, 2000). Under this effect, behavioural tendencies arising spontaneously through mental exploration and imitation set the context for further genetic changes crafted by natural selection. As such, the Baldwin effect could be of selective advantage by speeding up the rate of evolutionary change (Hinton and Nowlan, 1996) and/or discovering niche space that would otherwise not be available.

The above discussion is a more adventurous interpretation of the potential role of constraints than the conservative view of developmental constraints discussed widely in evolutionary biology. But it poses a deeper question of how selection might work on systems that generate spontaneous order? As constraints on natural selection become less local and more universal, it becomes unclear if we are remaining within the boundaries of the Darwinian tradition. Could self-organization be regarded as the driving force of large-scale, evolutionary dynamics rather than simply a constraint on natural selection’s role as the evolutionary engine? At this point, a fourth potential discursive niche comes into view.

D&W Vision 4: Natural selection <i>constrains</i> self-organization

The key example of this apparent role reversal that Depew and Weber cite is the controversial stance on the causes of phylogenetic branching adopted by Brooks and Wiley (1986). They suggest that the self-organization of ontogenetic programs can be coupled with the idea that species formation dissipates information into informational entropy, thereby generating a variety of new races and species over time. The notion of information applicable here is Shannon’s, implying that information is reduction of variety. Natural selection’s job, then, is to prune down the self-organized novelty that is being generated incessantly and autonomously by the requirements of the Second Law of thermodynamics, viewed as operative on macroscopic diversity in expanding systems (here, the biosphere).

To us, this merely exemplifies the view of self-organization proposing what natural selection disposes. Adopting this view, macroevolution might occur with little or no adaptation via micro-evolutionary natural selection. The role of the latter is restricted to removing incompetent genotypes. This view coheres with Ernst Mayr’s (1963) widely-accepted allopatric speciation model, wherein selection has no essential role at all. It merely speeds up the evolutionary process in some instances. Thus we feel that Visions 3 and 4 could be combined into the above mentioned single view: that self-organization proposes what selection disposes.

The issue of what role selection might play in macroevolution arises out of the problem of demonstrating its *efficacy* in the ‘improvement’ of traits in respect to their functional roles (to borrow Darwin’s term). Only forms of balancing and stabilizing selection have been demonstrated in nature (see Endler, 1986; Mitton, 1997; Kingsolver et al, 2001). Brooks and McLennan (1991) collected evidence showing that ecological adaptation occurs only in a minority of speciation events.

D&W Vision 5: Natural selection *instantiates* self-organization

According to Depew and Weber, a fifth vision comes into view with Swenson's work (Swenson, 1989; 1995). He argues that selection is a derived consequence of self-organization whenever a system is moving toward a state of maximum entropy production (Dewar, 2005). Swenson argues that selection is *entailed* by self-organization, and Darwinian selection is a special case where the components are replicating. By entailment or instantiation, is meant that selection arises as a necessary consequence of self-organization. Adopting this view, self-organization (order production) is not only necessary for, but ontologically prior to, selection. Thus, self-organization is vital to selection, but not the other way around. Once again, this view fits with our encompassing view that self-organization proposes that which selection disposes.

Swenson's view of selection is enigmatic, since he talks about a system 'selecting' the local constraints that will maximize entropy production in any given local situation. Salthe deems "this usage unfortunate, because it clearly cannot be the case that there is an array of definite potentialities present from which selection is made." (Salthe, 1993, p.108). Since only one configuration actually emerges, it seems reasonable to suppose that it emerges from more than one *potential* possibility. Presumably, a particular selection results from competition between several potential pathways for entropic dissipation. A cardinal principle of Darwinian natural selection theory is that several variants arise prior to the action of selection, while in this case only one variant situation emerges during the process of selection (Swenson, 1991).

