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Ontic openness: An absolute necessity for all developmental processes

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ABSTRACT

The physicist Walter M. Elsasser is mostly known for his work on the Earth's magnetism. Less attention has been paid to his efforts toward identifying what are the real differences between physical and biological systems. One essential distinction he recognized was that physical systems are largely *homogenous* while biological systems always revealed what he called *ordered heterogeneity*. Calculation of the possible configurations of such heterogeneous systems almost always leads to *combinatorial explosions* and to what Elsasser referred to as *immense numbers*. Such calculations have the consequence that any such systems are necessarily unique – mathematically speaking they represent *one-sets*.

Another consequence is that immense numbers automatically introduce enormous uncertainty and *indeterminacy* into the system. Such systems are said to be *ontically open*. Applying this perspective to the genome and employing the notion of *informational entropy* reveals a common drive behind all development. This means that both conventional Darwinian evolution as well as the genomic mistakes that are believed to lie behind processes like aging and diseases can be interpreted against the background of one and the same process.

At the same time the approach demonstrates how Darwinian evolution encompasses other notions such as Kauffman's "adjacent possible" (Kauffman, 1995, 2000) and Eldrege's and Gould's "evolution via punctuated equilibria" (e.g., Eldredge and Gould, 1972; Gould and Eldredge, 1977).

1. Introduction

In the literature two antagonistic concepts of entropy and information are used concurrently, often in very confusing manner and sometimes even conflated as if they were synonymous.

The source of the confusion dates back to Shannon's expropriation of the Boltzmann–Gibbs formulation for thermodynamic entropy as quantification of the positivist sense of information. These two concepts have opposing meanings and have been applied to a wide range of organizational forms often to contradictory ends. Unlike with the second law requiring ever-increasing thermodynamic entropy, no clear statement can be made concerning the evolutionary trend of the Shannon index.

One major issue needs to be resolved: Is the information (viz. entropy) of a system increasing or decreasing with time? The organismic theory launched by W.M. Elsasser, with its associated concepts of ontic openness, heterogeneity and immense numbers offers a resolution to this apparent problem.

In short, biological systems differ from purely physical systems in that the former are highly *heterogeneous* while the latter are largely *homogenous* (Bateson, 1972). Calculation of the *combinatorial possibilities* among the entities of a heterogeneous system leads to *numerical explosions*. The number of possibilities reaches orders of magnitude that no longer convey any physical meaning. Anything can and will happen, i.e., such complex systems are fundamentally unpredictable and said to be ontically open. As a result, the concept of ontic openness requires another metaphysic – one that can apply beyond the realm of finite or even infinite systems (Ulanowicz, 2009).

As will later be demonstrated, systems that are ontically open can proceed in either of two directions – they can increase or decrease in informational entropy, depending on the measure chosen. In fact, the concept of openness reveals a fundamental drive among all biological systems (Deacon, 2011) – which in turn prompts the following legitimate question.

2. Do processes such as natural evolution, aging and disease merely represent different facets of an underlying unity in ontic openness?

Introducing this perspective on evolution – *sensu lato* – on biological systems of any scale – provides a new interpretory

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framework upon which one may hang diverse processes from early morphogenesis and evolution of species to aging and disease. All are contingent upon a unitary and universal trend that contributes majority to explanatory power.

The examples provided above all involve digital structures, but analog systems are thought to behave similarly, provided one is careful about how the principle of openness is applied. Whereas Shannon is predicated for digital systems, classical thermodynamic entropy pertains as well to analog systems (see *code duality* below).

