

CHARACTERISTICS OF NESTED LIVING SYSTEMS

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Journal of Biological Systems,1:3 pp.257-274

Abstract

Living systems are nested and consist of basic materials, cells, organisms, ecosystems, and their environments, continuously interacting in time and space. Life is an integrated process of nested living systems. We synthesise and discuss exergy capturing and accumulation of organisational exergy; the structuring of the system towards maximum entropy production and export of high entropy products; autopoiesis; emergent attractors or optimum operating points; characteristics of nested systems and holarcic levels; and the role of working and latent information. It is concluded that 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-organising and nested living systems it is difficult to draw boundaries between living and non-living as well as human and non-human systems. Implications of this world-view is discussed in relation to environmental management.

Key words: self-organisation, autopoiesis, hierarchy, life processes, evolution

1. Introduction

The global call for sustainable development, the urgent need for ways to approach such a development, and the growing awareness of mankind's dependence on the life-supporting environment [40] has increased the interest for making explicit use of ecosystem processes and functions for the production and maintenance of valuable goods and services. Ecotechnology or ecological engineering [19,37] represent applications in this direction. These techniques imply the design of a human activity with its natural environment for the benefit of both. They are thus very different from conventional Western-oriented engineering and technologies that try to substitute or conquer the natural environment, a substitution that generally requires large amounts of industrial energies, other natural resources, as well as the often unrecognised but fundamental ecosystem services [11,20,41].

A major argument for using ecologically based technology is that such solutions generally are more cost-efficient than conventional technical measures [3]. However, we are convinced that these technologies are not only less costly, but also more sustainable because they are founded on basic principles of ecosystem functioning. As stated by Costanza [12] "Ecological systems are our best current models of sustainable systems. Better understanding of ecological systems and how they function and maintain themselves can yield insights into designing and managing sustainable economic systems".

Our purpose with this article is to contribute to the development of a theoretical foundation for the interdependent systems of humans and nature, which could provide a framework for human actions, in collaboration with the life-supporting environment on which we depend.

In the article we synthesise what we believe are fundamental life processes crucial for self-organisation and evolution of all living systems, natural as well as human [10,26,27,40,42,45,52,57,58].

Living systems are defined as systems exerting life-processes. These processes include systems' capturing of exergy, exergy storage [18,28], entropy export, maximum entropy production [51], autopoietic processes [53], and emergence of attractors or optimum operating points [29,30]. In addition, to these processes we discuss other characteristics that seem to appear in self-organising systems. We refer to them organisational exergy, working and latent information, nested systems [1,5,23], and holarctic levels.

We argue that life is an integrated process of nested living systems consisting of basic materials, cells, organisms, ecosystems, and their environments, continuously interacting at various holarctic levels in both time and space. From this perspective a living system can have more or less life, but not being referred to as alive or dead. We close the article with discussing the implications of such a perspective for natural resource and environmental management.

2. Order, Disorder and Entropy

It is easy to separate living systems, e.g., humans, animals and plants, from non-living e.g., machines. However, what makes a system "alive" is not as obvious, and even in the case of human beings there are ethical debates and need for legislative definitions of when life begins and ends.

Contrary to what would be expected, the question of what "life" is has not been particularly addressed by biologists, but rather by physicists dealing with thermodynamics. Ac-

According to the first law of thermodynamics, energy is indestructible. However, the same amount of energy can have very different quality, which is capability to conduct or maintain changes. A term, exergy, was introduced [6,31] to measure the difference in physical quality of energy. The exergy content of a system indicates how far it deviates from thermodynamic equilibrium. Exergy is related to how much entropy a certain amount of energy can produce, or expressed in another way, the amount of entropy that is possible to dissipate from a certain system when it moves towards thermodynamic equilibrium [24]. For an elaboration of the exergy concept see e.g. Keenan [31], Kestin [32] and Wall [56]. A living system must extract exergy from its environment (either directly from solar energy photosynthesis, or indirectly through food consumption) to structure itself. Eventually, the same amount of energy as extracted will be exported from the system. According to the second law of thermodynamics, the exported energy is always of a lower quality, in the sense that it has lower exergy content.

Schrödinger [50], in his book “What is life?”, concluded that a typical property of living systems is that they apparently break the second law of thermodynamics by maintaining a state of high order within their boundaries. Increase in internal order means that exergy is stored in living systems. Living systems with their low and internally decreasing entropy content contrast with the gradually increasing entropic state that is an elsewhere universal phenomenon for close-to-equilibrium processes in isolated systems. However, living systems are neither isolated nor close to equilibrium. A living system must exchange exergy (closed systems) or both exergy and matter (open systems) over its boundary. These attributes of living systems are typical for all far-from-equilibrium dissipative systems [27,46]. Entropy relations of living systems were discussed by physicists such as J.D. Bernal [8] and K.G. Denbigh [16]. Denbigh 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. As stated by Daly and Cobb [15], “what we live on is the qualitative difference between natural resources and waste, that is, the increase in entropy”.

Lovelock [34] summarised the conclusions by Schrödinger, Bernal and Denbigh as follows: “Life is one member of the class of phenomena which are open or continuous reaction systems able to decrease their internal entropy at the expense of free energy taken from the environment and subsequently rejected in degraded form.” The free energy that is mentioned by Lovelock in this citation is closely related to the exergy, the energy quality factor [55].

If the decrease in internal entropy by excretion of high entropy products and by processes leading to order is less than the internal production of entropy, disorder will accumulate and the system will ultimately deteriorate and cease to exist.