Swenson regards *natural* selection as a particular manifestation of deeper, directional laws governing all systems that select in favour of what is physically stable and entropy maximizing. Maximization of entropy production within the limits of constraints has been shown to be a bonafide physical principle in systems capable of reorganization (Dewar, 2005). This suggests that what results from evolution will be ecological situations that maximize entropy production. However, this would not necessarily impose directionality upon the phenotypic evolution of any given lineage, in so far as it would be only one component in any ecological situation.

In this regard, it is worthwhile noting that, during animal evolution, there has been an increased ability to dissipate prey or cadaver energy gradients as rapidly as possible. This has also occurred in the evolution of physiological systems that increase entropy production, like homeothermy and large central nervous systems (Salthe, 2004). At larger than organismic scale, there does appear to have been an increase in the diversity of living systems over time, (see e.g., Wagner et al, 2006), and this signifies an increase in the number of pathways for entropy production (Salthe, 2004). Such diversity growth corresponds to what Kauffman calls 'expanding into the adjacent possible at maximum speed.' Also, it implies an expansion of system workspace (as Kauffman notes), and therefore its entropy production.

D&W Vision 6: Natural selection *generates* self-organization

Some theorists have speculated that natural selection may be the author, or at least the shaper, of self-organization, in the sense that what can self-organize locally will have been materially prepared by previous selected forms. This was the substance of Ernst Mayr's view that natural selection was a creative force. For this view to be plausible, Depew and Weber suggest that natural selection must be viewed in the way that Dobzhansky, Lewontin and Levins view it.

In other words, it is there to allow populations or lineages to respond to changing environments. On this view, adaptability at the population level is itself a paradigmatic adaptation (Depew and Weber, 1995, p.484). It depends on maintaining plenty of variation and highly mobile genomes in populations.

Depew and Weber point to Wimsatt's models of the evolution of developmental programs as being illustrative of this viewpoint. Wimsatt has long insisted that living nature is distributed into modular systems that are only partially decomposable, stacking into various levels and units. Also, he believes that "generative entrenchment" and self-organization are key components of developmental systems (Wimsatt, 1986). Taking this view, the generative structure of the system (the organism plus relevant aspects of its environment) has a characteristic set of causal interactions. Wimsatt argues that these interactions could be represented as a directed graph, where nodes are parts, processes, or events, and arrows are consequences of the presence or operation of nodes on other nodes. For each node, consider how many other nodes can be reached from it by following the arrows. This indicates how much of the phenotype is downstream of, causally dependent upon, or affected by a given node. Wimsatt defines *generative entrenchment* (GE) of a node in his representation as the magnitude of this downstream dependency (see Wimsatt, 1986; Wimsatt and Schank, 2004).

By arguing that the downstream consequences of GE are limited to characteristic effects, systematic enough that they could be considered consequences of natural selection, Wimsatt's ideas resonate with Kauffman's. Where they differ is that Wimsatt believes that selection stabilizes developmental programs by selecting for arrangements favouring their self-organizing properties, whereas Kauffman regards ontogenetic stability as first and foremost a product of self-organization.

Consider generative structures produced in self-organizing systems such as social insect colonies. Several species of army ants go through emergent reproductive cycles of over a month in which they enter nomadic phases (Schneirla 1971; Camazine et al, 2003). These nomadic phases are driven in part by the development of larvae (nodes) and the emergence of new workers (nodes) both chemically and tactilely interacting (connections) with adult workers (downstream nodes), "agitating" them and initiating the nomadic phase with colony level patterns of behavior and spatial relationships (colony level phenotypic patterns of behavior). Here the rules of individual interactions (between nodes, larvae, newly emerging workers, and adult workers) become entrenched more generally in animal systems of reproduction.

