

On the consistency between thermodynamical and network approaches to ecosystems[☆]

Søren N. Nielsen ^{a,*}, Robert E. Ulanowicz ^b

^a *Environmental Chemistry Section, Department for Analytical and Pharmaceutical Chemistry, Royal Danish School of Pharmacy, Universitetsparken 2, DK-2100 Copenhagen Ø, Denmark*

^b *Chesapeake Biological Laboratory, University of Maryland, Solomons, MD 20688-0038, USA*

Abstract

If one assumes that biological systems develop in the direction of increasing thermodynamic efficiency, one is led to several conclusions about how interactions between parts of the system, as well as the system as a whole, should evolve. For example, one can show that maximizing efficiency will imply that inputs from the exterior should be maximized, internal transfers should be emphasized above negative exogenous links, the costs of structure maintenance should be minimized, and the heaviest imports should be those most easily accessible. In the network approach to ecosystem development, systems are assumed to change over time so as to increase the information inherent in their patterns of flow connections. This has been expressed quantitatively as a rise in the ‘ascendency’ of the flow pattern. That these two different views on ecosystem behaviour are essentially consistent is demonstrated by calculating the sensitivities of the ascendency index to individual types of flows. Those changes in flow patterns that augment the ascendency also contribute to increased thermodynamic efficiency. © 2000 Elsevier Science B.V. All rights reserved.

Keywords: Ascendency; Thermodynamics; Ecosystem network; Exergy

1. Introduction

Modern ecosystem theory offers two principal ontological approaches to ecosystem analysis. In other words, we deal with two different ways of viewing ecosystems and studying ecosystem phenomenology. One way is that ecosystems are

viewed as graphs and networks. They can be treated and analyzed as such using already existing and well established techniques. Alternatively, they may be viewed as dissipative structures that exist at the expense of energy and as a consequence of building energy into structure. This entails changes in the energy expended from high quality, low entropy forms to lower quality, intermediate entropy forms, finally ending up as the lowest entropy form, heat. In this case, thermodynamic efficiencies can be examined using methods for optimized functioning as suggested in current literature.

[☆] Presented at the 9th ISEM Conference held in Beijing, PR China, 11–15 August, 1995

* Corresponding author. Tel.: +45-353-06000; fax: +45-353-06001.

E-mail address: snn@dfh.dk (S.N. Nielsen).

Different perspectives usually lead to different conceptions about the systems under observation. That is, various ways of viewing a system usually lead to the formation of correspondingly different knowledge. For years, the two perspectives just mentioned have been leading to two different conceptions of how ecosystems behave.

Recently, the two perspectives have been cast as complementary theories. Either theory does not exclude the other, because a single theory does not tell us everything about ecosystems. Therefore, several views will be needed in order to understand the function of a particular system (Jørgensen, 1992).

The thermodynamical approach to ecosystems has been characterized by calculations and observations of the state components in dynamic flux. Network calculations, on the other hand, are based on flows within a system in steady state. Within the thermodynamic program several subdirections can be distinguished, as represented by different authors. Maximum entropy formation or dissipation (Aoki, 1987, 1988), minimum excess entropy (Mauersberger, 1995), minimum dissipation (Johnson, 1995), maximum exergy storage (Mejer and Jørgensen, 1979; Jørgensen and Mejer, 1981; Jørgensen, 1982), maximum exergy degradation or destruction (Kay and Schneider, 1992, 1994; Schneider and Kay, 1994a,b,c, 1995; Svirezhev, personal communication) and maybe even maximum exergy efficiency. The network direction was started by the works of Hannon (1973), Finn (1976) and Patten et al. (1976). During the last decades this approach has been further elaborated by Patten and Ulanowicz (summaries in Ulanowicz, 1986; Higashi and Burns, 1991). Both approaches overlap with H.T. Odum's notions of maximum power and emergy (Odum, 1983, 1996; Hall, 1995).