3. Expanded foundation of the hypothesis

Various approaches that find their origins in thermodynamics and information theory have for some years now been used to analyze the evolution of natural, biological systems (Brooks and Wiley, 1986; Chaisson, 2001; Demetrius, 1997; Gladyshev, 2004; Jørgensen, 1986, 2008; Jørgensen and Svirezhev, 2004; Kay and Schneider, 1992; Schneider and Kay, 1995; Schneider and Sagan, 2005; Weber and Depew, 1996; Wicken, 1998; Yockey, 2002; Zotin and Zotina, 1967). The extension of thermodynamics to the level of biological systems could be considered a new paradigm that bridges Darwinism to thermodynamics (Jørgensen and Mejer, 1979; Kauffman, 2000; Wicken, 1998; Wicken and Ulanowicz, 1988). Systems that organize themselves (self-organizing) while conforming to thermodynamic functional principles are usually referred to as dissipative structures, a term that originated out of the work of Prigogine and Nicolis (1971), Nicolis and Prigogine (1977), and Prigogine and Stengers (1984). It has widely been speculated that an as-yet-unformulated thermodynamic principle dictates the evolution of such systems (Kauffman, 2000). Debate persists as to whether such systems follow the “maximum entropy formalism” of Jaynes (1979, 1982) and Martyushev and Seleznev (2006), the “minimum dissipation density” of Prigogine and Nicolis (1971), a rule of optimal exergy storage/usage (Jørgensen, 1986; Schneider and Kay, 1995) or some one of a number of conjectures that have been proposed as candidates for a “fourth law” of phenomenology (e.g., Kauffman, 2000).

For biological systems at all scales, a distinct and general pattern can be observed. As the systems evolve, total entropy formation increases with system size, whereas the density of entropy formation decreases. This applies to the cellular as well as the organismic level (e.g., Zotin and Zotina, 1967).

At the same time, as species evolve over geological time, the statistical entropy of their genomes increases with time (Brooks and Wiley, 1986). Aging (Hayflick, 2007), disease (Azzone, 1996) and cancer (Waliszewski et al., 1998) all have been interpreted along the same line. All of the above have been interpreted as an increase in the disorder in the genome or in the biochemical processes within the cells (Reinhardt, 2007; Riggs, 1993, 1994, 1998; Rose, 1999; Rubin, 2006).

The systems covered by the works just mentioned are themselves at different levels of the biological hierarchy and hence not fully covered by classical thermodynamics. They are not even close enough to thermodynamic equilibrium to fall into the realm of what are usually referred to as far-from-equilibrium systems. It is beyond the scope of this paper to enter this domain, and so no attempt will be made to render judgments on the various approaches. In essence, each narrative along this spectrum of “thermodynamic” views has been fitted to an ontology appropriate to its level of application. It should be clear, therefore, that each approach is at best analogous to core classical thermodynamic concepts.

Moreover, the approaches reflect two basic thermodynamic analogies that have been used to analyze complex systems. The first is closer to classical thermodynamics and considers organisms to be machines doing work (W), allocating energy, carrying out metabolism, and exporting heat (Q) to the environment via respiration. This is the avenue taken in most eco-physiological or autecological studies. As an extension of thermochemistry, organisms are viewed in terms of their chemical potentials, the deviation of which from the surrounding environment can be estimated (Morowitz, 1968; Jørgensen and Mejer, 1979). While such estimates as they pertain to chemical constituents are widely accepted, such is not the case when the deviations are approximated in terms of their genomic compositions.

The other direction (and the one taken here) arises out of information theory as quantified by Shannon (1948). This approach has proved popular especially when applied to biological systems wherein molecular structures are organized in linear fashion, e.g., DNA, RNA and proteins.

These two thermodynamic conceptions of biological systems reflect the code-duality principle of Hoffmeyer and Emmeche (1991). A link between the original analog understanding and the later digital approach is to be found in the Boltzmann–Gibbs equation. The formal connection exists whether one is calculating the “information” inherent in the structural organization of constitutive processes or that of the composite elements themselves. Although our basic conjecture applies in both cases, we find our results easier to convey in terms of digital structures.

4. Hypothesis

Our conjecture is that ontic openness is an absolute necessity for the development of living systems. In counter tension to feedback dynamics, it is an integral part of the drive behind progressive evolution and constitutes a full exegesis of regressive devolution.

