

REFERENCE:

Schneider, E.D, Kay, J.J., 1995, "Order from Disorder: The Thermodynamics of Complexity in Biology", in Michael P. Murphy, Luke A.J. O'Neill (ed), "*What is Life: The Next Fifty Years. Reflections on the Future of Biology*", Cambridge University Press, pp. 161-172

Order from Disorder: The Thermodynamics of Complexity in Biology

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Introduction

In the middle of the nineteenth century, two major scientific theories emerged about the evolution of natural systems over time. Thermodynamics, as refined by Boltzmann, viewed nature as decaying toward a certain death of random disorder in accordance with the second law of thermodynamics. This equilibrium seeking, pessimistic view of the evolution of natural systems is contrasted with the paradigm associated with Darwin, of increasing complexity, specialization, and organization of biological systems through time. The phenomenology of many natural systems shows that much of the world is inhabited by nonequilibrium coherent structures, such as convection cells, autocatalytic chemical reactions and life itself. Living systems exhibit a march away from disorder and equilibrium, into highly organized structures that exist some distance from equilibrium.

This dilemma motivated Erwin Schrödinger, and in his seminal book *What is Life?* (Schrödinger, 1944), he attempted to draw together the fundamental processes of biology and the sciences of physics and chemistry. He noted that life was comprised of two fundamental processes; one "*order from order*" and the other "*order from disorder*". He observed that the gene generated *order from order* in a species, that is, the progeny inherited the traits of the parent. Over a decade later Watson and Crick (1953) provided biology with a research agenda that has led to some of the most important findings of the last fifty years.

However, Schrödinger's equally important but less understood observation was his *order from disorder* premise. This was an effort to link biology with the fundamental theorems of thermodynamics (Schneider, 1987). He noted that living systems seem to defy the second law of thermodynamics which insists that, within closed systems, the entropy of a system should be maximized. Living systems,

however, are the antithesis of such disorder. They display marvelous levels of order created from disorder. For instance, plants are highly ordered structures, which are synthesized from disordered atoms and molecules found in atmospheric gases and soils.

Schrödinger solved this dilemma by turning to nonequilibrium thermodynamics. He recognized that living systems exist in a world of energy and material fluxes. An organism stays alive in its highly organized state by taking high quality energy from outside itself and processing it to produce, within itself, a more organized state. Life is a far from equilibrium system that maintains its local level of organization at the expense of the larger global entropy budget. He proposed that the study of living systems from a nonequilibrium perspective would reconcile biological self-organization and thermodynamics. Furthermore he expected that such a study would yield new principles of physics.

This paper examines the *order from disorder* research program proposed by Schrödinger and expand on his thermodynamic view of life. We explain that the second law of thermodynamics is not an impediment to the understanding of life but rather is necessary for a complete description of living processes. We expand thermodynamics into the causality of the living process and show that the second law underlies processes of self-organization and determines the direction of many of the processes observed in the development of living systems.

Thermodynamic Preliminaries

Thermodynamics has been shown to apply to all work and energy systems including the classic temperature-volume-pressure systems, chemical kinetic systems, electromagnetic and quantum systems. Thermodynamics can be viewed as addressing the behaviour of systems in three different situations: 1) equilibrium, (classical thermodynamics), i.e. the actions of large numbers of molecules in a closed system, 2) systems that are some distance from equilibrium, and will return to equilibrium, i.e. molecules in two flasks connected with a closed stopcock; one flask holds more molecules than the other and upon opening the stopcock the system will come to its equilibrium state of an equal number of molecules in each flask, and 3) systems that have been moved away from equilibrium and are constrained by gradients to be at some distance from the equilibrium state, ie. two connected flasks with a pressure gradient holding more molecules in one flask than the other.

Exergy is a central concept in our discussion of *order from disorder*. As already mentioned, energy varies in its quality or capacity to do useful work. During any chemical or physical process the quality or capacity of energy to perform work is irretrievably lost. Exergy is a measure of the maximum capacity of an energy system to perform useful work as it proceeds to equilibrium with its surroundings (Brzustowski & Golem, 1978, Ahern, 1980).