These two ways of viewing ecosystems are not exclusive, in fact they are inseparable. In many ways, the flows of a system are consequences of its thermodynamical function, and vice versa. This is most readily seen when the ecosystem is viewed in the context of an open world of propensities (sensu Popper, 1990), that are subject to thermodynamical constraints.

Imposing thermodynamical constraints upon the functioning of biological systems makes it possible

to deduce certain features about how these systems should function optimally. Thus, it is hypothesized that ecosystems should tend to optimize their thermodynamic function: (1) to maximize inputs from the exterior, (2) to minimize the costs of structure maintenance and (3) to retain as much of the energy as possible flowing within the system.

Interpreting the ecosystem as a network and using the recently proposed formulation of ascendancy as the primary indicator of the system state, allows one to compare the behaviour of the ecosystem network against its thermodynamic performance. In this manner, the predictions of two different ways of viewing ecosystems, the network theoretical and the thermodynamical, can be tested against each other. The results presented below indicate a much closer relationship between the two perspectives than first might have been expected.

What follows, is a review of the functioning of ecosystems and an examination of what would happen if they hypothetically were to optimize their thermodynamic function in accordance with thermodynamic principles. The deductions from this analysis are then compared with an analysis of the behaviour of the ecosystem as if it were hypothetically increasing its ascendancy.

2. The propensity world

The late K.R. Popper in one of his last books (Popper, 1990) introduced a new world view. The world is seen, not in terms of deterministic forces, but rather as a world of propensities. Observed phenomena are considered to be outcomes of coinciding events that possess non-equiprobable distribution. That is, the world behaves not like the toss of a coin or a pair of dice, where all outcomes have the same probability of 1/2 or 1/6, respectively. Rather, it behaves more like a game where the coins or dice are loaded. Furthermore, the probabilities themselves can change as phenomena interact with each other, i.e. the probabilities themselves are not stationary. Any probability becomes conditional upon surrounding events. This represents a remarkable change from previous Popperian philosophy, which was dominated by a deterministic and reductionistic world view. It

would seem that late in his life Popper has renounced a fixed world in favour of one that is clearly non-deterministic and even holistic in character. The propensity world view recently has influenced a reinterpretation of the ascendancy principle originally formulated by Ulanowicz (1986, 1996, 1997).

3. Reformulated ascendancy

Applying the propensity view of the world to ecosystems allows us to view the fluxes of an ecosystem in terms of a set of conditional probabilities. Each flow between the compartments of an ecosystem is used to estimate the joint probability that a quantum of energy or matter leaves the given compartment and then enters the specified destination. The joint probabilities usually are presented as a matrix, where the compartments or state variables of the ecosystem, considered as output environs (sensu Patten, 1978, 1982) or transmitting compartments (or causes), are the rows, and the same compartments, now considered to be input environs or receivers (or effects), become the columns.

Let T_{ij} be the flow that leaves the i th compartment and enters the j th one. The index '0' corresponds to the input flows (from the input environ to the system). The indices ' $n+1$ ' and ' $n+2$ ' are used for the non-dissipative (exports) and dissipative flows, respectively (only ' $n+2$ ' flows, i.e. the dissipations, are considered in this paper). These are the flows from the system to the environment or output environ. Then the total flow through the system is equal to

$$T = \sum_{i=0}^n \sum_{j=1}^{n+2} T_{ij} \quad (1)$$

The joint and conditional probabilities can be combined into the index, I , which measures the average mutual information of the ecosystem (Ulanowicz, 1995):

$$I = \sum_{i=1}^m \sum_{j=1}^n p(a_i, b_j) \log \left[\frac{p(b_j|a_i)}{p(b_j)} \right] \quad (2)$$

where $p(a_i, b_j)$ is the joint probability that a_i and b_j occur and $p(b_j|a_i)$ is the conditional probability that b_j will occur, given that a_i has happened.