The authors of this paper are indebted to the philosophical works on living systems by the late Walter M. Elsasser (Elsasser, 1998; Rubin, 2005). Having achieved considerable fame as a physicist, Elsasser, like Bohr, dedicated his later professional life to speculating on the fundamental ways by which biological systems differ from nonliving ones.

Elsasser began his quest with arguments based on “concepts that could be no further reduced” (Rubin, 2002), or what he considered to be “logical primitives”. We consider ontic openness to be just such a logical primitive that plays a necessary role in all evolutionary processes – both progressive and regressive.

One of Elsasser’s basic concepts was that of *ordered heterogeneity*. Biological systems are heterogeneous and unique, as opposed to homogenous and generic atomic or molecular systems. In parallel with Schrödinger’s (1944) *order from order* principle, living organisms are able to harness this heterogeneity to create even more complex structures. Actually, several of Elsasser’s ideas can be traced to Schrödinger’s interpretations of the biological world beginning with the early 1940s. Given our detailed knowledge of molecular biology, many of these early notions might seem trivial, but at the time little knowledge existed about exactly how ontogenetic memory was stored.

At the very core of Elsasser’s take on biology one discovers a worldview that, once probed, appears to involve deeper aspects of nature than one might perceive at first glance.

To give an example of what biological heterogeneity really entails, Elsasser estimated the maximum number of events that could possibly have occurred in the universe since the “big bang”. This number lies in the order of 10^{110}. Details as to how Elsasser arrived at this threshold have been given elsewhere (e.g., Jørgensen et al., 2007, chap. 3). One could take a googol (10^{100}) as an approximation of the boundary, and values exceeding this limit will be referred to as *immense*.

As for the heterogeneity of biological systems, possible combinatorial rearrangements of known molecular compositions readily

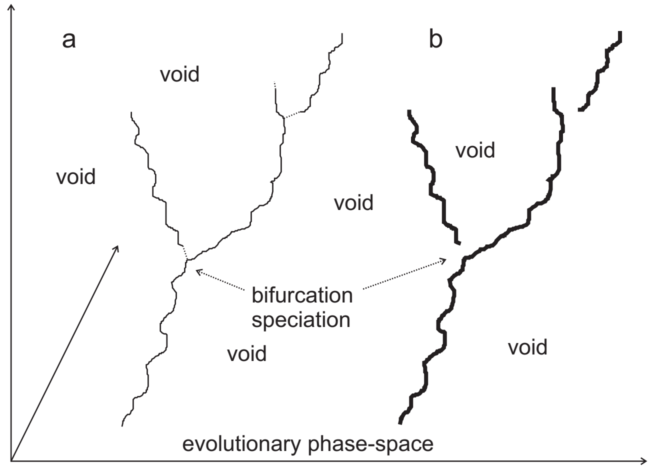

Fig. 1. Evolution of species is often illustrated by tree-like structure where a line represents a species position in a phase space of complexity, i.e., position in the phylogenetic tree. Here (a) the same is shown with fitness on the *y*-axis. Bifurcations corresponding to punctuated equilbria are indicated by broken lines. The evolutionary line of one single species will be surrounded by a part of the phase space with "possible" genomic constructs that will still be identified as the same species and should therefore rather be presented as a tube (b) is due to ontic openness composed of many strands.

surpass the threshold for immense numbers. For example, the strings of nucleic acids in a strand of DNA or of amino acids in proteins invariably lead to what are known as combinatorial explosions. According to Jørgensen et al. (1995) the length of an average protein is on the order of 700 amino acids. Given as how each position can be occupied by any of 20 different amino acids, the possible number of unique proteins of typical length would be 20^{700}, which lies enormously beyond the smallest immense numbers. Similar calculations performed on nucleotides in typical strands of DNA produces combinations on the order of 10^{1264} (more than a billion googols), a magnitude that becomes difficult even to contemplate. Thus, at the level of the genome, the number of possibilities is so extreme as to transcend any conceivable physical reality. Yet such numbers exist, – or do they? If so, what are the consequences?