If, on the other hand, the total internal decrease in entropy is larger than or equal to the internal production of entropy by the metabolism of the system, the system will have decreasing or constant entropy content and maintain its integrity. Therefore, an increase in the internal order leads to an increase in entropy production and export of high entropy products by the system (as indicated by Swenson [51, p.190] in one of his four propositions). Hence, *when living systems increase in organisation, they also increase their ability to produce entropy.*

Far-from-equilibrium system has a high exergy content [18]. Preliminary studies of a lake ecosystem [4] indicate that the entropy production of the ecosystem is about five times higher than the entropy of incoming shortwave radiation. This means that the exergy captured by the system is larger than what is exported. Therefore, there is an accumulation or build up of exergy reflected in the information/organisation of the components of the system and their interrelations. Schrödinger [50] mentioned “*Life consumes not food, but negative entropy*” (i.e. exergy). This could be interpreted as the exergy potential needed to maintain all living systems.

The above discussion points out that there is an upper limit for the use of energy if a system is to be sustainable. Increase in the use of exergy provides possibilities to increase in system organisation (“livingness”) or order *only if the system can evacuate the entropy produced*. Maximum energy abundance and use is therefore not necessarily equal to maximum organisation. This has been emphasised by Odum [43] stating that “the designs that prevail in self-organising systems are those that maximise *useful power*” (our italicisation), referring to ‘useful’ in the sense of power that *feeds back to amplify*. This amplifying power is different from just power maximisation. The latter often leads to linear flows, and throughput systems with few feed-back loops, little recycling, simplification and degradation of system structure and function [14].

3, Accumulation of Organisational Exergy

Most of the exergy accumulated in a system is used as chemical energy or is stored. Brooks et al. [10] refer to the use of chemical energy as *heat generating transformations*, and the accumulation of exergy as *conservative transformations*. The second type is further divided into what is stored as biomass and what is stored as increased diversity of the genetic information, termed instructional information.

With regard to instructional information we argue that such transformations are not solely those stored in genetic diversity, but also in the *relations* between (genetically determined) entities, what we term transformations of *organisational exergy*, that is, the part of the exergy transformed into structure of the system, for example when an ecosystem is undergoing succession.

Organisational exergy, like genetic diversity, accumulates during the entire development of the system, while biomass accumulation levels out as it is counteracted by heat generating transformations. We believe that this organisational exergy is crucial for the system, because it is the structure of the system that determines its ability to receive exergy and export entropy products. Since exergy is a concept related to the quality inherent in the system, we argue that *a system that holds a large amount of organisation has higher exergy content compared to a system with less organisation, but with the same mass and chemical composition.*

The accumulation of organisational exergy as genealogical (inherited) information storage is observed as evolution in biological systems [9]. The same accumulation is also guiding the succession of an ecosystem [36,42]. The increasing structure (organisation and biomass) during ecosystem succession and evolution increases the systems ability to produce entropy by increasing its efficiency in converting exergy to entropy, up to the limit of available exergy. This is referred to by Schneider and Kay [49] as the system's strive to reduce the applied exergy gradient.

By the accumulation of organisational exergy, the internal entropic state of a living system can continue to decrease until it is limited by a disturbance (entropy entrance) from outside, affecting the system's ability to excrete the entropy produced by its metabolism. Characteristics of ecosystems under stress have been discussed by Odum [39] and possible development pathways for disturbed systems by Holling [26] and Kay [30].

If biomass accumulation is restricted, organisation could still increase. In tropical rain forests and mature mammals, for example, the biomass increase has levelled out, but qualitative improvement can still take place. This could also be the case in human societies if economic growth or progress would be based on improvements in quality of the system's organisation instead of on physical expansion. High exergy inputs that do not induce feed-back loops for accumulation of organisational exergy (restoring a low entropy state) will instead break down organisation by accumulating entropy in the system, for example in terms of waste and pollutants. This is the case of modern agriculture where specialised production of biomass often increases but the organisation of the system diminishes [22]. The monocultural system is sustained by high industrial energy inputs diminishing self-organisation ability, not only in agriculture but also in the surrounding environments.

If biomass is diminishing it is still possible that the organisation of a living system could increase, as is the case when nutrient constraints on a system force more optimised utilisation of the available sources. Examples of this are the increase in chlorophyll content in plants growing under shadow conditions or the development of the highly diversified plant community in meadows.

4. Working Information and Communication in Living Systems

As discussed above living systems transform exergy entering the system into organisation. Organisation is working information (pragmatic information [27]; macroscopic information [10]). Such information has real effects on the receiver, resulting in for example feedback effects that will change the behaviour of both the receiver and the transmitter. In addition to working information there is latent information. Such information is there, but it does not affect the receiver, because there is no receiver. Examples of latent information are DNA transformed but not expressed in reproduction, or understudy or entrained species in ecosystems, that is species which are there but do not play an important role in the present processes and functions of the system (Holling C.S., Univ. of Florida, pers. comm.). Latent information might be transformed to working information if the system changes from one state to another. It has been argued that latent information is a crucial component for systems resilience and integrity [38]. Working information in one organisational level could also be considered latent on another.

The difference between latent and working information is that communication is involved in the latter. Communication is an essential part of any self-organising system.

Only working information can build system structures. Communication is necessary if a living system is to function [27,42].

Because of its cyclic nature (which is discussed below in relation to autopoietic processes) communication is a prerequisite for the stabilisation of living systems. This could be a reason why the internal communication ability is well developed in dissipative far-from-equilibrium self-organising systems.

The communication in simple self-organising systems could be exerted in a very simplistic way, as in the Belousov-Zhabotinsky reaction [59], where the communication between different parts of the system during the reaction is exerted by auto- or cross-catalytic steps. Communication in organisms or cells, is well understood. In the hypercycles [17] in cells the information is stabilised by chemical reactions. Examples of such a communication are the cycles of citric acid or glycolysis, or the co-ordinated transfer of information in the DNA-tRNA-protein system.

Also in systems with levels of organisation higher than the organism, such as ecosystems, communication is necessary for self-organisation. It could even be stated that communication is a prerequisite for self-organisation.