With a few qualifications, GE has been confirmed in all Wimsatt's simulations. His simulations were originally designed to test Kauffman's hypotheses on the evolution of genetic regulatory networks (Kauffman, 1985, 1993). Kauffman argued that selection could not maintain more than a small fraction of the connections in a gene control network of realistic size in the face of mutation. His model networks were directed graphs, with genes as nodes, and arrows (connections) between them representing influences of one gene on another. Mutations involved random reassignment of the head or tail of an arrow, changing gene interactions, and altering the connectivity of the network. The ratio of genes to connections determined the network's connectivity, and through this, many of its generic, topological properties (Kauffman 1985, 1993). Generic properties might include the average number of connections reachable from any node, the number of closed cycles in the network, and the mean cycle length. Since differential GE is also a generic property, but one that Kauffman excluded, Wimsatt and Schank examined the robustness of Kauffman's

conclusions in more realistic simulations which included the effects of GE. At least some of their results are more general, impacting any phenotypes whose genes or generative elements are subject to a diversity of selection forces of different magnitudes. This diversity may be produced by differential entrenchment, but need not be.

Darwinian processes almost inevitably give rise to generative processes. “*There is selection pressure, then for self-organized “locks” that keep ontogeny proceeding down Waddington’s canalized valleys*” (Depew and Weber, 1995, page 484). However, we are still left with some perplexing questions: How can complex adaptive systems evolve and continue to evolve in other than a predominantly accretional way if their generative elements become increasingly entrenched with increasing complexity? How can this allow modular evolvability to continue? This pattern of change is one of refinement of existing properties, characteristic of developmental systems, but it has not yet been argued to characterize organic evolution. Thus a fundamental research focus emanating from Wimsatt’s work is to figure out how complex systems can continue to evolve into new forms when evolutionary processes generically give rise to increasingly entrenched structures. Are elements of early stages entrenched within a lineage? Some of these questions may appeal to a wider group of evolutionary biologists because they might still be regarded as Darwinian in spirit. Thus this vision runs a lower risk of undermining the field’s autonomy than some others that we have been discussing.

D&W Vision 7: Natural selection and self-organization *are aspects of a single process*

Depew and Weber’s final vision seems to be attracting growing support, outside and even within evolutionary biology – perhaps because it says little more than that self-organization and selection are involved in a more encompassing process of organic evolution. In simple words, neither can get far without the other’s help. When Stuart Kauffman complements his stress on self-organization being a constraint on selection by arguing that the latter serves to keep living systems at the “edge of chaos”, his views fall into this niche. He claims that: “*Living systems exist in the solid regime near the edge of chaos, and natural selection achieves and sustains such a poised state.*” (Kauffman, 1983, p. 232). The implication is that complex systems that are constructed so that they are on the boundary between order and chaos are those best able to adapt by mutation and selection. In Michael Conrad’s (1983) computer models, natural selection works together with self-organization to “smooth out fitness landscapes” and thereby reduce the large differences in a Wrightian fitness landscape to shallow saddles, fostering evolutionary transit between fitness peaks.

Do we live in a world that is always in flux somewhere between chaotic and ordered states? Clearly, this is a markedly different world to the one portrayed by classical and neoclassical physics, since these discourses did not deal with truly complex systems. While in such a region of high complexity, Kauffman suggests that self-organization presents to selection entities that can play major roles in evolutionary change. Self-organization proposes what selection will dispose. According to Kauffman, selection maintains systems in precisely the region of phase space that affords them the greatest opportunity to evolve further. What selection has disposed invites further self-organization. Note that, in general, what this view replaces is the neoDarwinian concept of a random search for the new with self-organization of the new. Furthermore, complex systems may have convergent rather than divergent flow. The principle of homeostasis is a natural feature of many complex systems, and Kauffman calls it *order for free*.

Kauffman's emphasis on the edge-of-chaos as the key to evolvability is shared by Chris Langton and Norman Packard (who invented the term). At around the same time, James Crutchfield and others used the phrase *onset of chaos* to describe more or less the same concept. Depew and Weber allude to other authors (e.g. Campbell, 1987 and Wills, 1989) as arguing that natural selection will be seen to have favoured those traits that enhance the possibility of further evolution, thus revealing that evolvability might be the greatest adaptation of all. For these ideas to fit with the established materialist stricture that natural selection *cannot see the future*, but only what is immediately at hand, we note that evolvability is marked only by systems that have successfully evolved.

