

**Self-Organisation in Systems far from Thermodynamic Equilibrium:
Some Clues to the Structure and Function of Biological Systems**

by

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ABSTRACT

There is a large difference between systems that exist close to thermodynamic equilibrium and those existing far from it. Close to equilibrium, there is a tendency to a spontaneous increase of disorganisation into thermodynamic equilibrium. The existence of an exergy gradient over a system drives it away from equilibrium. It can then shift to a self-organising open system if there exists enough potential for change in the system. Simple self-organising systems have principles in common that invite to hypotheses about the function of biological systems. Such principles concern the organisation toward a system structure that degrades exergy at the highest possible rate, functional co-operation between subsystems and supersystems, autopoietic relationships during increase and maintenance of organisation, and the increased nestedness during the evolution of the system. Another important characteristic common for both simple and complex self-organising systems is the regenerative cycle, the tendency to keep limiting substances in tight cycles within the system. An explanation for nestedness proposed in this thesis is that it prevents the accumulation of low-exergy products necessarily excreted by self-organising systems. Such products are often used in the regenerative cycling of the supersystem.

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LIST OF PAPERS

This licenciate thesis is based on two complete papers which will be referred to by their Roman numerals:

(I) Günther, F. (1992): *Man in Living Systems*. Proceedings From The First International Symposium on Bioeconomics, November 28-30, 1991, Rome, Nagard; Milano

(II) Günther, F. and C. Folke (1993): *Characteristics of Nested Living Systems* Journal of Biological Systems, **1** (3), p 257-274

The discussions on the 'Fourth Law' draw on the manuscript:

Günther, F. (1994): *Converting Linear Flows into Cycles: The Phosphorus Flux in the Swedish Society as an Example*. Presented at the 2nd International Conference on Implications and Applications of Bioeconomics, Palma de Mallorca, Spain, Mars 11-13 1994

INTRODUCTION

In this thesis, I discuss some similarities that can be found between the behaviour of simple self-organising systems and complex self-organising systems at various organisation levels. There exists extensive knowledge on the particular behaviour of such systems from research in physics, medicine and ecology. However, they have only recently been discussed in terms of analogy (examples are Jørgensen and Mejer 1979, Jantsch 1980, Dalenoort 1986, Mayumi 1991, Müller & al. 1992, Jørgensen 1992, Schneider and Kay 1992). In order to provide perspectives that can be fruitful in further research in physics, medicine, ecology and related fields, this thesis exemplifies such analogies and invites to further discussions.

First, an overview of the reformulations of the second law of thermodynamics is discussed. The aim is to trace how its formulations have been transformed from a special, close to thermodynamic equilibrium view, to another, comprising all kinds of systems, even those far from thermodynamical equilibrium. Through this transformation, it has also become a base for the understanding of biological systems.

Second, the regenerative cycle, a model for the way cycling of basic elements and exergy utilisation mutually reinforce each other, is discussed. It is pointed out that this is a way to understand why high entropy products are not accumulated in a nested living system.

Last, some thoughts of the analogies between different types of self-organising systems are discussed, with citations taken from the two papers in the thesis. In order to make the discussion more understandable, I have added comments and explanations in bold italics.

THE REFORMULATIONS OF THE LAWS OF THERMODYNAMICS

The 1st¹, 2nd and 3rd² laws of thermodynamics are well known to scientists and students in physics. In this introduction, the second law of thermodynamics will be discussed in more detail. Primarily constructed to develop efficient steam engines, this fundamental principle has later proved to be relevant for physics as a whole, and for all kinds of phenomena and behaviour of the natural world. Among others, Clausius (1822-1888) formulated the second law of thermodynamics. His expression was:

It is impossible by a cyclic process to transfer heat from a colder to a warmer reservoir without net changes in other bodies.

Clausius also introduced the notion of entropy (S), and he proved that the change in this factor is always positive in any irreversible process in a closed system. Since the universe can be considered as a closed system, there is always an entropy increase in the universe.