5. Self-Organising Through Autopoietic Processes

In the previous section, we have argued that a prerequisite for living systems is to capture and store exergy, and by spontaneous self-organisation maximise the export of entropy produced by the system's metabolism. In this section we will analyse how the captured exergy could be transformed into the internal organisation of living systems, and how the system structure can reinforce itself in a self-organising process.

Major contributions to the understanding of the nature of living systems are those of Prigogine and co-workers. Their investigations on simple systems indicate that self-organising dissipative (energy dissipating) systems evolve automatically as a result of multiple irreversible processes in open systems far-from-thermodynamic-equilibrium. Prigogine and Stengers [46] state that "non-equilibrium is a source of order", and suggest that "both the biosphere as a whole as well as its components, living or dead, exist in far-from-equilibrium conditions". They continue:".. life, far from being outside the natural order, appears as the supreme expression of the self-organising processes that occur." ".once the conditions for self-organisation are satisfied, life becomes as predictable as the Bénard instability or a falling stone."

Varela, Maturana and Uribe [53] have coined the term *autopoiesis* 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 [27].

One example of autopoiesis is when a living system forms itself through a recursive process consisting of *structures* that determine bounded system *organisation* that generates bounded metabolic *pathways* that in turn produce structures (Fig. 1).

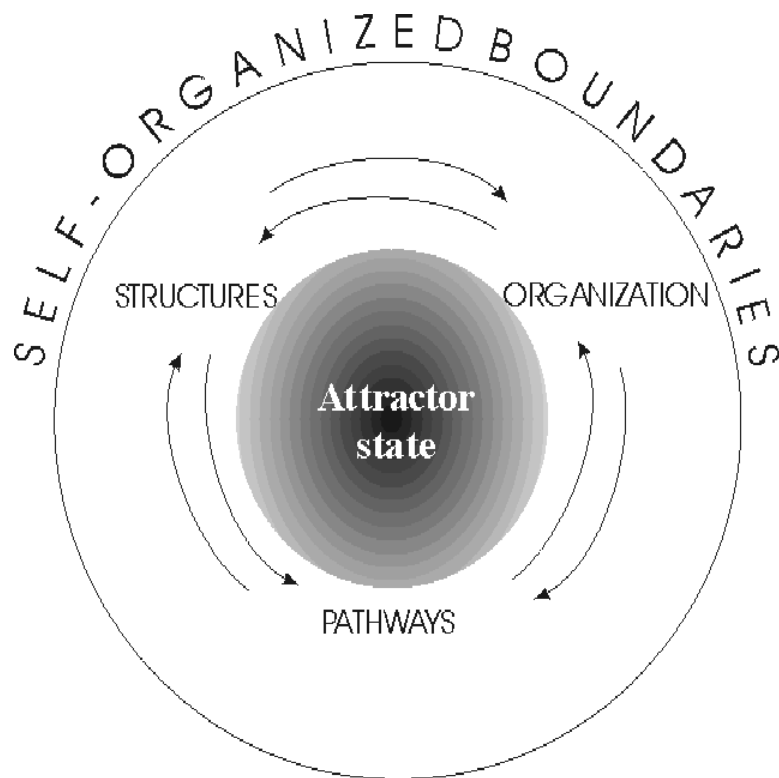


Figure 1. Principles of autopoiesis. The system forms its boundaries by its own actions (modified from 55).

In this system all factors influence the other factors, changing each other in an ever-decreasing rate of change until the system will come to rest in a dynamic balance between the influences of the compartments of the system and its environment, the emergent attractor state. Kay [30] has referred to this state as the optimum operating point(s) of the system. He suggests that the point is not unique and that there could be different possible states for the system. The point then reflects a state where self-organising thermodynamic forces and disorganising forces of external environmental change compensate each other.

The ordering processes in autopoiesis are associated with increased production of low grade thermal energy or other high-entropy products actively exported from the system [49]. The autopoietic system structure is a property that seems general to all living systems [23]. It has been stressed that recursive processes of this type are necessary for the evolving of ordered systems [27,43, 46]. The attractor state (optimum operating point) could in this case be understood as a metabolic (non-)equilibrium state typical for the autopoietic system in question, the “Gestalt” of the system. The position of this state is determined by the forces and products of the component processes and their interactions.

We suggest that it is processes of autopoietic type that create non-equilibrium emergent attractors in living systems. The autopoietic processes force the system as a whole towards a state of maximum entropy production by increasing the structure (biomass and organisation) of the system. In the attractor state the system utilises as much of the ingested exergy as possible and converts it to high entropy products.

One implication of the self-referentiality of autopoiesis is that the system does not exert any foresight or planning with respect to its environment. The emergent attractors are results of the components and their interactions. However, both the environment of the system and the components of the processes are often by themselves autopoietic systems, embedded in each other.

6. Autopoietic Shaping of all Living Systems

In ecosystems, information is transferred between genotype, phenotype and the ecosystem in an autopoietic, self-organising way. In an autopoietic system, it is impossible to point out any one-way relationship. The genotype is expressed in the phenotype, which is determined by both the genetic information and by the shaping forces of the ecosystem. By its actions, *the individual (the phenotype) contributes to the shaping forces that ultimately will influence the genetic constitution of its progeny* [27,48]. The attractor of this system is close to what is observed as the evolved system after a long time of autopoiesis.

Stabilising autopoietic processes exists both in cell systems [23], in organisms [27] 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 organisation and by that causing new conditions for the parts to react, modify and evolve [21].

Holling [26] has argued that in ecosystem development there are prolonged periods of accumulation and production (build up of organisational exergy), and short periods of renewal and restructuring that are caused by endogenously generated new attractor states. These changes both destroy and releases opportunity for innovation and reorganisation of system components, processes and functions. In the periods of renewal and restructuring there will be opportunity for latent information to become working information.