Compatible ideas have come out of the *autocatalytic* schools of thought in systems ecology, although they argue from a thermodynamic rather than a dynamical perspective. Wicken (1987) and others have stated that natural selection may be an emergent property of more basic kinds of selection in autocatalytic, energy-dissipating, open systems. In particular, Ulanowicz (1986, 1997) has developed a model of evolving autocatalytic cycles that will replace components with others that enhance a cycle's rate of cycling; drawing more materials into it and thereby out-competing others using the same resources. Such cycles, and dissipative structures in general, exist in a not too orderly (non-dynamic) realm on the one hand, and in a not too disorderly (chaotic) realm on the other; which Ulanowicz (2002) refers to as a "window of opportunity" for living systems.

Salthe (1993, 2000) suggests that the Second Law of Thermodynamics – in the form of the maximum entropy production principle (Swenson, 1989. Dewar, 2005) – is acting herein as a final cause. This amounts to asserting that selection (among different rates of energy throughput) is a phenomenon in its own right, an emergent process of complex dissipative systems that favours autocatalytic cycles that have acquired the ability to vary and retain information. Selection among such cycles results in the creation and maintenance of self-organizing networks of informed energy utilization and dissipation, and organisms may be construed as such nodes of informed patterns of thermodynamic flow. The fittest populations will be those, *ceteris paribus*, which best enhance the autocatalytic behaviour of the reward loops in which they participate.

Steven Frank (1997) analyses "developmental selection" as a self-organizing process. He argues that selective analysis emphasizes another path to self-organization: a clear division, and synergy, between generative mechanisms and selective filters. This idea is usually reserved for dynamics in which the direction of search is partly uncoupled from the ultimate target defined by the selective filter (fitness). This kind of system is sometimes called blind variation and selection, or "selection by consequences" (Skinner, 1981), to emphasize that discovery arises by random search, which is the traditional view in neoDarwinism. Although it has been discussed by many authors (including Frank), the idea that development and self-organization proceed by blind variation of developmental trajectories coupled with innately designed selective filters remains a minority view. The innate selective filters that are involved here have a theoretical function similar to the autocatalytic cycle in Ulanowicz's model.

3. FROM VISIONS TO LEVELS AND STAGES OF EVOLUTION

The study of self-organisation and natural selection faces a difficulty shared by all complex problems: the same processes can be analysed at different levels of representation

(Crutchfield 1994; Laughlin and Pines, 2000; Lemke, 2000; Shalizi, 2001; Salthe, 2002; Laughlin, 2005; Rabinowitz, 2005) and the relationships between these levels is often unclear. The question comes down to whether the drivers of a process, and the fundamental causal laws, belong to a single level (usually considered to be at the ‘finer’ resolution of physical laws) or to different levels. Hierarchies may be constructed by orders of magnitude (compositional hierarchies) or as physical, chemical, biological, ecological and cosmic levels (subsumption hierarchies), depending upon what the relationships are between these levels. This topic is addressed at length in the complexity and philosophy literature and details are beyond the scope of this review. Nevertheless, it is important to keep this framework in mind, since it strongly affects the way we view the relation between self-organisation and natural selection.

Salthe (1985) notes that systems organized as scale hierarchies: (for example: [organism[cell[macromolecule]]) are basically three-levelled, with the lowest level proposing what will be disposed at the intermediate level, under the guidance of the higher level. This higher-level constraint imposition amounts to a selection function on the possibilities generated in the lower level. As well, in the subsumption hierarchy: {physical{chemical{biological}}}, the biological arises out of, but also harnesses, the chemical in its interests – another top-down selection function².

Self organisation assumes the existence of at least two levels of representation: one related to the individual units (agents or organisms) that become coordinated, and another to the level of the community or structure which results from their organisation – as in the example of biology emerging from chemistry. As well, natural selection is a process acting at different levels. Environmental selection pressures act upon organismic interactors to select molecular genotypes in the gene pool. The relations here are not so obvious, however, since the gene pool belongs to the population. From the scale hierarchy point of view, we have organisms proposing what the environment will dispose with regard to a population’s gene pool.

