

An Integrated Ecosystem Theory

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Abstract

The paper presents an ecosystem theory based on ten propositions. The ecosystem theory is an integration of several contributions from a number of system ecologists. It is of importance to apply this theory to explain ecological observations and use it environmental management because the alternative is to rely entirely on observations which is very time consuming, costly and cumbersome. The presented integrated ecosystem theory is consistent with a recent published book *A New Ecology, A System Approach*, that is using some basic ecosystem properties to explain ecological observations.

Keywords

Ecosystem theory; Eco-exergy; Ecological Modelling; Environment; Toxic substance modelling; Ecotoxicological indicators; Ecosystem indicators; Ecosystem health indicators

Why do we need an Ecosystem Theory?

Humans have always strived toward finding a structure, a pattern, in their observations – to develop a theory. Science does not make sense without a theory. Without a theory our observations become only a beautiful collection of impressions that cannot be explained and not be applied to solve problems of human interest. Without a theory the observations would be like a collection of stamps. The alternative to a theory in a scientific discipline is to observe everything, which of course is not possible. With a theory in hand we can make predictions and we don't need to observe all details, but can at least partially rely on the theory.

All our knowledge in a scientific discipline has to be coherent to be able to apply the underlying theory and to explain our observations. Ecology has a long time only partially been able to condense the systematic collection of observations and knowledge about ecosystems into testable laws and principles. An ecological theory is *now* available as a tool in ecology due to the contributions of many system ecologists during the last decades. An integration of all these contributions forms the ecosystem theory. It has been difficult and taken long time to construct the theoretical building of system ecology, because of the enormous complexity of ecosystems, but nature has not been created to be easily understood by human beings. It has been necessary to break with the long reductionistic tradition in science and include the use of thermodynamics in a new holistic approach to understand ecosystems. It is today by many scientists considered the greatest challenge of science in the 21st century – to put together our many observations of complex systems to a completely understandable holistic picture.

A number of important contributions to system ecology have been published during the last three decades. They are all attempts to capture the features and characteristics of ecosystems, their processes and their reactions to changed conditions, i.e., changed forcing functions. The different theories look at the first glance not consistent, but when we examine

the different theories more carefully, it becomes clear that they represent different angles and view points. It was asserted in the first edition of S.E. Jørgensen's book "Integration of Ecosystem Theories: A Pattern" (1992), that the various theories actually form a pattern and the later editions (second edition 1997 and third edition 2002) have only enhanced the perception that the theories form a pattern and that they to a high extent are consistent. During the years 1995, 2000 and 2005 there have been several meetings where the fathers of the different contributions to the integrated theory have discussed the pattern. It is clear from this discussion that we today have an ecosystem theory which is rooted in a consensus of the pattern of ecosystem theories.

It is a very important progress in ecology and system ecology that we now have an integrated theory that several ecologists should be able to agree upon, as this is the prerequisite for further progress in system ecology and ecology. It makes it furthermore feasible to construct a network of laws, rules and explain our scientific observations, as we know it from physics, where a few fundamental laws can be applied to derive other laws which can be used to explain if not all then most physical observations. It is important to formulate and apply such a theory in ecology rather too early than too late, because only by the application of the theory to explain ecological rules and observations, can we assess how and where the theory needs improvements.

As a consequence of the changing paradigm direction of environmental management, we need to focus on ecosystem ecology. An ecosystem is defined as "a dynamic complex of plants, animals and microorganism communities and the nonliving environment, interacting as a functional unit. Humans are an integral part of ecosystems".

A well-defined ecosystem has strong interactions among its components and weak interactions across its boundaries. A useful ecosystem boundary is the place where a number of discontinuities coincide for instance in the distribution of organism, soil type, drainage basin or depth in a water body. At a larger scale, regional and even globally distributed ecosystems can be evaluated based on a commonality of basic structural units.

We are today able to formulate at least building blocks of an ecosystem theory in the form of useful propositions about processes and properties? We may prefer the word "propositions" and not laws because ecosystem dynamics are so complex that universal laws give way to contextual propensities. The propositions capture these general tendencies of ecosystem properties and processes that can be applied to understand the very nature of ecosystems, including their response to human impacts.

An ecosystem theory is a prerequisite for wider application of ecological sciences in environmental management because a theory can provide a strong guide for environmental management and resource conservation.