The upshot is that any realized state of the genomic system for any real species in time and space is *unique*. That particular genomic composition is but one out of an immense number of possibilities. Seeing as how the largest possible number of species known to exist is well under 10^{10}, we are forced to conclude that an overwhelming amount of evolutionary time – phase space must remain void (see Fig. 1a).

The ubiquity of combinatorial explosions has an additional consequence. Even if we could replicate genomes with the highest possible accuracy, let's say at "quantum level", the consequent magnitude of "mistakes" (variations) at the level of the individual organism will be even higher. Hence, the dissipation of information, uncertainty, and indeterminacy all become inherent in the dynamics of heterogeneous systems!

Furthermore, it is erroneous to assume that a one to one mapping of genomes to species exists. Rather, the genomic composition of any single species is represented in its basics by a suite of variations that can be realized and remain viable. Such variation contributes to the ontic open space. Hence, the genome is not to be understood as one particular state, but instead as a subset of possible states within which the morphology of the phenotypes can be identified as belonging the same species. This may be illustrated in Fig. 1b. Individuals are only approximately the same in many aspects, but in fact differ slightly in most regards. When it comes to the suite of physiological dynamics, organisms appear to be identical only to themselves. Such variation led Elsasser to accept Williams' (1998) notion of "biochemical individuality", but it should also be noted that individual variation has always been at the core of the Darwinian narrative. Upon close inspection, any group of organisms constitutes a set of realized genomic states (Fig. 2a) that cannot be separated from each other. This will be discussed further below (see Fig. 2b).

Although the possibilities in biological systems transcend the bounds of physical reality, it nevertheless remains possible to estimate their numbers. This is commonly done within the discipline of information theory. For example, a classical "gedanken experiment" (of unknown origin) sets an army of monkeys at work typing randomly, and the question is asked how long will it take on average before one monkey reproduces a particular sonnet of Shakespeare? The estimated time will likely exceed the age of the universe by a billion-fold – about the same result one would get for the time it would take to reproduce a particular genome from random. Both the sonnet and the genome are unique. Along the way, however, texts that resemble sonnets will be produced in much lesser time, just as some genomes could be produced that fall within the range of variation for what constitutes the particular species.

The digital character of genomes invites their analysis by information theory – in particular by what one might call informational

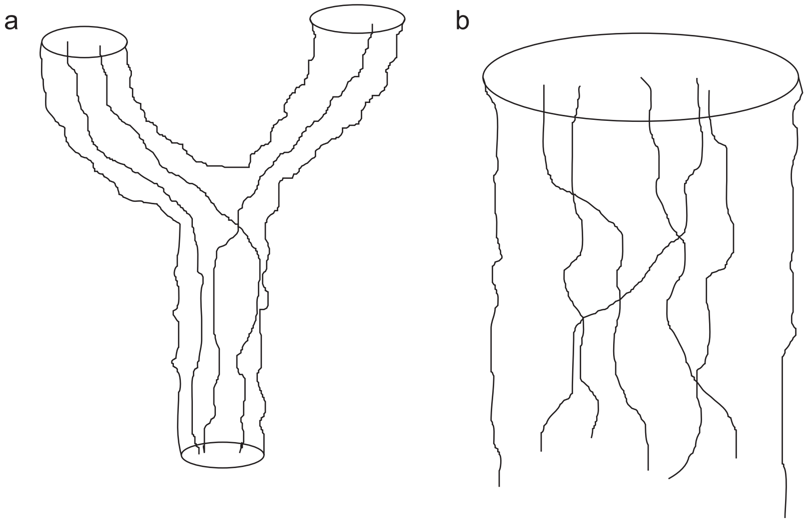

Fig. 2. Individuals of species will eventually bifurcate and result in formation if new species in the evolutionary tree (a). Within the tube belonging to one species only there will be tracks of individuals that are unique yet belong to the same species (b).