The seven visions reviewed above portray the possible relation between self-organisation and natural selection as interacting at different levels, as in [selective pressures [selection [self-organization]], or {self-organization {selection}}}. This is useful to classify our observations, but scientific explanations require a closer analysis of the drivers and how they act at these different levels. Adopting a physical perspective, for example, we find that, while entropy production occurs at the lowest scalar level of molecular particles, its mediation is largely accomplished at a macroscopic level by dissipative structures. Organismic interactions act as convections dissipating ecological energy gradients, garnered from unreflected radiation from the sun (Lotka, 1922). The biological information for the organismic dissipative structures is contained in their cells as molecular configurations which were mediated into organismic form by developmental processes. This information is stored in populations and species, which project some of their own informational constraints as well (Rapoport, 1982).

Far from suggesting any ultimate insight into this scientific problem, here we highlight a few aspects of how the interaction between different levels may take place in the interplay

² ² The [] brackets indicate systems nested by size and dynamical rate, as in [large, slowly changing [smaller, more rapidly changing]], while the { } brackets indicate the more particular nested within the more general, as in set theory {generality {particularity}}.

between self-organisation and natural selection. This, together with new mathematical insights into the study of levels of representation in complexity (Ryan, 2006) may lead to new avenues of research.

Our conjecture (which borrows heavily from the established literature) can be summarised as follows:

- 1) Self organisation is an avenue for the effective use of energy which is required, among other things at different levels, to achieve reproduction;
- 2) Natural selection interacts with self-organisation and often results in a change of context within which both can act. One of the results of this change of context is the ability to act at different levels. That is to say, selection itself becomes possible between populations and lineages (Stanley, 1979; Wilson, 2005);
- 3) This change of context implies self-referentiality, which is a pivotal driver for an increase in complexity.

In the remainder of this section we try to justify our claims. That self-organisation is an avenue for effective use of energy is readily demonstrated with a few simple observations. Suppose we ask how much energy is needed to motivate my friend Harry (weight 80 Kg, height 190 Cm) to go to the local pub. Very little, a phone call will suffice. How likely is it to find 100 birds on the same tree at the same time? Quite unlikely if the birds belong to different species, and far more likely if they fly in a flock. While it is quite time consuming to deliver electoral certificates by mail to each single citizen, it is fairly easy to deliver a drug to most cells of our body. We just swallow a pill and the blood circulation does the rest. The common feature in the above examples is that *existing organization allows a small energy/information input to achieve an outcome of considerably larger magnitude*³: ($Magnitude(response) \gg Magnitude(input)$).

It should be noted, however, that a considerable energy gradient has been consumed in carrying out these activities. Information serves to reduce the energy barriers to gradient dissipation, which is then entrained to the interests of that information. From a physical perspective, the necessary conditions for this process to occur are the existence of some potential energy to be released and a structure which allows for such energy to be channelled in a particular fashion rather than dissipated randomly; both (potential energy and structure) of which required some sort of dissipative symmetry breaking to have previously occurred⁴.

This idea was hinted at long ago by Russell (1921, chapter 7). More recently, Kauffman (2000) capitalized on the same idea in his definition of a living organism as an autonomous agent: an “*autonomous agent is a collectively autocatalytic system that performs one or more thermodynamic work cycles*”. In order to survive as dissipative structures, organisms need to

³ We are not suggesting any violation to the First Law of Thermodynamics. Energy conservation still needs to be respected by all involved systems, in their internal dynamics. Here we refer merely to the input provided by an external observer and the magnitude of the system’s response to it.