The basic scientific Results and Ideas behind the presented Ecosystem Theory

The scientific world was very optimistic when it enters the 20th century: science was very close to a complete understanding of nature – maybe not all details but all important fundamental features of nature. A few more problems should be solved and science would have finished the jigsaw puzzle of nature. Science developed, however, very differently from this prediction due to mainly seven different new general scientific theories that changed our perception of nature radically: the two relativity theories, the quantum theory, the complementarity theory, Gödel's theory about the theories, the chaos theory and Prigogine's thermodynamic theory for far from thermodynamic equilibrium systems. Due to these seven theories, we understand to day that nature is much more complex than we thought 108 years

ago, but we have also got tools to understand this complexity better, which has entailed that we have an ecosystem theory today.

The speed of the light is the absolute upper limit for any transmission of matter, energy and information according to the special relativity theory. This has given a completely new meaning of the concept locality. It has also in system ecology brought another meaning of network: links among components that share a locality and of the hierarchical organization: networks of smaller and smaller localities that are linked together on the next level of the hierarchy. The relativity theory gives us also a clear understanding of the lack of absolute measures, which was the governing scientific perception before the 20th century. When we use ecological indicators to assess the ecosystem health, we can only apply them relatively to other (similar) ecosystems and when we use thermodynamic calculations of ecosystems we know that we cannot get the absolute value but only an index or relative value, because ecosystems are too complex to be able to include all the components of an ecosystem in our calculations. The quantum theory and later the chaos theory destroyed the deterministic world picture: we cannot determine the future in all details, even if we would know all the details of the present conditions. Our planet is both physical and ontic open. In the nuclear world the uncertainty is due to our inevitable impact on the nuclear particles, while the uncertainty in ecology is due to the enormous complexity (Jørgensen, 1990 and 2002). Ecosystems are middle number systems (Jørgensen, 2002) understood as systems with a number of components that are smaller than the number of atoms in a normal room, but opposite the atoms that are represented by a few different types, all the components in an ecosystem are different even among the organisms of the same species. A room may contain 10^{28} components but they are represented by only 10 or 20 different types of molecules with exactly the same properties. An ecosystem contains in the order of 10^{15} - 10^{20} different components all with different properties. It makes also the possible interactions among these components different and it would be impossible to observe all the components and even more impossible to observe all the possible interactions among these 10^{15} - 10^{20} different components. So, of course we can fully accept the non-deterministic world picture in ecology.

In accordance to the complementarity theory, the properties of the light can only be described by an interpretation of the light as both waves and particles (photons). An ecosystem is much more complex than the light. Therefore, a full (holistic) description of an ecosystem will also, not surprisingly, require two or more descriptions. Margalef (1991 and 1995) describes ecosystems as dissipative, self-organizing systems, H.T. Odum (1983, 1988 and 1996) uses emergy, Ulanowicz (1986, 1996 and 1997) ascendancy and Jørgensen (1990, 1995 and 2002) eco-exergy for the description of the dynamics of ecosystems, they are all right, because they cover simply different aspects of ecosystems, that are extremely complex systems with an extremely complex dynamics. We need all the descriptions to understand in all details how the dynamics of ecosystems are working and functioning. However, different description methods may be more useful than the other for solving different specific types of ecosystem problems.

Gödel's theorem that there is no complete theories – they are all based on some assumptions is of course also valid for ecological theories. We shall with other word not expect a complete theory based on no assumptions and which can be used in all possible contexts.

The Newtonian physics is based on the reversibility of all processes. Prigogine has by his new interpretations of the Second Law of Thermodynamics clearly shown that time has an arrow. All processes are irreversible and the evolution is rooted in this irreversibility. We cannot explain the evolution without referring to the irreversibility. The speed of light is the

maximum possible speed in the universe, which means that it is not possible to go faster than the light and overtake and thereby maybe be able to change the light signals which give information about a previous event. Therefore, Einstein's special relativity theory also makes it absolutely necessary to accept the principle of irreversibility. We cannot change the past but only the future. With the enormous complexity of ecosystems it implies also that the same conditions will never be repeated in an ecosystem. Ecosystems are always confronted in space and time with new challenges, which explain the enormous diversity that characterizes the biosphere.

The proposed ecosystem theory consists of ten laws. As the interpretation of some of the laws is using the concept of eco-exergy, it is necessary before the presentation of the laws to present briefly in the next section the concept of eco-exergy.