The first law of thermodynamics arose from efforts to understand the relation between heat and work. The first law says that energy cannot be created or destroyed and that the total energy within a closed or isolated system remains unchanged. However, the quality of the energy in the system (i.e the exergy content) may change. The second law of thermodynamics requires that if there are any processes underway in the system, the quality of the energy (the exergy) in that system will degrade. The second law can also be stated in terms of the quantitative measure of irreversibility, entropy, which for any process is greater than zero. The second law can also be stated as: any real process can only proceed in a direction which results in an entropy increase.

In 1908 thermodynamics was moved a step forward by the work of Carathéodory (Kestin, 1976) when he developed a proof that showed that the law of "entropy increase" is not the general statement of the second law. The more encompassing statement of the second law of thermodynamics is that "In the neighbourhood of any given state of any closed system, there exists states which are inaccessible from it, along any adiabatic path reversible or irreversible" Unlike earlier definitions this does not depend on the nature of the system, nor on concepts of entropy or temperature.

More recently Hatsopoulos & Keenan (1965) and Kestin (1968) have subsumed the 0th, 1st and 2nd Laws into a Unified Principle of Thermodynamics: "When an isolated system performs a process after the removal of a series of internal constraints, it will reach a unique state of equilibrium: this state of equilibrium is independent of the order in which the constraints are removed". This describes the behavior of the second class of system, which are some distance from equilibrium but are not constrained to be in a nonequilibrium state. The importance of this statement is that it dictates a direction and an end state for all real processes. This statement tells us that a system will come to a local equilibrium as constraints permit.

Dissipative Systems

These principles outlined above hold for closed isolated systems. However a more interesting class of phenomena belong to the third class of systems that are open to energy and or material flows and reside at quasi-stable states some distance from equilibrium (Nicolis and Prigogine, 1977, 1989). Nonliving organized systems (like convection cells, tornados and lasers) and living systems (from cells to ecosystems) are dependent on outside energy fluxes to maintain their organization and dissipate energy gradients to carry out these self-organizing processes. This organization is maintained at the cost of increasing the entropy of the larger "global" system in which the structure is imbedded. In these dissipative systems, the total entropy change in a system is the sum of the internal production of entropy in the system (which is always greater or equal than zero), and the entropy exchange with the environment which may be positive, negative or zero. For the system to maintain itself in a nonequilibrium steady state the entropy exchange must be negative, and larger than the entropy produced by internal processes, such as metabolism.

Dissipative structures which are stable over a finite range of conditions are best represented by autocatalytic positive feedback cycles. Convection cells, hurricanes, autocatalytic chemical reactions and living systems are all examples of far-from-equilibrium dissipative structures which exhibit coherent behavior.

The transition in a heated fluid between conduction and the emergence of convection (Bénard cells) is a striking example of emergent coherent organization in response to an external energy input (Chandrasekhar, 1961). In the Bénard cell experiments, the lower surface of a fluid is heated and the upper surface is kept at a cooler temperature. The initial heat flow through the system is by molecule to molecule interaction. When the heat flux reaches a critical value the system becomes unstable and the molecular action of the fluid becomes coherent and convective overturning emerges resulting in highly structured coherent hexagonal to spiral surface patterns (Bénard Cells). These structures increases the rate of heat transfer and gradient destruction in the system. This transition between non-coherent, to coherent structure is the system's response to attempts to move it away from equilibrium (Schneider and Kay, in press). This transition between non-coherent, molecule to molecule heat transfer, to coherent structure results in excess of 10^{22} molecules acting in an highly organized manner. This seemingly improbable occurrence is the direct result of the applied temperature gradient, the dynamics of the system at hand, and is the system's response to attempts to move it away from equilibrium.

To deal with this class of nonequilibrium systems we have proposed a corollary to Kestin's Unified Principle of Thermodynamics. His proof shows that a system's equilibrium state is stable in the Lyapunov sense. Implicit in this conclusion is that a system will resist being removed from the equilibrium state. The degree to which a system has been moved from equilibrium is measured by the gradients imposed on the system.

As systems are moved away from equilibrium, they will utilize all avenues available to counter the applied gradients. As the applied gradients increase, so does the system's ability to oppose further movement from equilibrium.

We shall refer to this as the "restated second law" and the pre-Carathéodory statements as the classical

second law. In chemical systems, LeChatelier's principle is an example of the restated second law.