Different pathways for living system development after external disturbances have been discussed by Kay [30], from a non-equilibrium thermodynamic perspective. The possible reactions to disturbance are that

- 1) the system may not move from its original attractor(s) or optimum operating point(s),
- 2) it may move away but return to the original point,
- 3) the system may permanently move away from it. In the latter situation the system may
 - a) break down because there exists no alternative attractor,
 - b) remain on its original development path but self-organise through autopoiesis to a new (set of) attractor or optimum operating point,
 - c) develop on a bifurcation from the original development path,
 - d) or attractors may emerge on a different path and the system undergoes a catastrophic reorganisation to reach it.

By changing a part of the system radically (e.g. hydrology by draining a wetland system), one also may change the attractor of the system, which may cause a flip to a new type of system with other compartments. If these properties are found to be generally valid for living systems, it will have extensive implications for natural resources and environmental management.

7. Nested Autopoietic Systems

We argue that cells, organisms and ecosystems, even the entire ecosphere, are autopoietic far-from-equilibrium dissipative systems [27,46]. Living systems self-organise in the presence of exergy potentials. This process occurs in every level of the system. Supersystems (e.g. ecosystems or organisms) consists of subsystems (organisms respectively cells). 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-organising parts or *holons* [33]. 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 [5,44]. Holons are open subsystems of systems of higher order, with a continuum from the cell to the ecosphere.

The hierarchy of holons we prefer to call *holarchy* [33]. In a holarchy the higher organisational levels *consist of* the lower levels. This is different from a hierarchy of rank, such as an army, where the higher ranked men *does not consist* of the lower ranked men. The distinction between different types of hierarchical systems is further discussed in Allen and Starr [1], and the concept of hierarchy in relation to ecosystem is thoroughly treated in O'Neill et al. [44].

Table 1. Homologous holarcic levels and their connecting forces

| Basic unit: | Biomonomer (amino acids, simple sugars, fatty acids, nukleotide bases) | The Cell (muscular-, nervous-, epithelial-) | The Organism: > human > bird > tree | The Ecosystem: > lake > forest > town with agriculture |
|---|---|--|---|--|
| SIGNALS (binding primary units together) (making congregations) | Physical - chemical bonds : <i>molecular</i> bonds : <i>ionic</i> bonds : <i>hydrogen</i> bonds | Chemical signals <i>binding</i> cells together : agglomerations : <i>growth inhibition</i> : <i>transmittor</i> substances) | Signals : visual, sexual signals, dominance signs, flags : feromones : sounds (bird songs, speech, radio) | Flows information, energy flows, critical substances, means for adaption : nutrient flows: : water flows : migrations |
| Polymers (basic units connected) | Biopolymers > Proteins > Complex carbohydrates > Membranes > Nucleic acids | Tissues similar cells cooperating > muscles > nerves > epithels | Populations several organisms of the same type > spruces in a wood > humans in a town > perches in a lake | Trophotypes Similarly adapted ecosystems in the same biological region. > lakes in a forest > oases in a desert > forests patches in agricultural areas |
| TRANSACTIONS ("services" between polymeric units) making cooperative units | : <i>Energy transactions</i> (ATP) in cells : <i>Information transactions</i> (DNA, RNA) | : Energy transport (glucose) : Oxygen transport : Protection, support, nutrition : Immune system services | : Symbiosis (parasitism, commensalism, mutualism) : Energy transactions - population regulation (prey-predator relationships) : Mutual defence (insect eating, tree-dwelling birds) | : <i>Transfer</i> of critical substances : Transfer of organisms (=information) : Adaption to the same energy costs and disturbances (f.ex. those prevailing within the tundra-area) |
| Polymer aggregations (Cooperations btw. polymers) | Organelles: >cellular nucleus > endoplasmic reticulum > mitochondries > procaryotes | Organ: > heart > lungs > nervous system > skin > skeleton | Communities > pelagic organisms of a lake > meadow > town > farm | Biom trophotypes in the same region > Subarctic areas > Tropics |
| MUTUAL DEPENDENCE (Btw. polymer aggregations) => organisation of functions | <i>Coordination</i> of transactions : DNA -> RNA - >protein synthesis : Cellular division : Cellular metabolism | : <i>growth regulation</i> : <i>oxygen transport</i> : <i>distribution</i> and absorption of nutrients : <i>disease defence</i> : <i>excretion</i> | : <i>Transactions</i> of critical substances (N, P, CO ₂ , O ₂) : <i>Feedback</i> mechanisms : <i>Regulation</i> of energy transactions between societies | <i>Regulation of:</i> : the salinity of the seas : mean temperature of earth : atmosphere gas composition : climate |
| New holon: | The (eucaryote) cell | The organism | The ecosystem | The ecospere, Gaia system |

In Table 1, we propose what could be regarded as homologous levels in different levels of the *holarcic* system of life. It is divided in two types of features, the *physical composition* of the holon (unit, polymer, aggregated polymers, new unit) and the *combining forces* (signals making congregations, transactions making co-operative units, mutual dependence making organisation of functions). A few examples are listed under each item.

8. What Delimits Living and Non-Living Matter?

Accepting the perspective that open living systems of different order (cells, organisms, ecosystems, ecosphere) are embedded in each other, makes it very difficult to speak of living and non-living matter. Does non-living water become living, when we drink it and integrate its components in our bodies? How do we regard the sodium ion in the water, which the moment before drinking was a non-living inorganic ion, and that will become an integrated part of the mind, in the sodium pumping in a nerve cell of the brain?