The thermodynamic concept of eco-exergy

Eco-exergy has successfully been used to develop structurally dynamic models (see Jørgensen, 2002) and as a holistic ecological indicator (see Jørgensen et al., 2004). Eco-exergy expresses the work capacity presuming a reference environment that represents the same system (ecosystem) at the same temperature and pressure at the thermodynamic equilibrium, which means that all the components are inorganic at the highest possible oxidation state and all the components are homogeneously distributed in the system (no gradients) (Fig. 1).

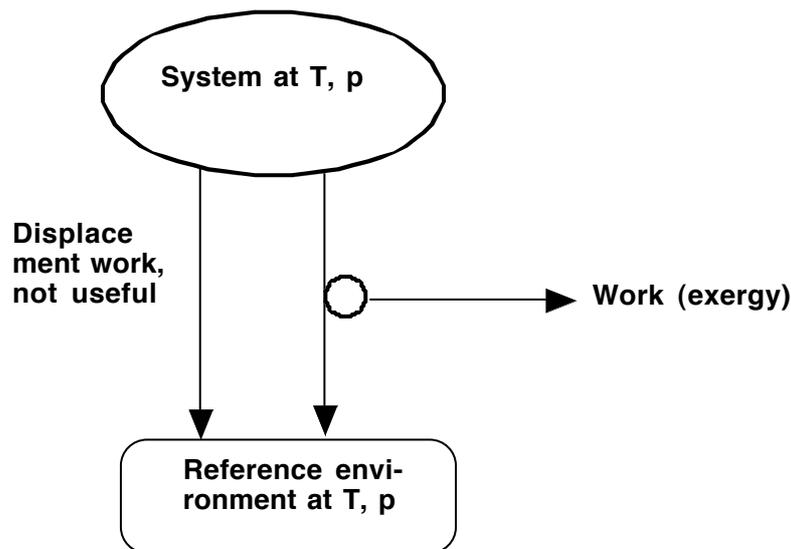


Fig. 1. The exergy content of the system is calculated in the text for the system relatively to a reference environment of the same system at the same temperature and pressure, but as an inorganic soup with no life, biological structure, information or organic molecules

Technological exergy is not practical to use in the ecosystem context, because it presumes that the environment is the reference state which means for an ecosystem the next ecosystem. As the energy embodied in the organic components and the biological structure and information contributes far most to the exergy content of the system, there seems to be no reason to assume a (minor) temperature and pressure difference between the system and the reference environment. Under these circumstances we can calculate the exergy, which has been denoted eco-exergy to distinguish from the technological exergy defined above, as coming entirely from the chemical energy:

$$\sum_c (\mu_c - \mu_{c0}) N_i.$$

This represents the non-flow biochemical exergy. It is determined by the difference in chemical potential ($\mu_c - \mu_{c0}$) between the ecosystem and the same system at thermodynamic equilibrium; N_i is the number of moles. This difference is determined by the activities (approximated by the use of the concentrations) of the considered components in the system and in the reference state (thermodynamic equilibrium), as it is the case for all chemical processes. We can measure the concentrations in the ecosystem, but the concentrations in the reference state (thermodynamic equilibrium) could be based on the usual use of chemical equilibrium constants. Eco-exergy is a concept close to Gibb's free energy but opposite Gibb's free energy, eco-exergy has a different reference state from case to case (from ecosystem to ecosystem) and it can furthermore be used far from thermodynamic equilibrium, while Gibb's free energy in accordance to its exact thermodynamic definition is a state function close to thermodynamic equilibrium. In addition, eco-exergy of organisms is mainly embodied in the information content and should therefore not to be considered the same as the chemical energy of fossil fuel.

As ($\mu_c - \mu_{c0}$) can be found from the definition of the chemical potential replacing activities by concentrations, we get the following expressions for the exergy:

$$Ex = RT \sum_{i=0}^{i=n} C_i \ln (C_i / C_{i,0}) \quad (1)$$

where R is the gas constant (8.317 J / K moles = 0.08207 liter· atm / K moles), T is the temperature of the environment, while C_i is the concentration of the i'th component expressed in a suitable unit. $C_{i,0}$ is the concentration of the i'th component at thermodynamic equilibrium and n is the number of components. $C_{i,0}$ is of course a very small concentration (except for $i = 0$, which is considered to cover the inorganic compounds), corresponding to a very low probability of forming complex organic compounds spontaneously in an inorganic soup at thermodynamic equilibrium. $C_{i,0}$ is even lower for the various organisms, because the probability of forming the organisms is very low with their embodied information which implies that the genetic code should be correct.