However, there has been some debate of the seeming contradiction between the second law of thermodynamics, stating that every spontaneous process in the universe will increase the entropy, and the existence of life that apparently is the antithesis of entropy increase. In the early forties, Erwin Schrödinger (1944) discussed this apparent contradiction. Later, it has been understood that those systems studied when the first and second laws of thermodynamics were formulated belong to *another class* of phenomena than living systems. The former are steady state phenomena *close to* thermodynamic equilibrium, but the latter are steady state phenomena *far from* thermodynamic equilibrium, not isolated but depending on a steady flux of energy that is dissipated to maintain a local state of organisation (Nicholis and Prigogine 1977, Prigogine and Stengers 1984, Nicholis and Prigogine 1989), apparently following other laws. Among else, these "laws" result in an accumulation of organisation, the opposite of the universal entropy increase.

Efforts have been made to find a reconciliation between the global laws of thermodynamics and their apparent contradictions existing far from thermodynamic equilibrium. As early as 1908, Caratheodory (Kestin 1976) was able to prove that "entropy increase" was not the correct formulation of the second law. Instead, he formulated it in the following way:

In the neighbourhood of any given state of any closed system, there exists states that are inaccessible from it along any adiabatic path, reversible or irreversible.

¹ Stating that energy can not be produced nor destroyed.

² Stating that there is no temperature below 0°K

In this formulation, the notion of entropy is not necessary, and it is a more general statement than the one made by Clausius. Further progress in the generalisation of this principle was made by Hatsopoulos and Keenan (1965) and Kestin (1966) by formulating the Unified Principle of Thermodynamics (as it was called by Kestin. Hatsopoulos and Keenan called it the Law of Stable Equilibrium). This principle epitomised the former three laws 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 principle is generally valid only for isolated systems. However, Kestin showed that such a system is stable in the Lyapunov sense, which means that it will resist being moved from its equilibrium state. Schneider and Kay (1992,1993) used this information to make a corollary of the principle that is valid also for systems far from thermodynamic equilibrium. The distance is measured as the gradient imposed on a system, moving it away from thermodynamic equilibrium:

The thermodynamic principle which governs the behaviour of systems as they are moved away from equilibrium is that they will utilise all means available to them to dissipate the applied gradients. Furthermore, as the applied gradients increase, so will the system's resistance to being moved away from equilibrium.

Examples of such gradients are the heat → heat sink gradient of a Bénard cell, the food → excrement gradient of an animal, or the gradient between +15°C on the surface of the earth and the -18°C in the outer atmospheric layer of the ecosphere (Murota and Tsuchida 1985). These examples could be described in terms of an exergy gradient. Exergy is a measure of how far a system deviates from thermodynamic equilibrium (Keenan 1951, Eriksson, Eriksson and Wall 1978). Living systems are formed by their exergy gradients (II). Their dissipation activities can be described as exergy degradation activities. The principle formulated by Schneider and Kay is valid without the use of the term 'entropy production', which is an improvement, since the definition of entropy far from equilibrium has been problematic (Prigogine 1955).

There is a close connection between a system's capacity to dissipate exergy and the exergy content of the system itself. This follows directly from the reformulation of the Unified

Principle of Thermodynamics for far-from-equilibrium conditions made by Schneider and Kay and Keenan's definition of exergy.

This formulation has been analysed by Jørgensen (1992), who proposes it to be a core principle of ecosystem ecology:

If a system has a through-flow of exergy, it will attempt to utilise the flow to increase its exergy, i.e., to move farther away from thermodynamic equilibrium; if more combinations and processes are offered to utilise the exergy flow, the organisation that is able to give the system the highest exergy under the prevailing conditions and perturbations will be selected.

(Jørgensen 1992, p.186)

It is important to note the association of exergy degradation (which Jørgensen in this citation refers to as exergy flow) with information or organisation content of the system itself. This means that *as systems deviate from equilibrium, they become more organised, and increase in exergy dissipating capacity*. This quality has been discussed by Swenson (1989), and it is also considered by Schneider and Kay (1992). They observe that as the maturity of an ecosystem increases, so does also its capacity to degrade the exergy of sunlight to low temperature radiation. That is: mature ecosystems have a lower surface temperature than less mature systems under the same solar radiation circumstances. This was shown by measurements made both from aeroplanes and satellites. (Schneider and Kay 1992).