Rocks are commonly regarded as non-living matter. But through the pumping of carbon dioxide by plant roots into the soil, the siliceous matter of the rock is dissolved and transported by water to the sea. There it is taken up by diatom algae and turned into a stabilising siliceous skeleton of the algae. When the alga dies, the siliceous skeleton sinks towards the bottom of the sea. Some of the silica is dissolved and goes through another loop, and eventually the silica rests as deposits on the sea bottom. There it becomes integrated in the sediments, which during the millennia will be packed to sedimentary slate sinking towards the hot lower parts of the crust, ultimately becoming metamorphous rock, moved by the plate tectonics (which have been suggested to be induced by biological processes [2]) to the surface by earthquakes and upheavals, where it again is exposed to erosion by wind, rain and plant roots [35]. It has been argued that a very large part of the “non-living” rocks of the upper crust has been integrated parts of living matter some time during life’s existence on Earth (K. Brood, Museum of Natural History, Stockholm, Sweden, pers.comm.).

Similarly, basic components are concentrated in plants, plants are eaten by herbivores, and herbivores are eaten by carnivores. The components are returned to the soil as excrements, carcasses and so on, and are decomposed by micro-organisms, making the basic components available to plant growth where they are reloaded with exergy - the so called regenerative cycle [25]. The regenerative cycle is internally formed through autopoietic processes. In an ecosystem, the main components of the regenerative cycle are the consumers (e.g. animals), recyclers (e.g. fungi and bacteria) and reconstructors (green plants) (Fig. 2)

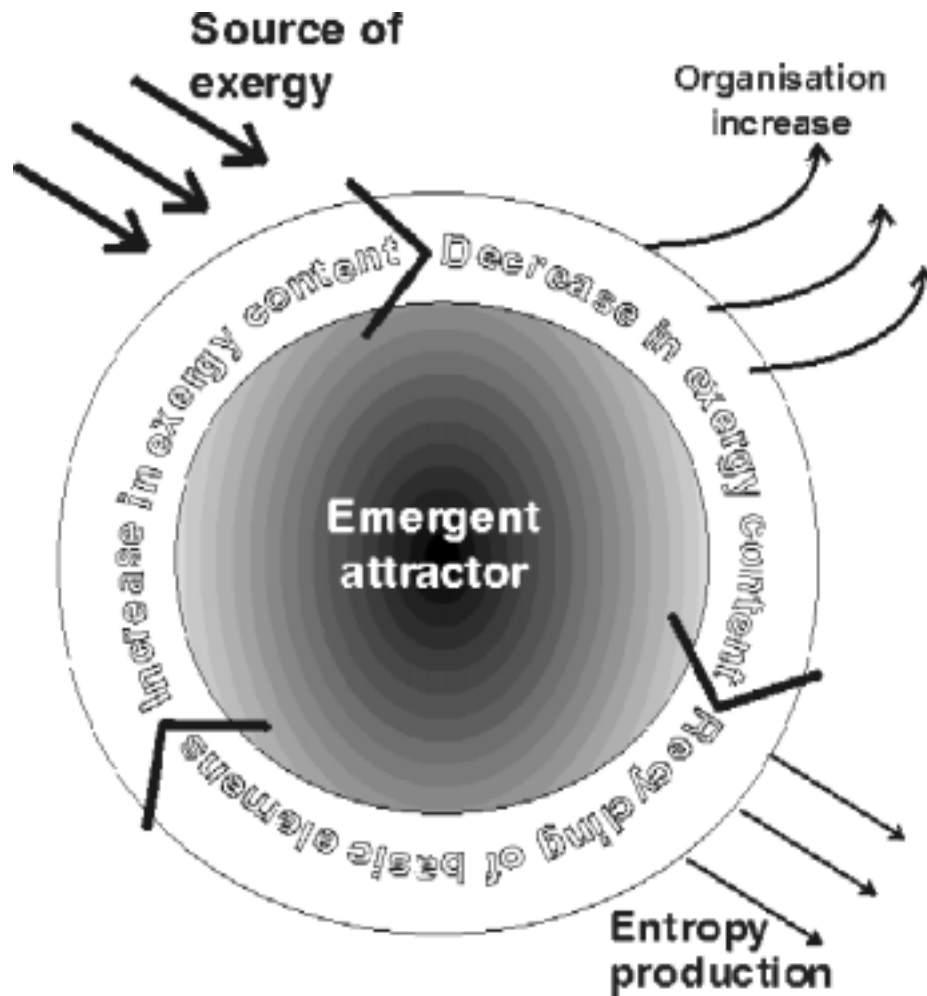


Figure 2. The regenerative cycle describes the relationships between exergy destruction, material flows and organisational increase in self-organising systems. Crucial materials (e.g. nutrients, mineral salts, organic matter) are circulated and reloaded with exergy by the combined actions of the system's compartments (e.g. cells, individuals, populations etc.). This enhances the system's capacity to absorb exergy, convert it to entropy and evolve its own structure. The regenerative cycle is a general phenomena of the different levels of the holarchy of living systems.

We suggest that the 'livingness' of a certain molecule (or system) only could be defined by the system processes of which it is a part. It should therefore be realistic to define *living matter by the process of which it is a part*. Referring to its chemical structure in isolation is not enough. Any particular subunit is not a prerequisite for the life processes to prevail. The processes of exergy loading and dispersion of high entropy products continue even if an individual unit is replaced. Life is a process, and living matter is the matter integrated in this process.

9. What Delimits Living Systems?

If we accept the nested world-view, however, even the process oriented description of life will be confused. If a cell of our body disintegrates, for example as a result of functional cell death during morphogenesis, most of its constituents are used by other cells within the body for further growth. The unit “dies”, but its components are integrated in the system that it was a part of. Further, if the living system would be of higher hierarchical order, for example a rabbit, which is eaten by a fox, the supersystem of the cell - the organism - disintegrates, but its components are still integrated parts in the ecosystem. Hence, a certain molecule integrated in one living process becomes a part of another living system, but of another holarchical order.

By this even the process-defined separation of living and non-living matter becomes inconsistent. A definition of life has to encompass the entire living system consisting of identifiable parts at various hierarchical levels.