By using this particular exergy based on the same system at thermodynamic equilibrium as reference, the eco-exergy becomes dependent only on the chemical potential of the numerous biochemical components.

It is possible to distinguish in equation (1) between the contribution to the eco-exergy from the information and from the biomass. We define p_i as C_i / A , where

$$A = \sum_{i=1}^n C_i$$

is the total amount of matter density in the system. With introduction of this new variable, we get:

$$Ex = A RT \sum_{i=1}^n p_i \ln (p_i / p_{i0}) + A \ln (A / A_0) \quad (2)$$

As $A \approx A_0$, eco-exergy becomes a product of the total biomass A (multiplied by RT) and Kullback measure:

$$K = \sum_{i=1}^n p_i \ln (p_i / p_{i0}) \quad (3)$$

where p_i and p_{i0} are probability distributions, a posteriori and a priori to an observation of the molecular detail of the system. It means that K expresses the amount of information that is gained as a result of the observations. For different organisms that contribute to the eco-exergy of the ecosystem, the eco-exergy density becomes $c RT \ln (p_i / p_{i0})$, where c is the concentration of the considered organism. $RT \ln (p_i / p_{i0})$, denoted β is found by calculation of the probability to form the considered organism at thermodynamic equilibrium, which would require that organic matter is formed and that the proteins (enzymes) controlling the life processes in the considered organism have the right amino acid sequence. These calculations can be seen in Jørgensen et al., 2000 and Jørgensen et al., 2005. In the latter reference the latest information about the β -values for various organisms is presented; see Table 1. For human, the β -value is 2173, when the eco-exergy is expressed in detritus equivalent or 18.7 times as much or 40635 kJ/g if the eco-exergy should be expressed as kJ and the concentration unit g/unit of volume or area. The β -value has not surprisingly increased as a result of the evolution. To mention a few β -values from Table 1: bacteria 8.5, protozoa 39, flatworms 120, ants 167, crustaceans 232, mollusks 310, fish 499, reptiles 833, birds 980 and mammals 2127. The evolution has in other words resulted in a more and more effective transfer of what we could call the classical work capacity to the work capacity of the information. A β -value of 2.0 means that the eco-exergy embodied in the organic matter and the information are equal. As the β -values; see above are much bigger than 2.0 (except for virus, where the β -value is 1.01 – slightly more than 1.0) the information eco-exergy is the most significant part of the eco-exergy of organisms.

Table 1

β -values = Exergy content relatively to the exergy of detritus

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Early organisms	Plants	Animals
Detritus		1.00
Virus		1.01
Minimal cell		5.8
Bacteria		8.5
Archaea		13.8
Protists	(Algae)	20
Yeast		17.8
		33
		Mesozoa, Placozoa
		39
		Protozoa, amoeba
		43
		Phasmida (stick insects)
Fungi, moulds		61

	76	Nemertina
	91	Cnidaria (corals, sea anemones, jelly fish)
Rhodophyta	92	
	97	Gastroticha
Prolifera, sponges	98	
	109	Brachiopoda
	120	Platyhelminthes (flatworms)
	133	Nematoda (round worms)
	133	Annelida (leeches)
	143	Gnathostomulida
Mustard weed	143	
	165	Kinorhyncha
Seedless vascular plants	158	
	163	Rotifera (wheel animals)
	164	Entoprocta
Moss	174	
	167	Insecta (beetles, flies, bees, wasps, bugs, ants)
	191	Coleodia (Sea squirt)
	221	Lepidoptera (butter flies)
	232	Crustaceans
	246	Chordata
Rice	275	
Gymnosperms (incl. pinus)	314	
	310	Mollusca, bivalvia, gastropodea
	322	Mosquito
Flowering plants	393	
	499	Fish
	688	Amphibia
	833	Reptilia
	980	Aves (Birds)
	2127	Mammalia
	2138	Monkeys
	2145	Anthropoid apes
	2173	Homo Sapiens

The eco-exergy due to the “fuel” value of organic matter (chemical energy) is about 18.7 kJ/g (compare with coal: about 30 kJ/g and crude oil: 42 kJ/g). It can be transferred to other energy forms for instance mechanical work directly, and be measured by bomb calorimetry, which requires destruction of the sample (organism), however. The information eco-exergy = $(\beta - 1) c$ is taken care of the control and function of the many biochemical processes. The ability of the living system to do work is contingent upon its functioning as a living dissipative system (Ulanowicz, 1986). Without the information eco-exergy the organic matter could only be used as fuel similar to fossil fuel. But due to the information eco-exergy,

organisms are able to make a network of the sophisticated biochemical processes that characterize life. The eco-exergy (of which the major part is embodied in the information) is a measure of the organization (Jørgensen and Svirezhev, 2004). This is the intimate relationship between energy and organization, that Schrödinger (1944) was struggling to find.