Recently, Jørgensen, Schneider and Kay (pers. comm.) have proposed a formulation of a general system principle valid for any self-organising system as well as ecosystems which they call 'The non-equilibrium principle':

If a system is moved away from thermodynamic equilibrium by the application of a flow of exergy, it will utilise all avenues available, that is, to build up as much dissipative structure as possible, to reduce the effects of the applied gradient.

From this, they draw the following conclusions:

*Exergy capture, degradation, use and storage increase with organisation.
As the applied gradients increase, so does the system's ability to oppose further movement from equilibrium.*

This is a step further toward a rule that connects ecosystem theory, systems theory and general thermodynamics. It could, however, be objected that the expressions 'all avenues available' and 'as much dissipative structure as possible' are a bit too vague to be included in a general rule of that importance. Therefore, I propose to use an expression drawn from mathematical complex system theory, the attractor³, to make it easier to test the hypothesis and express it mathematically:

If a system is moved away from thermodynamic equilibrium by the application of a gradient of exergy, an attractor for the system can emerge for the system to organise in a way that reduces the effect of the applied gradient.

As in the case mentioned above, the consequence will be:

An increase of the applied gradient will also increase the strength of the attractor.

REGENERATIVE CYCLING

Accepting the Non-equilibrium Principle by Jørgensen, Schneider and Kay in its simplified form above, two important questions arise: How is the exergy degradation maximisation attained in real, self-organising systems, *and* what determines the limits for the capacity of a certain system to evolve efficient exergy destroying structures? Clearly, all self-organising structures do not appear the same under the same circumstances of solar radiation. A desert and a tropical rain forest can receive about the same amount of solar exergy, yet they appear very different.

To destroy exergy, self-organising systems use the same general strategy: They load high exergy energy into compounds which later will give it away in degraded form. For efficient exergy uptake, a constant supply of compounds with *low* exergy must be available. These are often provided by an internal organisation supplying the site of exergy loading in the system with degraded material to be "reconstructed". If degraded material exist in ubiquitous amounts, there is no need for the organisation to provide it, but if the material is limited, a cyclic organisation delivering the material to the site of exergy uptake has survival value for the system. The more a substance is limiting, the higher the survival value for an organisation that keeps it within the system and transports it efficiently to the "re-loading" area of the system. This phenomenon is called *the regenerative cycle (I and II)*.

³This is also the view of Jørgensen (1992) in his propositions of ecosystem properties.

Typical for all self-organising systems

The phenomenon of regenerative cycling can be found in any self-organising system. The simplest example is the Bénard-cell, where the circulation of water provides cooler water to the heated bottom. Any organisation that provides chilled water to the bottom surface, and transports heated molecules for cooling-off at the upper surface will have an advantage before possible systems that do not manage to do this. After a very short time of change, the 10^{23} or more non-purposeful, indifferent molecules in the experimental set-up are cooperating in a unanimous way to accomplish this! The Bénard apparatus is enclosed in a glass container, so the only thing connecting it to the supersystem is high and low exergy heat.

Other examples of the regenerative cycle can be found in a cell, where the Krebs-cycle uses acetyl CoA as an exergy source to produce molecules of carbon dioxide, water and ATP. They have together a lower exergy content than the initial material. The cell cycle then delivers the end-product, malic acid, for reloading with acetyl CoA. The glucose metabolism and the oxidative phosphorylation in the cell consist of a series of such regenerative cycles. In the Krebs cycle, acetyl CoA, carbon dioxide, water and ATP are substances connecting to the supersystem.

At the organism level, an example of regenerative cycling can be found in the blood circulation, where the net reaction is the uptake of oxygen and exergy-rich material (food) and the oxidation of that material into carbon dioxide and water. The blood itself is conserved within the system and continuously reloaded with glucose and oxygen. The end products leave the lungs with outgoing breath. The conveying substance, the blood, is kept within the system in a regenerative cycle. Food, oxygen, excrements, carbon dioxide and water vapour are here the connecting substances to the supersystem.