Thermodynamic systems exhibiting temperature, pressure, and chemical equilibrium resist movement away from these equilibrium states. When moved away from their local equilibrium state they shift their state in a way which opposes the applied gradients and attempt to move the system back towards its local equilibrium attractor. The stronger the applied gradient, the greater the effect of the equilibrium attractor on the system. The more a system is moved from equilibrium, the more sophisticated are its mechanisms for resisting being moved from equilibrium. If conditions permit, self-organization processes will arise that abet the gradient dissipation. This behaviour is not sensible from a classical perspective, but is expected given the restated second law. No longer is the emergence of coherent self-organizing structures a surprise, but rather it is an expected response of a system as it attempts to resist and dissipate externally applied gradients which would move the system away from equilibrium. Hence we have *order emerging from disorder* in the formation of dissipative structures.

So far our discussion has focused on simple physical systems and how thermodynamic gradients drive self-organization. Chemical gradients also result in dissipative autocatalytic reactions, examples of which are found in simple inorganic chemical systems, in protein synthesis reactions, and in phosphorylation, polymerization and hydrolysis autocatalytic reactions. Autocatalytic reaction systems are a form of positive feedback where the activity of the system or reaction augments itself in the form of self-reinforcing reactions. Autocatalysis stimulates the aggregate activity of the whole cycle. Such self-reinforcing catalytic activity is self-organizing and is an important way of increasing the dissipative capacity of the system.

The notion of dissipative systems as gradient dissipators holds for nonequilibrium physical and chemical systems and describes the processes of emergence and development of complex systems. Not only are the processes of these dissipative systems consistent with the restated second law, but it should be expected that conditions permitting, such systems will emerge if there are gradients present. Schrödinger's notion of *order from disorder* is about the emergence of these dissipative systems, a phenomena which is generally observed in these class 3 thermodynamic systems.

Living Systems as Gradient Dissipators

Boltzmann, recognized the apparent contradiction between the heat death of the universe, and the existence of life in which systems grow, complexify, and evolve. He realized the sun's energy gradient drives the living process and suggested a Darwinian like competition for entropy in living systems:

"The general struggle for existence of animate beings is therefore not a struggle for raw materials - these, for organisms, are air, water and soil, all abundantly available - nor for energy which exists in plenty in any body in the form of heat (albeit unfortunately not transformable), but a struggle for entropy, which becomes available through the transition of energy from the hot sun to the cold earth. " (Boltzmann, 1886).

Boltzmann's ideas were further explored by Schrödinger who noted that some systems, like life, seem to defy the classical second law of thermodynamics (Schrödinger, 1944). However, he recognized that living systems are open and not the adiabatic closed boxes of classical thermodynamics. An organism stays alive in its highly organized state by importing high quality energy from outside itself and degrading it to support the organizational structure of the system. Or as Schrödinger said

"the only way a living system stays alive, away from maximum entropy or death is to be continually drawing from its environment negative entropy. Thus the device by which an organism maintains itself stationary at a fairly high level of orderliness (= fairly low level of entropy) really consists in continually sucking orderliness from its environment. ...plants of course have their most powerful supply in negative entropy in sunlight," (Schrödinger, 1944).

Life can be viewed as a far-from-equilibrium dissipative structure that maintains its local level of organization, at the expense of producing entropy in the the environment.

If we view the earth as an open thermodynamic system with a large gradient impressed on it by the sun, the restated second law suggests that the system will reduce this gradient by using all physical and chemical processes available to it. We suggest that life exists on earth as another means of dissipating the solar induced gradient and as such, is a manifestation of the restated second law. Living systems are far from equilibrium dissipative systems and have great potential for reducing radiation gradients on earth (Kay, 1984, Ulanowicz and Hannon, 1987).

The origin of life is the development of another route for the dissipation of induced energy gradients. Life ensures that these dissipative pathways continue and has evolved strategies to maintain these dissipative structures in the face of a fluctuating physical environment. We suggest that living systems are dynamic dissipative systems with encoded memories, the genes, that allows dissipative processes to continue.

We have argued that life is a response to the thermodynamic imperative of dissipating gradients (Kay, 1984 and Schneider, 1988). Biologic growth occurs when the system adds more of the same types of pathways for degrading imposed gradients. Biologic development occurs when new types of pathways for degrading imposed gradients emerge in the system. This principle provides a criteria for evaluating growth and development in living systems.