The eco-exergy is a result of the evolution and of what Elsasser (1975) call re-creativity to emphasize that the information is copied and copied again and again in a long chain of copies where only minor changes are introduced for each new copy. The energy required for the copying process is very small, but it has of course required a lot of energy to come to the “mother” copy through the evolution for instance from prokaryotes to human cells. To cite Margalef (1997) in this context: the evolution provides for cheap – unfortunately often “erroneous” i.e. not exact – copies of messages or pieces of information. The information concerns the degree of uniqueness of entities that exhibit one characteristic complexion that may be described.

A tentative ecosystem theory consisting of ten basic propositions

Jørgensen and Fath (2004) have previously presented a tentative ecosystem theory consisting of 8 basic laws, but it seems to be an advantage to split one of the laws into 3 due to some recent results, which are presented below. The other seven proposed laws have basically not been changed in this chapter. Some comments based on various valuable inputs to the ecosystem theory by system ecologists during the last 2-3 decades and based on the paradigm shift which took place during the 20th century, see the second section of the chapter, are presented here together with the proposed laws to facilitate the understanding of how the laws are rooted in the general scientific development. However, the proposed laws 3-5 are based on the fundamental laws of thermodynamics and the fundamental biochemical knowledge and observations, which are applied again and again in our interpretation of ecological observations and rules.

1. *All ecosystems are open systems embedded in an environment from which they receive energy–matter input and discharge energy–matter output.* From a thermodynamic point of view, this principle is a prerequisite for the ecological processes. If ecosystems would be isolated, they would be at thermodynamic equilibrium without life and without gradients.

This law is rooted in Prigogine’s use of thermodynamics far from thermodynamic equilibrium. The openness explains according to Prigogine why the system can be maintained far from thermodynamic equilibrium without violating the Second Law of Thermodynamics.

2. *Ecosystems have many levels of organization and operate hierarchically.* This principle is used again and again when ecosystems are described: atoms, molecules, cells, organs, organisms, populations, communities, ecosystems and the ecosphere.

The law is based on the differences in the locality. The distance between components becomes essential because it takes time for events and signals to disseminate. The complexity of biological systems makes it therefore practical to distinguish between different levels with different locality.

3. *Thermodynamically, carbon-based life has a viability domain determined between about 250-350 K.* It is within this temperature range that there is a good balance between the opposing ordering and disordering processes: decomposition of organic matter and building

of biochemical important compounds. By a lower temperature the process rates are too slow and by higher temperatures the enzymes catalyzing the biochemical formation processes will decompose too rapidly. At 0 K there is no disorder, but no order (structure) can be created. At increasing temperature, the order (structure) creating processes increases, but the cost of maintaining the structure in the form of disordering processes also increases.

4. *Mass, including biomass, and energy are conserved.* This principle is used again and again in ecology and particularly in ecological modelling.

5. *The carbon based life on earth, has a characteristic basic biochemistry which all organisms share.* It implies that many biochemical compounds can be found in all living organisms. They have therefore almost the same elementary composition and the composition of all organisms can be represented as a relatively narrow range of about 25 elements (Morowitz 1968). This principle is used when stoichiometric calculations are made in ecology, i.e. an approximate average composition of living matter is applied.

6. *No ecological entity exists in isolation but is connected to others.* The theoretical minimum unit for any ecosystem is two populations, one that fixes energy another that decomposes and cycles waste, but in reality viable ecosystems are complex networks of interacting populations. It can be shown by observations and ecological network calculations that the network has a synergistic effect on the components: the ecosystem is more than the sum of the components. This principle has been used in numerous ecological network papers; see for instance Patten 1991 and Patten et al., 1990.

The number of components interacting in such networks is very high (ecosystems are middle number systems). The complexity of the network becomes therefore extremely high, which makes it impossible to assess all the properties of the ecological networks that are characteristic for ecosystems.

7. *All ecosystem processes are irreversible* (this is probably the most useful way to express the Second Law of Thermodynamics in ecology). It is widely used in ecology that living organisms need energy to cover the maintenance of the life processes. This energy is lost as heat to the environment which is in agreement with the Second Law of Thermodynamics.