The product of T and I gives the ascendancy of the system:

$$A = T \times I \quad (3)$$

If we assume that the corresponding probabilities are equal to the frequencies, so that

$$p(a_i, b_j) = \frac{T_{ij}}{T}; p(a_i) = \sum_j \frac{T_{ij}}{T}; p(b_j) = \sum_i \frac{T_{ij}}{T}; \quad (4)$$

and

$$p(b_j|a_i) = \frac{p(a_i, b_j)}{p(a_i)} \quad (5)$$

then the expression for the ascendancy can be presented in the form:

$$A = \sum_{i=0}^n \sum_{j=1}^{n+1} T_{ij} \log \left(\frac{T_{ij} T}{\sum_{i=0}^n T_{ij} \sum_{j=1}^{n+1} T_{ij}} \right) \quad (6)$$

Using the last expression, it is possible to calculate the sensitivity of the ascendancy to any particular flux in the system. It happens that the sensitivity takes a surprisingly simple formulation equal to the component of the average mutual information of the system divided by the corresponding flow (Eq. (10)).

4. Thermodynamic optimum of biological systems

The traditional thermodynamic view of individual components of a biological system or ecosystem as a dissipative structure can be illustrated with a figure redrawn from the works of Prigogine and coworkers (Fig. 1).

Difference between thermodynamical balances according to Prigogine and Exergy principle(s)

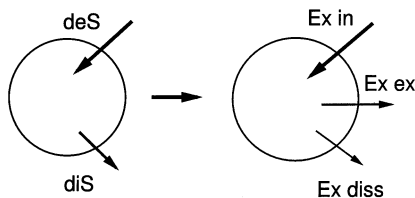


Fig. 1. The development of a Prigogine/Schrödinger interpretation of the thermodynamical function of a biological system (a) into an interpretation formulated in terms of exergy (b).

Energy Flow of a Foodchain reformulated according to Exergy Principle(s)

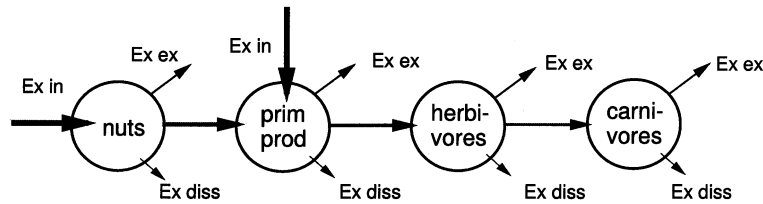


Fig. 2. The thermodynamical function of biological systems formulated in terms of exergy extending to a trophic chain. The appearance of exergy transfers occurs.

The directions of the arrows pertaining to d_iS and d_eS (Fig. 1) have caused some confusion.

The internal dissipation of the system, d_iS , is shown pointing out of the system. It represents the export of entropy to the surroundings. As a result, d_eS can be mistakenly interpreted as an import of entropy from the surroundings. But the direction of this arrow refers instead to the import of Schrödingers negentropy. Since the process symbolized by this arrow acts to move the system away from thermodynamical equilibrium, i.e. the opposite of entropy formation, the arrow logically is given the direction opposite to d_iS .

Having clarified the direction of processes, we now state the entropy balance of the system as

$$d_{\text{tot}}S = d_iS + d_eS \quad (7)$$

where $d_{\text{tot}}S$ must be non-positive if a given biological system is to persist. Because d_iS is always positive, d_eS must be a negative quantity of greater magnitude, i.e.

$$d_eS < -d_iS \quad (8)$$

If this relation holds, the system can grow and develop. If the two balance out, the system is in steady state. The criterion may be violated for short periods of time during which the system may draw from its storages, e.g. during hibernation. If such conditions persist, however, it will eventually lead to the decay and death of the system.