Regenerative cycling of phosphorus in an ecosystem

In an ecosystem, the reconstruction takes place in the green plants receiving high exergy radiation from the sun. The presence of animals and other consumers in the system facilitates efficient exergy degradation. The organisms also carry the genetic code providing information of the most efficient way to use exergy and to convert it into low exergy energy products. Such products are for example carbon dioxide, water and for the organism itself unusable products as faecal matter and urine containing nitrogen and phosphorus. However, in a terrestrial ecosystem nitrogen is seldom limiting, because it is conveyed by the air. Neither is carbon, and in many cases not even water. Phosphorus however is often limiting, since it has no (non-poisonous) gaseous phases. Therefore, regenerative cycling of phosphorus is common

in an ecosystem. In an advanced ecosystem, as a tropical rain forest, the regenerative cycling of phosphorus is very efficient (e.g., see Stark and Jordan 1978). As phosphorus is limiting the general exergy degrading activity of the system, this promotes self-organisation toward effective regenerative cycling of phosphorus. The components of the system would rather be called *consumers*, *recyclers* and *reconstructors* than the common denomination consumers, decomposers and producers, since it is a cyclic, not a linear system, which easily is inferred from the later set of terms. In this case, solar radiation, carbon dioxide and water are the substances connecting the ecosystem to the supersystem, the ecosphere.

The regenerative cycle describes the relationships between exergy degradation, material flows and the organisational increase in self-organising systems. Crucial materials (e.g., nutrients, mineral salts, organic matter) are circulated and reloaded with exergy by the combined actions of the system's compartments (e.g., cells, individuals, populations etc.). This enhances the system's capacity to absorb exergy, convert it to low exergy energy and improve its own structure. The regenerative cycle is formed through autopoietic self-organisation. It is a general phenomenon in all far-from-equilibrium systems, of which living systems are the most abundant. Tapping off the elements necessary for re-loading the system with exergy, will make the system unstable and eventually cease to exist. Examples of this are the bleeding of an animal and the constant deprivation of nutrients from a farm producing food used in other places.

To keep or increase its organisation, any self-organising system must export more entropy (i.e. low exergy compounds or low temperature thermal radiation) than it produces by its internal metabolism (Denbigh 1951). This is more or less a definition of self-organisation. Self-organising, exergy destroying systems are nested in each other (Mayumi 1991, II). I suggest that an explanation of this can be that the entropy (low exergy) produced by the system in the form of low exergy products (e.g., water vapour, carbon dioxide, inorganic ions) are used in the regenerative cycle of the supersystem as products to be reloaded. In this way, there is no accumulation of low exergy products, "garbage". The only type of low exergy exported by the total nested system is radiation. The materials will successfully be used in a complicated construction of nested systems that together destroy the incoming exergy from solar radiation in the highest rate allowed by the amount of material. An additional explanation may be that nested complex systems have a larger capacity to degrade exergy than non-nested, because of the multiple layers of the network reinforcements by feedback pointed out by Patten (1992).

Adapting the view of an attractor for the system emerging when a gradient is strong enough to push it away from equilibrium, the regenerative cycle could be the factor limiting the descent of the system into the attractor basin of efficient exergy

degradation. Inefficient cycling of limiting substances can limit the extent of the organisation increase that the system is open to, i.e., its exergy content. Any spontaneous change increasing the capacity of regenerative cycling will then promote the development of new organisation which is more efficient in exergy capture and degradation, i.e., a further descending into the attractor basin.

(For a diagram of the regenerative cycle, see fig. 3 in I)

SOME PRINCIPLES OF SELF-ORGANISING SYSTEMS

In the last part of this discussion, I will consider some thoughts concerning the general principles of self-organising systems common to simple systems, as Bénard cells, and complex systems, as organisms and ecosystems. The discussions are only very briefly outlined, and only meant as "food for the thought".