Time has an arrow. The evolution can only be understood in the light of the irreversibility principle rooted in the Second Law of Thermodynamics. The evolution is a step-wise development that is based on the previously achieved good solutions to survival in a changeable and very dynamic world. Due to the memory of the good solutions, which are the eco-exergy expressed by Kullback's measure of information, the evolution has been towards more and more complex solutions.

8. *Biological processes use captured energy (input) to move further from thermodynamic equilibrium and maintain a state of low-entropy and high exergy relative to its surrounding and to thermodynamic equilibrium.*

This is just another way of expressing that ecosystems can grow. Svirezhev (1992) has shown that eco-exergy of an ecosystem corresponds to the amount of energy that is needed to break down the system.

9. *After the initial capture of energy across a boundary, ecosystem growth and Development is possible by 1) an increase of the physical structure (biomass), 2) an increase of the network*

(more cycling) or 3) an increase of information embodied in the system. All three growth forms imply that the system is moving away from thermodynamic equilibrium (Jørgensen et al., 2000) and all three growth forms are associated with an increase of 1) the eco-exergy stored in the ecosystem, and 2) the energy through flow in the system (power). When cycling flows increase, the eco-exergy storage capacity, the energy use efficiency and space-time differentiation all increase (Ho and Ulanowicz, 2005). When the information increase, the feed back control becomes more effective, the animal get bigger, which implies that the specific respiration decreases, and there will be a tendency to replace r-strategist with K-strategists, which means that less energy is wasted on reproduction.

Notice that the first growth form corresponds to the eco-exergy of organic matter, the above mentioned 18.7 kJ/g, while the increase of the network + the increase of the information will correspond to the eco-exergy calculated as $(\beta - 1) c$. Notice also that the three growth forms are in accordance with what is denoted Odum's attributes (Odum, 1969). The explanation is given in Table 2, where the growth forms corresponding to the usually applied attributes are indicated. A typical development according to the growth forms is represented in the graph Fig. 2. Firstly, mainly the biomass is increasing (growth form 1) which implies that the ecosystem is also able by the use of biomass to capture more solar radiation.

Table 2

Differences between initial stage and mature stage according to Odum (1959 and 1969) are indicated with reference to the three growth forms

Growth form	Properties	Early stages	Late or mature stage
1 (biomass)	Production /respiration	$\gg 1$ $\ll 1$	Close to 1
	Production/Biomass	High	Low
	Respiration/Biomass	High	Low
	Yield (relative)	High	Low
	Total biomass	Small	Large
	Inorganic nutrients	Extra biotic	Intra biotic
2 (network)	Patterns	poorly organized	well organized
	Niche specialization	Broad	Narrow
	Life cycles	Simple	Complex
	Mineral cycles	Open	Closed
	Nutrient exchange rate	Rapid	Slow
	Life span	Short	Long
	Ecological network	Simple	Complex
	Stability	Poor	Good
	Ecological buffer capacity	Low	High

3 (infor- Mation)	Size of organisms	Small	Large
	Diversity, ecological	Low	High
	Diversity, biological	Low	High
	Internal symbiosis	Undeveloped	Developed
	Stability (resistance to external perturbations)	Poor	Good
	Ecological buffer capacity	Low	High
	Feedback control	Poor	Good
	Growth form	Rapid growth	Feedback controlled growth
	Types	r-strategists	K-strategists