Plant growth is an attempt to capture solar energy and dissipate usable gradients. Plants of many species arrange themselves into assemblies to increase leaf area so as to optimize energy capture and degradation. The gross energy budgets of terrestrial plants show that the vast majority of their energy use is for evapotranspiration, with 200-500 grams of water transpired per gram of fixed photosynthetic material. This mechanism is a very effective energy degrading process with 2500 joules used per gram of water transpired (Gates, 1962). Evapotranspiration is the major dissipative pathway in terrestrial ecosystems.

The large scale biogeographical distribution of species richness is strongly correlated with potential annual evapotranspiration (Currie, 1991). These strong relationships between species richness and available exergy suggest a causal link between biodiversity and dissipative processes. The more energy available to be partitioned among species the more pathways there are available for total energy degradation. Trophic levels and food chains are based upon photosynthetic fixed material and further dissipate these gradients by making more highly ordered structures. Thus we would expect more species diversity to occur where there is more available energy. Species diversity and trophic levels are vastly greater at the equator, where 5/6 of the earth's solar radiation occurs, and there is more of a gradient to reduce.

A Thermodynamic Analysis of Ecosystems

Ecosystems are the biotic, physical, and chemical components of nature acting together as nonequilibrium dissipative processes. Ecosystem development should increase energy degradation if it follows from the restated second law. This hypothesis can be tested by observing the energetics of ecosystem development during the successional process or as they are stressed.

As ecosystems develop or mature they should increase their total dissipation, and should develop more complex structures with greater diversity and more hierarchical levels to assist in energy degradation. (Schneider, 1988), and Kay and Schneider, 1992). Successful species are those that funnel energy into their own production and reproduction and contribute to autocatalytic processes thereby increasing the total dissipation of the ecosystem.

Lotka (1922) and Odum and Pinkerton (1955) have suggested that those biological systems that

survive are those that develop the most power inflow and use it to best meet their needs for survival. A better description of these "power laws" may be that biological systems develop so as to increase their energy degradation rate, and that biological growth, ecosystem development and evolution represent the development of new dissipative pathways. In other words ecosystems develop in a way which increases the amount of exergy that they capture and utilize. As a consequence, as ecosystems develop, the exergy of the outgoing energy decreases as ecosystems develop. It is in this sense that ecosystems develop the most power, that is, they make the most effective use of the exergy in the incoming energy while at the same time increasing the amount of energy they capture.

This theory suggests that disorganizing stresses will cause ecosystems to retreat to configurations with lower energy degradation potential. Stressed ecosystems often appear similar to earlier successional stage ecosystems and reside closer to thermodynamic equilibrium.

Ecologists have developed analytical methods that allow analysis of material-energy flows through ecosystems (Kay, Graham and Ulanowicz, 1989). With these methods it is possible to detail the energy flow and how the energy is partitioned in the ecosystem. We have recently analyzed a data set for carbon-energy flows in two aquatic tidal marsh ecosystems adjacent to a large power generating facility on the Crystal River in Florida (Ulanowicz, 1986). The ecosystems in question were a "stressed" and a "control" marsh. The "stressed" ecosystem was exposed to hot water effluent from the nuclear power station. The "Control" ecosystem is not exposed to the effluent but is otherwise exposed to the same environmental conditions. In absolute terms all the flows dropped in the stressed ecosystem. The implication is that the stress has resulted in the ecosystem shrinking in size, in terms of biomass, its consumption of resources, in material and energy cycling and its ability to degrade and dissipate incoming energy.

Overall the impact of the effluent from the power station heating water has been to decrease the size of the "stressed" ecosystem and its consumption of resources while impacting on its ability to retain the resources it has captured. This analysis suggests that the function and structure of ecosystems follow the development path predicted by the behavior of nonequilibrium thermodynamic structures and the application of these behaviors to ecosystem development patterns.

The energetics of terrestrial ecosystems provides another test of the thesis that ecosystems will develop so as to degrade energy more effectively. More developed dissipative structures should degrade more energy. Thus we expect a more mature ecosystem to degrade the exergy content of the energy it captures more completely than a less developed ecosystem. The exergy drop across an ecosystem is related to the difference in black body temperature between the captured solar energy and the energy reradiated by the ecosystem. If a group of ecosystems are bathed by the same amount of incoming energy, we would expect that the most mature ecosystem would reradiate its energy at the lowest exergy level, that is the ecosystem would have the coldest black body temperature.

Luvall and Holbo (1989, 1991) have measured surface temperatures of various ecosystems using a Thermal Infrared Multispectral Scanner (TIMS). Their data shows one unmistakable trend, that when other variables are constant the more developed the ecosystem, the colder its surface temperature and the more degraded it's reradiated energy.