I will focus on a few issues, namely those of autopoiesis, ecosystems as self-organising elements, the internal co-operation of the subsystems with supersystems, and the discussions of nestedness.

The thinking is illustrated with citations from (I) and (II). I try to clarify these thoughts by adding some comments. ***These comments are written in bold italics.*** For simplicity reasons, the references in the citations are not included, but can be found in the papers.

Autopoiesis

One basic term pertaining self-organisation is autopoiesis. Its effect is to reinforce adaptive behaviour in self-organising systems.

(I:4) One example of autopoiesis is a living system forming itself through a recursive process consisting of *structures* that determine system *organization* generating metabolic *pathways* that in turn produce structures. In this system all factors influence the other factors, changing each other in a logistic way until the system will come at rest in a balance of the influences between the different factors. This balance could be seen as determined by the system dynamics general for dissipative systems proposed by Swenson, the force towards maximum entropy production. Thus, also when autopoietic processes come into play, spontaneous processes guided by nonequilibrium attractors emerges.

It is possible to follow the sequence of complexity from autocatalysis via hypercycles and ultracycles to autopoiesis.

(II:5) ..the term *autopoiesis (is used)* for the recursive cybernetic processes occurring in living systems at all hierarchical levels (the system-logic counterpart of autocatalysis).

Autopoiesis is the cyclic interactions of three or more different parts of a system, mutually shaping each other to a metabolic network. In an autopoietic system, the system boundaries and the components necessary for its transformations are *endogenously generated*. The autopoietic system transformations are composed by interrelationships between its components. This means that the system is both self-reliant and self-referential. It is produced by itself .

Examples of autopoietic processes can quite easily be found in natural systems:

(II:6) Stabilizing autopoietic processes exists both in cell systems, in organisms as well as in ecosystems. One example of the latter is the development of wetland ecosystems where biological subsystems modify hydrology that affect chemical and physical properties of the substrate, which in turn have a decisive effect on the ecological succession of the biological subsystem. The interactions of the parts change the total system organization and by that causing new conditions for the parts to react, modify and evolve.

The ecosystem as a self-organising system

Two fundamental questions in this discussion are: Are living systems fundamentally different from 'dead' systems, and in what respect? Could ecosystems, the ecosphere and other systems of higher order of organisation than the organism be described as 'living'? These questions were discussed in both (I) and (II):

(I) Denbigh (1951) expressed the fundamental processes of living systems in the following way:

$$dS = dS_i + dS_e$$

where dS is the *total entropy* change of a system, dS_i is the *entropy production within* the system due to its metabolism of ingested free energy (this factor is always positive or zero), and dS_e is the *entropy exchange* with the environment. The exchange can be both positive or negative, that is, entropy can either increase in the system by disturbances from outside or it can decrease by means of active export of high entropy energy through the excretion of metabolic products of higher entropy content than the "ingested" exergy, or through processes that increase order within the system. It seems to be a general tendency for living systems to actively produce entropy from low entropy inputs.

Actually, this formula could be seen as a general description of self-organising, since it reflects the continuous increase (if $dS_i < dS_e$) or conservation (if $dS_i = dS_e$) of organisation in a system. If $dS_i > dS_e$, the internal disorganisation exceeds the export of high entropy products, which means that the system deteriorates and, ultimately, dies.

If an exergy gradient is applied over a system, it may start self-organising. One example of a simple system of that type is the Bénard cell :

(I): This system consists only of water molecules which could not be expected to exert any foresight or planning, but anyhow the molecules cooperate in a way that leads to an organized system. This *teleonomic*, or self-organizing, behaviour seems to be a very common feature in living systems.

...It demonstrates that far from thermodynamic equilibrium, ordered systems form spontaneously.