⁴ In principle, this does not necessarily require life forms; driving a bulky 4-wheel-drive to a local pub also involves an energy/information input from the driver several order of magnitude smaller than the physical work the 4-wheel-drive will accomplish by simply exploiting an artificial organization (the 4-wheel-drive) and an external energy source (fuel). In this specific case some priori biological intervention is responsible for both building the 4-wheel-drive and for storing energy in the fuel, but it does not necessarily have to be so, as we will discuss below.

use energy to carry out certain tasks (looking for food, reproducing, fleeing predators, etc). In order to perform these tasks, they need to constrain the ways that such energy is released, channelling the dissipation used for moving, allowing necessary chemical reactions, etc. As Kauffman suggests, the key to such constrained release of energy is *organization*. “Organization is fundamentally related to that coordination of matter and energy which enables and controls the constrained release of energy - work - to be propagated” (Kauffman, 2000).

Seemingly simple, the insight provided by Russell and Kaufman is powerful because it allows us to cast, within a unified framework, the concepts of self-organisation and complexity and their relation to the physical and chemical processes underpinning life. Also, it suggests a possible relation between self-organisation and natural selection at different levels.

According to our current understanding, replication is a defining feature of life. At a biochemical level, replication requires a set of non trivial autocatalytic reactions. For these specific reactions to occur, both energy release and matter need to be *organised* according to specific spatial and temporal structures. This can happen only far from equilibrium, achieved thanks to a certain amount of symmetry breaking. In turn, energy needs to be employed for this symmetry break to occur. At the simplest level, only the most trivial form of natural selection can be at work; autocatalytic structures which can replicate can reproduce and thus can be selected. According to this view, only a particular kind of organisation can lead to replication. Thus only this kind of organisation can lead to reproduction, and consequently this kind of organisation is a necessary requirement for natural selection (and thus organic evolution) to take place.

According to the Computational Mechanics school (Crutchfield and Young, 1989), organisation implies an increase in statistical complexity. In its non-organised form, matter can display a considerably large number of statistically similar behaviours. In its organised form, however, we can observe only a small variety of behaviours which are significantly different among themselves (e.g. moving, feeding, replicating, etc). Since, roughly speaking, statistical complexity measures the probability distribution of these behaviours, we see that organisation implies an increase in complexity⁵.

There is an apparent anomaly in this view. On the one hand, symmetry breaking and organisation reduce the number of effective configurations available to the system. On the other hand, the constrained release of energy which becomes possible thanks to organisation, allows for such energy to be used to ‘do’ particular tasks. As a result, certain behaviours which would in principle be possible but highly unlikely in its non-organised form (replication, for example), become effectively possible. In principle the potential behaviours are reduced; in practise the organised system can ‘do’ things which would have not happened without organisation. This shows the establishment of new degrees of freedom in the system, even while many older degrees of freedom have become frozen out.

⁵ It is important to notice that other measures of complexity which account for all possible configurations the same matter could display, like Kolmogorov-Chaitin algorithmic complexity, would instead detect a decrease in complexity, since some configurations would not be available to the organised matter as a result of symmetry breaking.

So far, things are fairly straightforward. But now the conditions are present for self-referentiality to arise, and the outcome becomes far more interesting. A first form of self-referentiality stems from the fact that the energy channelled by the existing organisation can be used to build further constraints to further harness the release of energy. The result is that more energy becomes available to ‘do’ more, the results of which reflect the existence of that particular system.

The second form of self-referentiality stems from the fact that complexity inevitably increases, since more structured organisation is needed to manage the increasingly complicated set of constraints. Thus more available energy can lead to the maintenance of increasing complexity, and the increasing complexity can provide for more and more energy channelling, with a potential open loop. At this stage, selection can start to work in earnest. It can now act not only to trivially discriminate what replicates from what does not, but also to discriminate what replicates ‘faster’. It can discriminate increasingly sophisticated ways of duplication, leading to the selective pressures we normally associate with natural selection.

A third level of self-referentiality now becomes possible, because different levels of organisation are in open competition with one another. Organisation is no longer merely a tool to exploit resources from the environment, but also a way to prevail over or cooperate with other forms of organisation. Selection now has more subtle ways to discriminate what duplicates ‘better’, entraining group selection between populations (Wilson, 2005) and lineage selection (Stanley, 1979), as well as the natural selection of organisms.