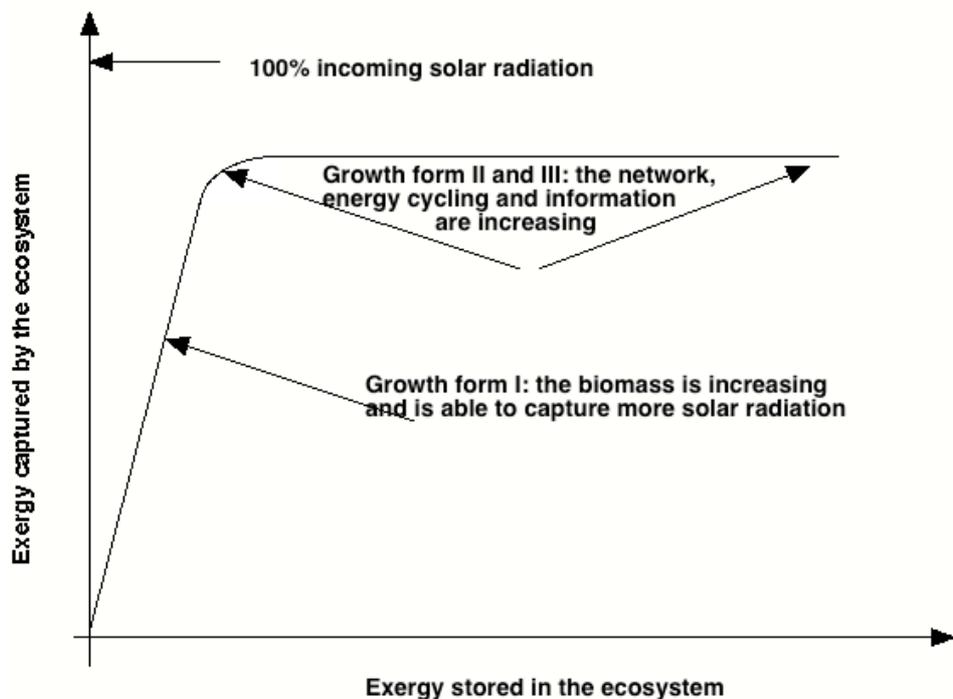


Fig. 2. The development of an ecosystem is illustrated by plotting exergy captured from the inflowing solar radiation toward the exergy stored in the ecosystem. Growth form I is dominant in the first phase of the development from an early stage ecosystem to a mature ecosystem. By increasing the biomass the percentage of solar radiation captured increases up to about 80% corresponding to what is physically possible. Growth forms II and III are dominant in the intermediate phase and when the ecosystem is in a mature stage. Thereby more exergy is stored without increasing the exergy needed for maintenance. The system becomes with other words more effective in the use of the solar radiation according to Prigogine's minimum entropy principle. The exergy stored is increased for all three growth forms.

When the system is capturing about 75%, it is not possible to increase the amount of solar radiation captured further. One or more of the available elements to build biomass may also

have been used up. The ecosystem can therefore not benefit more from growth form 1 and is therefore using growth form 2 and 3. Thereby the efficiency with which the system uses the exergy is increased. In the ecological succession the information is transferred from the present to the future and the shift is manifest in a historical way that has many aspects. One of them is the production and accumulation of biomass prevails at the beginning, and this result in what is often described as “bottom up” control. Later on the high trophic levels take more control, “top-down-control”, becomes more apparent.

Jørgensen and Svirezhev (2004) have shown that the efficiency with which the incoming energy is used to gain eco-exergy, n_{ex} , can be expressed by the following equation:

$$n_{ex} = (1 - n_{rad}) K + (1 - n_{rad}) \ln (1 - n_{rad}) + n_{rad} \quad (4)$$

where n_{rad} is the fraction of the incoming energy in form of solar radiation, the ecosystem is able to capture and K is Kullback’s measure of information; see above.

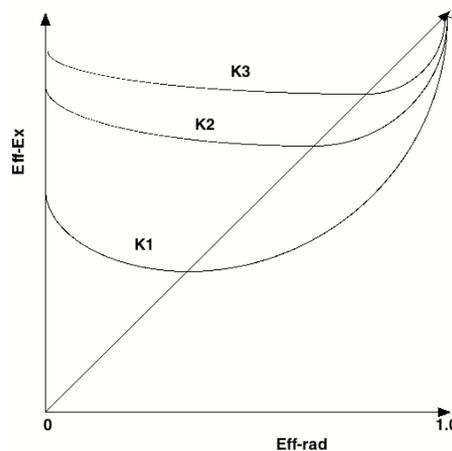


Fig. 3. n_{ex} is plotted versus n_{rad} for three information level $K3 > K2 > K1$. Increasing Kullback’s measure of information implies that the ecosystem will generate information up to a higher n_{rad}

Fig. 3 shows the dependency of the eco-exergy efficiency on the radiation efficiency for two different K values according to this equation. As it can be seen from the graph. The eco-exergy efficiency $>$ the radiation efficiency at sufficient high radiation efficiency. The higher the K value the sooner will the ecosystem reach the radiation efficiency that means that the eco-exergy $>$ radiation efficiency. This is a strong support for the 9th tentative law.