An eddy in a river is clearly definable and measurable, but it is still a part of the river, entirely dependent on the river’s dynamics and flows. It is impossible to think of an eddy as separated from the river.

The living system on Earth, with a holarchy from the ecosphere, consisting of ecosystems consisting of organisms consisting of cells (Table 1) could metaphorically be described as whirls consisting of smaller whirls consisting of eddies consisting of smaller eddies (Fig. 3). Each succession of whirls stabilises and is a constituent of the next. When an eddy is disintegrated, its components are incorporated by the system of which it was a part. In due course its components could be a part of another eddy in the same river.

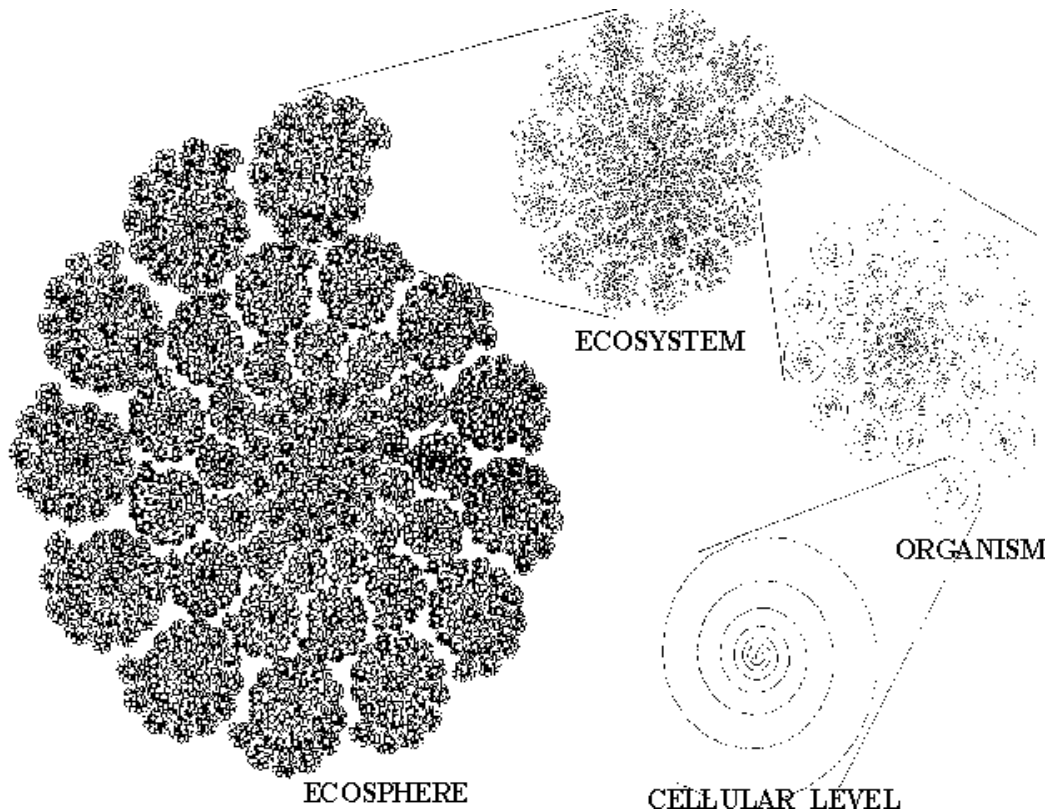


Figure 3. Successive levels of organisation in nested living systems.

We suggest that it is important for the understanding of nested systems to conceive that the attractors typical for every autopoietic system is the result of forces between autopoietic subsystems that have their own attractors also. The systems are thus stabilised by the attractors of the subsystems as well as the presence of their own attractors.

Table 2. Properties of living systems.

A) Basic system requirements

| |
|--|
| Life can only exist where there are possibilities to convert an exergy source to entropy |
| Living systems can only exist in a state far-from-thermodynamic equilibrium |
| Life is an organisational process towards maximum conversion of available exergy sources to entropy products |
| Organisational processes can only be a result of system cooperation between components |
| Living systems are <i>nested</i> , consisting of subsystems |
| This leads to a holarctic structure of living systems (cells, organisms, ecosystems, ecosphere), with an interconnectedness between subsystems and supersystems. |
| For survival the supersystem has to export equal or more entropy products than its subsystems produces. |

B) Basic living system characteristics

| | |
|---|---|
| <i>Openness</i> | Exchange of energy and material over the boundaries of the system. |
| <i>Far-from-equilibrium</i> | A source of high quality energy (exergy) and basic materials for maintenance. |
| <i>Communication</i> | Information channels between different parts of the system. |
| <i>Autopoietic pathways</i> | Loops that promote their own generation, autocatalytic feedbacks. |
| $dS_i \leq dS_e$, <i>exergy enhancement or maintenance</i> | Export of entropy products which exceeds (or equals) the entropy production of the “ingested” free energy source, and the disturbances that enter the system. |
| <i>Material conservation, maintaining physical parts</i> | A structural basis for channelling and storing the acquired organisational exergy. |

Cells, organisms, ecosystems and the ecosphere are features of different holarctic levels of the living system. They all show general characteristics of living systems listed in Table 2. Since all of the concepts in this table could be attributed with more/less values, not only false/true values, one could conclude that *the “livingness” of a system is only possible to describe in a continuous way*. That is, a system can have more or less life (organisation, structure etc.), but a system cannot be “living” or “non-living” in an absolute sense, as a false/true function.

10. Humanity as Integrated Parts of Nested Living Systems

What are the management implications of a world view of nested human-nature systems? The theoretical principles that we have discussed in this article would imply that

it is a social trap to continue to exclude the role of ecosystems for a prosperous development of human societies. However, 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 [7,13,27].