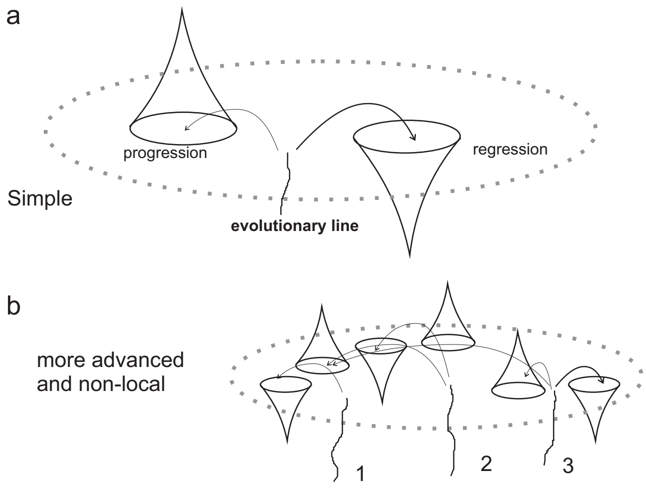

Fig. 3. The individual species track will evolve due to ontic openness into either a progressive or regressive evolutionary state (a). Ontic openness leads to a more sophisticated view where individuals may either evolve in forwards or retrowards direction (1) or both (2) or even move to evolutionary cones far from the original evolutionary line (3).

entropy (as distinct from thermodynamic entropy). Brooks and Wiley (1986) conflated the statistical and thermodynamic meanings of the term entropy to draw conclusions about the nature of the evolutionary process. While such a move remains controversial, it may nevertheless be possible to draw insights about evolution from the mathematical analogy. Others have taken this same path to interpret different phases of the life cycle of organisms (e.g., Rubin, 2006).

As mentioned above, the assumption of variation is fundamental to the neo-Darwinian scenario for evolution. That such variation constitutes ontic openness, which rests comfortably with the conventional paradigm, is illustrated in Fig. 1. There are depicted attempts by the realized parts of the subset to experiment with the various possibilities presented by the adjacent possible. As natural evolution proceeds, one may identify pathways leading to improved efficiency or increased reproductive fitness of the organism, as illustrated in Fig. 3.

Those pathways are generally guided by self-organizing dynamics, notably by autocatalytic ones (Kauffman, 1995). In configurations of autocatalytic processes any constituent process amplifies its own activity via its interaction with others. The magnitude of such amplification can vary in response to chance changes in the constituents. Such variation is asymmetric, however, in that those changes that increase amplification are rewarded, while those that decrement it become self-diminishing. At one level, the effects of autocatalysis appear to oppose those of ontic openness – autocatalysis builds up, while ontic openness tears down. At a higher level, however, autocatalysis could not increase, were it not for the chance perturbations provided by ontic openness (Ulanowicz, 1997). Whence, ontic openness makes an absolutely necessary contribution to the dynamics of self-organization.

Contemporaneous with self-organization, there will be trajectories among the adjacent possible leading to diminished efficiency and decreased fitness. Ontic openness requires that some of these avenues will be accessed during evolution. Those experiments represent steps backward in the sense that the genome produced will be less fit. If the decrease in performance is the result of a direct malfunction of the gene or protein, such consequence will be recognized as disease and eventually will lead to exclusion of the genome via the death of the organism.

Thus, the exploitation of ontically open time-space phase by random variation is in the end absolutely necessary to progressive evolution and at the same time provides a full accounting of any regressive evolution, such as aging or disease such as cancer.

On a closing note, it should be mentioned that evolution, progressive as well as regressive, does indeed correlate with Kauffmann's concept of the adjacent possible, and that notion in turn accords fully with the idea of ontic openness. Ontic openness is didactically present as the void spaces alongside the evolutionary trajectories. These void regions were never occupied and constitute what could be referred to as the "adjacent impossible". In this picture the next step in the evolutionary process will always be a question of success vs. non-success, and whatever happens will be the result of intrinsic dynamics and imposed extrinsic constraints.

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Beyond being a scientist deeply rooted in thermodynamics (which plays a major role in this essay), Enzo Tiezzi was also an ardent admirer of arts. In particular, we shared an enthusiasm for music. Enzo was one of the first to grasp the necessary role that ontic openness plays in music, and he immediately encouraged us to point to the function of openness in music in the chapter devoted to openness that appeared in the book written pursuant to several meetings by its group of authors that took place in Møn and Pacina. We dedicate this work to the memory of a colleague and friend who was truly ontically open!