The teleonomic behaviour of self-organising systems induces a system behaviour that is basically different from the system behaviour of close-to-equilibrium systems. This is pointed out in I:

Living systems exist only far from thermodynamic equilibrium. This means that one has to be *very careful* when making analogies between reaction assemblages that are close to equilibrium (for example mechanisms, as cars, watches etc.) and living systems. To stress this difference, we chose the term self-organizing systems (Jantsch 1980) to encompass assemblages that exist only far from equilibrium and react as wholes, in such a way that their behaviour governs the behaviour of their parts. Such systems react upon their environment in a seemingly purposeful way, a *teleonomic* way, to maintain their individuality and to maximize their access to exergy. Examples of self-organizing systems are then cells or organisms, ecosystems, the ecosphere, and possibly also eddies or complicated cyclic reaction assemblages of hypercyclic or ultracyclic type. Close-to-equilibrium systems as the mechanisms mentioned above react by means of programs instructed from outside and are *exopoietic* "constructed from outside". Therefore, analogies between mechanisms as watches, computers or other exopoietic systems and evolutionary systems as organisms or other self-organizing systems could easily be erroneous or at least misleading.

As concluded in paper II:

(II:1) ..it is only possible to describe the livingness of a system in a continuous way, and that living matter should be defined by the processes of which it is a part. Hence, from the perspective of self-organizing and nested living systems it is difficult to draw boundaries between living and non-living as well as human and non-human systems.

The question of 'living' and 'dead' systems could then be changed into the grouping of systems into self-organizing and not self-organizing systems. Clearly, systems that are open, exergy destroying and self-maintaining, as cells, organisms, ecosystems and the ecosphere, could be seen as belonging to the former group. This apprehension is clearly expressed in II, as the title in paragraph II:5: Self-organizing through autopoietic processes, and in II:7: We argue that cells, organisms and ecosystems, even the entire ecosphere, are autopoietic far-from-equilibrium dissipative systems. Living systems self-organize in the presence of exergy potentials. This process occurs in every level of the system.

From the system perspective hold in this thesis, ecosystems could be conceived as belonging to the same class of systems as cells and organisms, that is: self-organising, far from thermodynamic equilibrium systems.

Functional co-operation

In I, the Bénard cell experiment is discussed:

This system consists only of water molecules which could not be expected to exert any foresight or planning, but anyhow the molecules cooperate in a way that leads to an organized system. This *teleonomic* or self-organizing, behaviour seems to be a very common feature in living systems.

In a self-organising situation, the internal order of the system is increased or maintained. It is hard to imagine how such a situation could evolve if the supersystem consists of elements that do not cooperate, or internally compete with each other in some other manner than being the most supportive to the general evolution of the supersystem. Furthermore:

(II:5) Both the environment of the system and the components of the processes are often by themselves autopoietic systems.

It is pointed out that the human socio-economic system in itself is a subsystem of its supporting ecosystems:

(II:10) Hence, there is an urgent need to redirect the behaviour of socioeconomic systems from the throughput based operation of increased resource use, waste accumulation, and

environmental degradation towards a development path where human resources flows are integrated with biogeochemical cycles, and ecosystem processes in a synergistic fashion. **

Nestedness

The structure of nested, or holarchic systems, is described in II:

(II:1).. life is an integrated process of nested living systems consisting of basic materials, cells, organisms, ecosystems, and their environments, continuously interacting at various holarchic levels in both time and space.

(II:7) Supersystems (e.g. ecosystems or organisms) consist of subsystems (organisms and cells respectively). They are *nested* within each other, and from this view inseparable, since they, though clearly individual, consist of each other. The nested system consists of identifiable, self-organizing parts or *holons*. A holon refers to entities that are ordered to constitute a new entity in the living system. It is itself a whole composed of parts, but at the same time a part of some greater whole. Holons are open subsystems of systems of higher order, with a continuum from the cell to the ecosphere.

(II:9) ..important for the understanding of nested systems to conceive that the attractors typical for every autopoietic system are the result of forces between autopoietic subsystems that have their own attractors also.

(II:10) ..in the fields of ecological economics, human ecology and also more recently in environmental economics the dominant western worldview of mankind as superior and independent of nature is shifting towards a view of human societies as sub-systems of the overall ecosphere

A possible explanation of why self-organising systems are nested in each other is suggested in the discussion on the regenerative cycle.

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