To summarise, we propose a view according to which the relation between self-organisation and natural selection can be divided into three stages:

- 1) During the first stage, the emergence of organisation is a necessary requirement for natural selection to occur. Without organisation, behaviours which can be selected upon are statically so unlikely that the process cannot even start. In this situation, *self-organisation constrains selection*. In other words, organization proposes what selection might dispose.
- 2) In the second stage, primordial forms of organisation provide the material for natural selection to act upon, which in turn results in increasingly complex forms of organisation to develop. Here *natural selection provides a form of constraints on self-organisation*. Selection passes on contexts for further self-organization.
- 3) In a third stage, the relation (both competition and collaboration) between ever increasing complex forms of organisation and their impact on the environment is such as to affect the *context* within which natural selection can act (for example, the current cultural selection occurring in human society could not be conceived in the context of the early primordial soup) hereby making *natural selection and self-organization complementary aspects of a single process*.

Although the suggested assignments may not be perfect, the potential relationships of these three stages of evolution to the seven visions discussed earlier are shown in Table 1.

Table 1: Stages and Visions of Evolution

Stage 1: Natural selection drives evolution	
a.	and is unrelated to self-organization (Vision 1)
b.	and views self-organization as an auxiliary force (Vision 2)

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|----|--|
| c. | and is constrained by self-organization (Vision 3) |
| d. | and is the architect of self-organization (Vision 6) |

Stage 2: Self-organization drives evolution
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|----|--|
| e. | and is constrained by natural selection (Vision 4) |
| f. | and natural selection arises as its consequence (Vision 5) |

Stage 3: Natural selection and self-organization are complementary aspects of a single evolutionary process (Vision 7)

4. CONCLUSIONS

We agree with Depew and Weber's assertion that, as we consider successively more dynamically enriched ways in which selection and self-organization might interact, we are moving steadily towards a deeper appreciation of the probabilistic and statistical character of the world; a world in which non-living and living organisms, including ourselves, coexist. This probabilistic vision of nature can come into full view only when theoretical biology internalizes the nonlinear dynamics of complex systems. What exist at any moment locally are contingent, historically derived, path dependent configurations that materially mediate the laws of nature and matter, as well as possibly reflecting the influence of structural attractors.

What we have attempted in this paper is a naturalizing of the process of natural selection, as it has been discussed for several generations in evolutionary biology. From the viewpoint of *that* evolutionary biology, there was no need to understand how variant forms arose. The task was to trace their fortunes in the context of other forms. Nature would provide, by way of accidents and contingencies, all the variants needed to promote evolution. This *idealistic* evolutionary biology was lacking any material grounding. The latter has been gained from the self-organizing discourse of complexity studies, which has uncovered the generativity of the material world.

With this gain in scope, we can now see clearly that selection occurs within frameworks at higher levels than the place where generativity is located. Organisms are selected as members of populations; chemical entities are selected within cells. The selection is frameworked by boundary conditions imposed upon the selected entities from a higher level of organization. We can conveniently present the entire complex picture in terms of the Aristotelian causal categories. Material causes of evolutionary change are the mutated forms that are generated spontaneously by way of self-organization, which are deployed in conditions set by the formal causes of boundary conditions which will favour some types and not others. Efficient causation is carried by multiple energy dissipations at work at many moments within the framework. As note by Fisher (1929), the result of selection is always to increase the fitness of a population to local conditions (if it survives), and so, inasmuch as it cannot be otherwise, it is appropriate to locate fitness increase as a final cause of natural selection.

Finally, we suggest that the self-organizing forces of nature propose multiple possibilities, which will be disposed of by natural selection acting on their suitability to conditions. Those kinds that survive this fitness review will partially define conditions for further selection on upcoming generations of new variants. Natural selection disposes what self-organization proposes, based in part on what selection had disposed in the past.

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