The insight is spreading that socio-economic systems not only need, but also depend on natural resources and ecological services for evolution and survival. Similar to ecosystems, socio-economic systems require exergy for organisation on a daily, annual, cultural or any other time scale. The use of industrial exergy has been a major reason for the ability of human societies to shift from the direct limits to growth set by solar energy based systems [41]. The availability of industrial exergy in combination with human ingenuity has made substantially more matter available to human economic development. The rapid expansion of human activity and population on a global level has made mankind approaching new limits to growth [54]. Some authors' even claim that the global carrying capacity limits have already been reached, reflected in ozone depletion, global warming threats, and severe environmental degradation [47]. Hence, there is an urgent need to redirect the behaviour of socio-economic 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. For this purpose we believe that the theoretical foundation of self-organising living systems needs to be further established. We hope that what we have discussed in this article could contribute to such a development and serve as a useful framework for the ongoing debate on the potentials for sustainability in human-nature interrelations.

Acknowledgements

We have got valuable comments on the manuscript from J. Barkley Rosser Jr., Stephen Cousins, Stefan Hellstrand, C.S. Holling, Ann Mari Jansson, James Kay, Joseph Potvin, Hans-Erik Wanntorp and from participants at a research seminar on nested systems at Department of Systems Ecology, Stockholm University. We appreciate their interest in our work. Many thanks also to Professor Ingemar Dahlstrand, Department of Datorology and Numerical Analysis on the Technical Highschool of Lund, for helping us constructing Figure 3. This work was made possible by a grant from the Swedish Council for Planning and Coordination of Research (FRN). Carl Folke's work was partly financed through a grant from the Swedish Council for Forestry and Agricultural Research.

References

- [1] Allen TFH and Starr TB, *Hierarchy: Perspectives for Ecological Complexity* (University of Chicago Press, Chicago, 1982).
- [2] Anderson P, The Earth as a planet: paradigms and paradoxes. *Science* **223** (1984) 347-355
- [3] Andréasson-Gren I-M, Costs for nitrogen source reduction in a eutrophicated bay in Sweden. In *Linking the Natural Environment and the Economy: Essays from the Eco-Eco Group*, ed. by Folke C and Kåberger T (Kluwer Academic Publishers, Dordrecht, 1991) pp. 173-188.
- [4] Aoki I., Entropy balance in Lake Biwa. *Ecological Modelling* **37** (1987) 235-248.
- [5] Auger P, *Dynamics and Thermodynamics in Hierarchically Organized Systems* (IFSR Series on Systems Science, Pergamon Press, Oxford, 1989).
- [6] Baehr HD, *Energie und Exergie* (VDI-Verlag, Düsseldorf, 1965).
- [7] Berkes F and Folke C, A systems perspective on the interrelations between natural, human-made and cultural capital. *Ecological Economics* **5** (1992) 1-8.
- [8] Bernal JD, *The Physical Basis of Life* (Ruthledge and Kegan P., London, 1951).
- [9] Brooks DR and Wiley EO, *Evolution as Entropy: Toward a Unified Theory of Biology* ((2:nd ed.), University of Chicago Press, Chicago, 1988).
- [10] Brooks DR, Collier J, Maurer BA, Smith JDH and Wiley EO, Entropy and information in evolving biological systems. *Biology & Philosophy* **4** (1989) 407-432.
- [11] Cleveland CJ, Natural resource scarcity and economic growth revisited: economic and biophysical perspectives. In *Ecological Economics: The Science and Management of Sustainability*, ed. by Costanza R (Columbia University Press, New York, 1991) pp. 289-318.
- [12] Costanza R, Ecological economics as a framework for developing sustainable national policies. In *Towards an Ecologically Sustainable Economy*, ed. by Aniansson B and Svedin U (The Swedish Council for Planning and Coordination of Research (FRN), 1990) Report 90:6.
- [13] Costanza R, ed. *Ecological Economics: The Science and Management of Sustainability*, (Columbia University Press, New York, 1991).
- [14] Daly HE, The economic growth debate: what some economists have learned but many have not. *Journal of Environmental Economics and Management* **14** (1987) 323-336.

- [15] Daly HE and Cobb JB, *For the Common Good: Redirecting the Economy Toward Community, The Environment and a Sustainable Future* (Beacon Press, Boston, 1989).
- [16] Denbigh KG, *The Thermodynamics of The Steady State* (Methuen, London, 1951).
- [17] Eigen M and Schuster P, The hypercycle: a principle of natural self-organization. In three parts: Part A, Emergence of the hypercycle. *Naturwissenschaften* **64** (1977) 541-565. Part B, The abstract hypercycle. *Naturwissenschaften* **65** (1978) 741-565. Part C, The realistic hypercycle. *Naturwissenschaften* **65** (1979) 347-369. Appeared under the same title as a book, 1979, Springer-Verlag, Berlin.
- [18] Eriksson B, Eriksson K-E and Wall G, *Basic Thermodynamics of Energy Conversions and Energy Use* (Department of Theoretical Physics, University of Göteborg, Göteborg, Sweden, 1978) Report No. 77-41
- [19] Etnier C and Guterstam B, ed. *Ecological Engineering for Wastewater Treatment*, Proceedings from an International Conference at Stensund Folk College, Sweden, March 24-28, 1991 (Bokskogen Publisher, Lund, 1991).
- [20] Folke C, Socio-economic dependence on the life-supporting environment. In *Linking the Natural Environment and the Economy: Essays from the Eco-Eco Group*, ed by Folke C and Kåberger T. (Kluwer Academic Publishers, Dordrecht, 1991) pp. 77-94.
- [21] Folke C, The societal value of wetland life-support, in C. Folke and T. Kåberger (eds), *Linking the Natural Environment and the Economy: Essays from the Eco-Eco Group*, ed. by Folke C and Kåberger T (Kluwer Academic Publishers, Dordrecht, 1991) pp. 141-171.
- [22] Folke C and Kautsky N, Aquaculture with its environment; prospects for sustainability, *Ocean and Coastal Management* **17** (1992) 5-24
- [23] Fleischaker GR, *Origins of Life: An Operational Definition in Origins of Life and Evolution of the Biosphere* Vol 20 (No 2) Special Issue, 1989 (ISSOL Conference, 1990).
- [24] Gibbs JW, *A Method of Geometrical Representation of The Thermodynamical Properties of Substances by Means of Surface*, The collected works, Vol 1 1928, (Yale University Press, New Haven, 1873).
- [25] Günther F, Man in living systems. Proceedings from *Entropy and Bioeconomics*, the First International Conference of the European Association for Bioeconomic Studies (Dragan Foundation, Rome, 1993). in press.
- [26] Holling C, The resilience of terrestrial ecosystems: local surprise and global change. In *Sustainable Development of the Biosphere*, ed. by Clark WC and Munn RE (Cambridge University Press, London, 1986). pp. 292-317.