10. *An ecosystem receiving solar radiation will attempt to maximize eco-exergy storage or maximize power such that if more than one possibility is offered, then in the long-run the one which moves the system furthest from thermodynamic equilibrium will be selected.*

The eco-exergy storage is increasing with all three growth forms – see above. When an ecosystem evolves it can therefore apply all three growth forms in a continuous Darwinian selection process. It is intuitively obvious why the nested space-time differentiation in organisms optimizes thermodynamic efficiency as expressed in the tenth law, because it allows the organism to simultaneously exploit equilibrium and non-equilibrium energy transfer with minimum dissipation (Ho and Ulanowicz, 2005).

It has been shown (Jørgensen, 1995, Jørgensen et al, 2000, Jørgensen 2002 and Fath et al., 2004) that to maximize eco-exergy storage means also that the power (see Odum, 1983, 1988

and 1996) and the ascendancy (see Ulanowicz, 1986 and 1997) are maximized. The three different formulations by using eco-exergy, power and ascendancy are three different view points that are consistent. Eco-exergy storage focuses on the accumulated structure and information (Svirezhev, 2001), power focuses on the outcome of more storage: more flows and ascendancy focuses on an ecological network information measure that accounts for the flows. The three formulations are equally valid, which is consistent with the complementarity theory. This law has been used to explain numerous ecological observations. It is therefore not possible here to go into details. Some comments with reference to examples on the application of the theory to explain ecological observations and rules are, however, given below.

A special issue of Ecological Modelling volume 158 issue 3 was devoted to use the entire proposed ecosystem theory to explain 39 ecological observations that were unexplained in the ecological literature.

Jørgensen et al. (2000) has applied the tenth law to explain that the sequence of the use of oxidators for microorganism oxidizing organic matter is oxygen, nitrate, manganese (IV), iron (III), sulfate, carbon dioxide because the amount of eco-exergy accumulated in form of ATP as a result of the oxidation process is decreasing in the same sequence. One more example from Jørgensen et al. (2000) should be mentioned, namely that the rate of cycling of a nutrient is increasing with the abundance of the nutrient relatively to its use. This observation that originates from the examination of OECD lakes in the late seventies can easily be explained by the proposed tenth law. The eco-exergy of a lake is simply increasing when the most abundant nutrient relative to its use is cycling faster, which can be shown by the use of well examined eutrophication models (see Jørgensen et al., 2000).

It should finally be mentioned that it has been possible to develop structurally dynamic models, i.e. models that can describe changes in the properties of the species due to adaptation or even due to a shift in the species composition by applying eco-exergy as the goal function. By adaptation and shift in species composition a Darwinian selection takes place, which can be described quantitatively accordance to the tenth law by the use of eco-exergy.

It is all by all been attempted to challenge the tenth law by the use of ecological observations and rules, but in vain. The many example where the tenth law seems valid, can of course not be considered a proof of the tenth law, as the thermodynamic laws cannot be proved. It is, however, necessary to test the law against as wide a spectrum of ecological observations and a positive test can be applied as a support – not as a proof.

Discussion of the presented ecosystem theory

Recently, June 2005, at a brainstorming meeting about the possibilities to apply wider a general ecosystem theory, it was concluded that the here presented ecosystem theory approximately covers what a basic ecosystem theory should contain. It was furthermore agreed to write a book together in a general ecological language to try to get a wider acceptance of ecology as a theoretical science. As the best method to present an ecosystem theory for ecologists in general, it was decided to use in stead of the ten laws presented here the basic properties of ecosystem, which in principle only is another more down to earth presentation of an ecosystem theory. The properties that explain the dynamic and the

reactions of ecosystems are:

I) Ecosystems are physical and ontic open, meaning that they can exchange mass, energy and information with the surroundings and that it is not possible to make exact predictions on their development due to their enormous complexity; see the discussion above.

II) Ecosystems have directionality

III) Ecosystems have connectivity

IV) Ecosystems have emergent hierarchies

V) Ecosystems have a complex dynamics (growth but also reactions toward disturbances)

Property I corresponds to law 1, property IV corresponds to law 2 and property III corresponds to law 6. The laws 3, 5,7,8,9 and 10 are embodied in the properties II and V.

It is clear that any step toward a wider application of an ecosystem theoretical explanation of ecological rules and observations will reinforce the theoretical fundament of ecology. The experience from physics shows that the wider theoretical explanations are used the better becomes the basis theory, because every application will either support the theory or improve it, if the theory is failing, because it becomes obvious where the theory needs modifications. So, the overall conclusion of this chapter is: we have an ecosystem theory and let us use it wider.

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