TIMS data from a coniferous forest in western Oregon, showed that ecosystem surface temperature varies with ecosystem maturity and type. The warmest temperatures were found at a clearcut and over a rock quarry. The coldest site, 299deg.K, some 26deg. colder than the clear cut, was a 400 year old mature Douglas Fir forest with a three tiered plant canopy. A quarry degraded 62% of the net incoming radiation while the 400 year old forest degraded 90%. Remaining aged sites fell between these extremes, increasing energy degradation with more mature or less perturbed ecosystems. These unique data sets show that ecosystems develop structure and function that degrades imposed energy gradients more effectively (Schneider and Kay, 1994).

Our study of the energetics of ecosystems treats them as open systems with high quality energy pumped

into them. An open system with high quality energy pumped into it can be moved away from equilibrium. But nature resists movement away from equilibrium. So ecosystems, as open system, respond, whenever possible, with the spontaneous emergence of organized behaviour that consumes the high quality energy in building and maintaining the newly emerged structure. This dissipates the ability of the high quality energy to move the system further away from equilibrium. This self-organization process is characterized by abrupt changes that occur as a new set of interactions and activities by components and the whole system, emerge. This emergence of organized behaviour, the essence of life, is now understood to be expected by thermodynamics. As more high quality energy is pumped into an ecosystem, more organization emerges to dissipate the energy. Thus we have *order* emerging from *disorder* in the service of causing even more disorder.

Order from DISORDER and order from order

Complex systems can be classified on a continuum of complexity from ordinary complexity (Prigoginean systems, tornadoes, Bénard Cells, auto-catalytic reaction systems) to emergent complexity perhaps including human socio-economics systems. Living systems are at the more sophisticated end of the continuum. Living systems must function within the context of the system and environment they are part of. If a living system does not respect the circumstances of the supersystem it is part of, it will be selected against. The supersystem imposes a set of constraints on the behaviour of the system and living systems which are evolutionarily successful have learned to live within them. When a new living system is generated after the demise of an earlier one, it would make the self-organization process more efficient if it were constrained to variations which have a high probability of success. Genes play this role in constraining the self-organization process to those options which have a high probability of success. They are a record of successful self-organization. Genes are not the mechanism of development, the mechanism is self-organization. Genes bound and constrain the process of self-organization. At higher hierarchical levels other devices constrain the self-organization process. The ability of an ecosystem to regenerate is a function of the species available for the regeneration process.

Given that living systems go through a constant cycle of birth/development/regeneration/death, preserving information about what works and what does not, is crucial for the continuation of life (Kay, 1984). This is the role of the gene and, at a larger scale, biodiversity, to act as information data bases about self-organization strategies that work. This is the connection between the *order from order* and *order from disorder* themes of Schrödinger. Life emerges because thermodynamics mandates *order from disorder* whenever sufficient thermodynamic gradients and environmental conditions exist. But if life is to continue, the same rules require that it be able to regenerate, that is create *order from order*. Life cannot exist without both processes, *order from disorder to generate life* and *order from order to ensure the continuance of life*.

Life represents a balance between the imperatives of survival and energy degradation. To quote Blum (1968):

"I like to compare evolution to the weaving of a great tapestry. The strong unyielding warp of this tapestry is formed by the essential nature of elementary non-living matter, and the way in which this matter has been brought together in the evolution of our planet. In building this warp the second law of thermodynamics has played a predominant role. The multi-colored woof which forms the detail of the tapestry I like to think of as having been woven onto the warp principally by mutation and natural selection. While the warp establishes the dimensions and supports the whole, it is the woof that most intrigues the aesthetic sense of the student of organic evolution, showing as it does the beauty and variety of fitness of organisms to their environment. But why should we pay so little attention to the warp, which is after all a basic part of the whole structure? Perhaps the analogy would be more complete if something were introduced that is occasionally seen in textiles, the active participation of the warp in the pattern itself. Only then, I think, does one grasp the full significance of the analogy."

We have tried to show the participation of the warp in producing the tapestry of life. To return to Schrödinger, life is comprised of two processes, *order from order*, and *order from disorder*. The work of Watson and Crick and others described the gene, and solved the *order from order* mystery. This work supports Schrödinger's *order from disorder* premise and better connects macroscopic biology with physics.

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