- [27] Jantsch E, *The Self-Organising Universe: Scientific And Human Implications of The Emerging Paradigm of Evolution*. (Pergamon Press, Oxford, New York, 1980).
- [28] Jörgensen S-E, and Meijer H, A holistic approach to ecological modelling. *Ecological Modelling* **7** (1979) 169-189.
- [29] Kay JJ, *Self-organisation in Living Systems* PhD thesis, Univ. of Waterloo, Ontario, 1984.
- [30] Kay JJ, A nonequilibrium thermodynamic framework for discussing ecosystem integrity. *Environmental Management* **15**, (1991) 483-495.
- [31] Keenan JH, Availability and irreversibility in thermodynamics', *British Journal of Applied Physics* **2** (1951).
- [32] Kestin J, *A Course in Thermodynamics*. (Blaisdell, 1966)
- [33] Koestler A, *The Ghost in The Machine* (Hutchinson, London, 1967).
- [34] Lovelock JE, A physical basis for life detection experiments, *Nature* **207**, (1965) 568-570
- [35] Lovelock JE, *The Ages of Gaia* (Oxford University Press, Oxford, UK, 1988).
- [36] Margalef R, *Perspectives in Ecological Theory* (University of Chicago Press, Chicago, 1968).
- [37] Mitsch WJ, and Jörgensen SE (eds.), *Ecological Engineering: An Introduction to Ecotechnology* (John Wiley, New York, 1989).
- [38] Norton BG and Ulanowicz RE, Scale and biodiversity policy: a hierarchical approach. *Ambio* **21** (1992) 244-249.
- [39] Odum EP, Trends to be expected in stressed ecosystems. *BioScience* **35** (1985) 419-422.
- [40] Odum EP, *Ecology And Our Endangered Life-Support System* (Sinauer, Sunderland, Massachusetts, 1989).
- [41] Odum HT, Energy, ecology and economics. *Ambio* **2** (1973) 220-227.
- [42] Odum HT, *Living with Complexity*, Crafoord Lecture, The Crafoord Prize in the Biosciences (Royal Swedish Academy of Sciences, Stockholm, Sweden, 1987).
- [43] Odum HT, *Systems Ecology*, (John Wiley, New York, 1983).
- [44] O'Neill RV, DeAngelis DL, Waide JB and Allen TFH, *A Hierarchical Concept of Ecosystems* (Princeton University Press, Princeton, New Jersey, 1986).

- [45] Prigogine I, Order through fluctuation: self-organisation and social system. In *Evolution and Consciousness: Human Systems in Transition*, ed. by Jantsch E and Waddington CH (Reading, Mass., London and Addison-Wesley, Amsterdam, 1976).
- [46] Prigogine I and Stengers E, *Order out of Chaos* (Bantam Books, New York, 1984).
- [47] Rees WE, Sustainable development of the biosphere: concepts and principles. The American Teilhard Association for the Future of Man. *Teilhard Studies* **23** (1990) 1-26.
- [48] Riedl R, A systems-analytical approach to macro-evolutionary phenomena. *Quarterly Review of Biology* **52** (1977) 351-370.
- [49] Schneider ED and Kay JJ, *Life as a Manifestation of The Second Law of Thermodynamics*. Working Paper Series, Department of Environment and Resource Studies (University of Waterloo, Ontario, 1992).
- [50] Schrödinger E, *What Is Life?* (Cambridge University Press, Cambridge, U.K, 1944).
- [51] Swenson R, Emergent attractors and the law of maximum entropy production: foundations to a theory of general evolution. *Systems Research* **6** (1989) 187-197.
- [52] Ulanowicz R, *Growth and Development: Ecosystem Phenomenology* (Springer-Verlag, New York, 1986).
- [53] Varela FJ, Maturana HR and Uribe R, Autopoiesis: the organisation of living systems, its characterization and a model. *BioSystems* **5**, (1974) 187-196.
- [54] Vitousek PM, Ehrlich PR, Ehrlich AH and Matson PA, Human appropriation of the products of photosynthesis. *BioScience* **36** (1986) 368-373.
- [55] Wall G, *The Exergy Conversion in the Swedish Society* (Chalmers University of Technology, Göteborg, Sweden, 1981).
- [56] Wall G, *Exergy - A Useful Concept* (Chalmers University of Technology, Göteborg, Sweden, 1986).
- [57] Weber BH, Depew DJ and Smith JD (eds.), *Entropy, Information and Evolution: New Perspectives on Physical and Biological Evolution* (MIT Press, Cambridge, Massachusetts, 1988).
- [58] Weber BH, Depew DJ, Dyke C, Salthe SN, Schneider ED, Ulanowicz RD and Wicken JS, Evolution in thermodynamical perspective; an ecological approach. *Biology and Philosophy* **4** (1989) 373-405.
- [59] Zhabotinsky AM, *Self-Oscillating Concentrations* (Nauka, Moscow, 1974).