References

Azzone, G.F., 1996. The nature of diseases: evolutionary, thermodynamic and historical aspects. Hist. Philos. Life Sci. 18, 83–106.

Bateson, G., 1972. Steps to an Ecology of Mind: Collected Essays in Anthropology, Psychiatry, Evolution and Epistemology. University Of Chicago Press.

Brooks, D.R., Wiley, E.O., 1986. Evolution as Entropy. Toward a Unified Theory of Biology. University of Chicago Press, Chicago, 415 pp (reprinted 1988).

Chaisson, E.J., 2001. Cosmic Evolution: The Rise of Complexity in Nature. Harvard University Press, Cambridge, MA.

Deacon, T.W., 2011. Incomplete Nature: How Mind Emerged from Matter. W.W. Norton & Co., New York.

Demetrius, L., 1997. Directionality principles in thermodynamics and evolution. Proc. Natl. Acad. Sci. U.S.A. 94, 3491–3498.

Elsasser, W.M., 1998. Reflections on a Theory of Organisms. Holism in Biology Johns? Hopkins University Press.

Eldredge, N., Gould, S.J., 1972. Punctuated equilibria: an alternative to phyletic gradualism. In: Schopf, T.M. (Ed.), Models in Palaeobiology. Freeman Cooper, pp. 82–115.

Gladyshev, G.P., 2004. Macrothermodynamics of biological evolution: aging of living beings. Int. J. Mod. Phys. B 18 (6), 801–825.

Gould, S.J., Eldredge, N., 1977. Punctuated equilibria: the tempo and mode of evolution reconsidered. Paleobiology 3 (2), 115–151.

Hayflick, L., 2007. Biological aging is no longer and unsolved problem. Ann. N.Y. Acad. Sci. 1100, 1–13.

Hoffmeyer, J., Emmeche, C., 1991. Code duality and the semiotics of nature. In: Anderson, F., Merrell, F. (Eds.), On Semiotic Modeling. Mouton de Gruyter, Berlin, New York, pp. 117–166.

Jaynes, E.T., 1979. Where do we stand on maximum entropy'? In: Levine, R.D., Tribus, M. (Eds.), The Maximum Entropy Formalism. M.I.T. Press, Cambridge, MA.

Jaynes, E.T., 1982. On the rationale of maximum-entropy methods. Proc. IEEE 70 (9), 939–952.

Jørgensen, S.E., 1986. Structural dynamic model. Ecol. Model. 31, 1–9.

Jørgensen, S.E., 2008. Evolutionary Essays. A Thermodynamic Interpretation of the Evolution. Elsevier, Amsterdam, 206 pp.

Jørgensen, S.E., Mejer, H., 1979. A holistic approach to ecological modelling. Ecol. Model. 7, 169–189.

Jørgensen, S.E., Svirezhev, Y., 2004. Toward a Thermodynamic Theory for Ecological Systems. Elsevier, Amsterdam, 366 pp.

Jørgensen, S.E., Fath, B., Bastianoni, S., Marques, J.C., Müller, F., Nielsen, S.N., Patten, B.C., Tiezzi, E., Ulanowicz, R.E., 2007. A New Ecology – Systems Perspective. Elsevier, Amsterdam, 288 pp.

Jørgensen, S.E., Nielsen, S.N., Mejer, H.F., 1995. Emergy, environ, exergy and ecological modelling. Ecol. Model. 77, 99–109.

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

Kauffman, S.A., 2000. Investigations. Oxford University Press, 302 pp.

Kay, J., Schneider, E., 1992. Thermodynamics and measures of ecosystem integrity. In: McKenzie, D., Hyatt, D., McDonald, J. (Eds.), Ecological Indicators. Elsevier, New York, pp. 159–181.