The resolution of the entropy flows, together with the need for more pragmatic formulation of fluxes that can be compared to network approaches, leads us to reformulate the thermodynamic relationships of a biological system in

terms of exergy. Exergy is defined as useful, available energy. The forms of exergy are, as we shall see later, dominated by the free biogeochemical energies of the system. Thus, the above diagram from Prigogine (Fig. 1a) can be redrawn as shown in Fig. 1b.

Exergy, or high quality energy, Ex_{in} , now enters the system across its boundaries. This exergy is slowly transformed by the system processes. As these processes are irreversible, a part of the exergy will be degraded into the lowest quality energy form, heat, Ex_{diss} , that is lost to the system or to any other system forever. (This remark, allows for the possibility that heat might be used as input to facilitate other processes.) Most biological systems are 'leaky' in one form or the other. By leaky we mean that material and its accompanying intermediate quality energy is lost, and the exergy thus transferred can be of use to other neighbouring systems. This we call the exported exergy, Ex_{ex} . We note that the exergy balance is strictly non-conservative in contrast to the first law of thermodynamics. The difference between exergy input and the exergy lost, either as dissipation or export, represents the exergy built into and stored in the organism, i.e. growth in its broadest sense. Thus, for any system representing a single unit, such as an individual organism, one may write

$$Ex_{\text{st}} = Ex_{\text{in}} - Ex_{\text{ex}} - Ex_{\text{diss}} \quad (9)$$

The extension of these considerations to a trophic chain is depicted in Fig. 2. The designation of the flows is the same as in Fig. 1b.

The expansion of this scheme to include more (sub)systems merely involves moving system

boundaries. In doing so, however, the characteristics of several of the exergies in Fig. 1b are changed. Two important features of the figure should be noted.

First, exergy crosses the system boundaries to drive the system at only two places — from the pool of inorganic nutrients and by the capture of solar energy by autotrops. The implicit assumption is that systems boundaries are wide enough to internalize other possible inputs, e.g. allochthonous inputs or migration.

Second, the formulation of the ecosystem as a food chain allows one to denote a new ‘type’ of exergy, i.e. those intermediate flows that are exported from a subsystem, but not from the whole system. Some exported exergies remain, but these are mainly dependent on the forcing functions, whereas the exergies transferred internally are influenced primarily by the characteristics of the ecosystem structure, its history and potential for evolution. Any individual component should be able to optimize its thermodynamic relationship with respect to its surroundings in two ways. The first is by increasing its imports of high quality energy (exergy) from the surroundings. The second is by optimizing the efficiency with which the transfers are taking place. The first action corresponds to taking up as much energy as possible,

the second to lowering the costs of transfer up the chain, i.e. to minimize dissipation.

The characterization of various energies in terms of their relative qualities is taken from Brillouin (1966), according to whom the highest form of energy consists of short-wave electromagnetic radiation, and the lowest is heat, long-wave, infrared radiation. In between, one encounters intermediate quality energies, such as chemical or bio-geochemical energies.

The extension of this representation to a network of organisms or populations is illustrated in Fig. 3. It should be noticed that additional thermodynamic flows occur internal to the system.

One sees that not only has the system boundary been moved, but cycling also is present.

It has previously been argued that there are two kind of flows of energy in an ecosystem: energy proper and energy bound in chemical compounds. It should be noted, that energy proper can enter the ecosystems only via autotrophic compartments! That is, the only input of high quality energy enters the system via photosynthesis. This entry point usually is unique, or at least few in number. The only proper energy leaving the system (dissipation) is respiration. It takes the form of heat, the lowest form of energy, and exits from all compartments.