Martyushev, L.M., Seleznev, V.D., 2006. Maximum entropy production principle in physics, chemistry and biology. Phys. Rep. 426, 1–45.

Morowitz, H.J., 1968. Energy Flow in Biology. Academic Press.

Nicolis, G., Prigogine, I., 1977. Self-organization in Non-equilibrium Systems: From Dissipative Structures to Order Through Fluctuations. Wiley.

Prigogine, I., Nicolis, G., 1971. Biological order, structure and instabilities. Quart. Rev. Biophys. 4 (2–3), 107–148.

Prigogine, I., Stengers, I., 1984. Order Out of Chaos. Man's New Dialogue with Nature. Heinemann Ltd., London.

Reinhardt, K., 2007. Evolutionary consequences of sperm cell aging. Quart. Rev. Biol. 82 (4), 375–393.

Riggs, J.E., 1993. Aging, genomic entropy and carcinogenesis: implications derived from longitudinal age-specific colon cancer mortality rate dynamics. Mech. Ageing Dev. 72 (3), 165–181.

Riggs, J.E., 1994. Carcinogenesis, genetic instability and genomic entropy: insight derived from malignant brain tumor ages specific mortality rate dynamics. J. Theor. Biol. 170, 331–338.

Riggs, J.E., 1998. Aging, increasing genomic entropy, and neurodegenerative disease. Neurol. Clin. N. Am. 16 (3), 757–770.

Rose, S., 1999. Précis of lifelines: biology, freedom, determinism. Behav. Brain Sci. 22, 871–921.

Rubin, H., 2002. Complexity, the core of Elsasser's theory of organisms. Complexity 7 (1), 17–20.

Rubin, H., 2005. Walter Elsasser, prophet of biological complexity, seeker of simplifying rules. Cell. Mol. Biol. 51, 599–606.

Rubin, H., 2006. What keeps cells in tissues behaving normally in the face of myriad mutations. BioEssays 28, 515–524.

Schneider, E.D., Kay, J.J., 1995. Order from disorder: the thermodynamics of complexity in biology. In: Murphy, Michael P., O'Neill, Luke A.J. (Eds.), What is Life: The Next Fifty Years. Reflections on the Future of Biology. Cambridge University Press, pp. 161–172.

Schneider, E.D., Sagan, D., 2005. Into the Cool – Energy flow, Thermodynamics and Life. University of Chicago Press, 378 pp.

Schrödinger, E., 1944. What is Life – the Physical Aspect of the Living Cell. Cambridge University Press.

Shannon, C.E., 1948. A mathematical theory of communication. Bell Syst. Tech. J. 27, 379–423, pp. 623–656, July and October.

Ulanowicz, R.E., 1997. Ecology the Ascendent Perspective. Columbia University Press, New York.

Ulanowicz, R.E., 2009. A Third Window: Natural Life Beyond Newton and Darwin. Templeton Foundation Press, West Conshocken, PA.

Waliszewski, P., Molski, M., Konarski, J., 1998. On the holistic approach in cellular and cancer biology: nonlinearity, complexity, and quasi-determinism of the dynamic cellular network. J. Surg. Oncol. 68, 70–78.

Weber, B.H., Depew, D.J., 1996. Natural selection of self-organization. Dynamic models as clues to a new evolutionary synthesis. Biol. Philos. 11, 33–65.

Wicken, J.S., 1998. Evolution and thermodynamics: the new paradigm. Syst. Res. Behav. Sci. 15, 365–372.

Wicken, J.S., Ulanowicz, R.E., 1988. On quantifying hierarchical connections in ecology. J. Social. Biol. Struct. 11, 369–377.

Williams, R.J., 1998. Biochemical Individuality: The Basis for the Genetotrophic Concept, first ed. 1956. John Wiley & Sons.

Yockey, H.P., 2002. Information theory, evolution and the origin of life. Inf. Sci. 1441, 219–225.

Zotin, A.I., Zotina, R.S., 1967. Thermodynamic aspects of developmental biology. J. Theor. Biol. 17, 57–75.