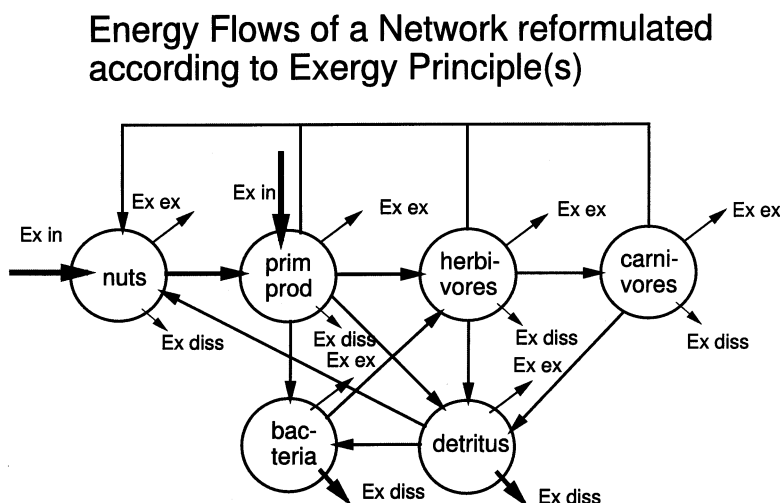


Fig. 3. The thermodynamical function of biological systems formulated in terms of exergy extending to an ecosystem network. The appearance of cycles of exergy transfers serving to retain exergy within the system occurs.

As regards the materially bound energies, they have multiple points of entry to the system. These inputs can be further differentiated. Generally, they are inorganic nutrients or organic materials that enter from other systems. Inorganic nutrients usually enter only the autotrophic compartment(s). In the remainder of the system, the nutrients enter compartments bound into organic compounds. Most of the materially bound energies in organic material are of internal origin, and they cycle within the system according to the characteristics of the food chain or network.

The materially bound energies are not actually dissipated from the system, but rather lost over the boundaries via advective or dispersive fluxes. They enter other systems as inputs, or forcing functions, that are important constraints on the ecosystem in its progression towards a higher structure.

Based on these considerations, we hypothesize the following directions to characterize the thermodynamical evolution of an ecosystem network.

5. Hypotheses

1. An ecosystem network should evolve so as to increase its sources of energies, which can be done by increasing the efficiencies by which energies are captured from the outside.
2. An ecosystem network should evolve in a way that minimizes its dissipations, i.e. lowers the costs of its maintenance.
3. An ecosystem network should evolve so as to retain energies within the system by passing them on to other components, or by storing them as efficiently as possible in any of the compartments.

The primary advantage of exergy as the numerarie of energy in an ecological network is that it directly reflects the quality of the energy. This attribute embellishes the information otherwise inherent in network energy flows. Energy not only is retained in the system as a result of cycling, but cycling also makes it possible to combine several quanta of relatively poor energy quality, and join them with compounds of higher energy quality, albeit at the cost of much accompanying dissipa-

tion. This may in fact be one explanation of the observations made by Patten that energy can be utilized more than once in an ecological network. In addition, exergy implicitly invokes the second law, and thus facilitates the interpretation of ecosystems as dissipative, far-from-equilibrium structures. The normal energy interpretation does not take us that far since it only relates to the first law.

6. A network analysis

We now wish to consider how an ecosystem will evolve in response to changes in both its input and output environs in the light of hypotheses 1 and 2. In the network analysis of ecosystems, the principal exchanges across the system boundaries can be identified as inputs (the D-vector), respirations (the R-vector), and exports (the E-vector), using the notations of Ulanowicz (1986). All the remaining element transfers comprise the elements, T_{ij} , of the directed flowmatrix (T-matrix).

An increase in the cycling within a system (i.e. exergy transfers) contributes positively to the ascendancy of the system mostly through the amplifying effect it has on the total system throughput. So hypothesis 3, as formulated above, has already been confirmed. What remains are the relationships to the exterior, especially the exergy input and the exergy dissipated. These fluxes can, following the terminology of Ulanowicz (1986), be identified with the $T_{0,i}$'s and $T_{i,n+2}$'s of the system, respectively.

The performance of the ecosystem network is expressed by the ascendancy. How the system should respond to changes in specific flows, should be mirrored by the sensitivity of the ascendancy to changes in various components of the system. This sensitivity to changes in flows was formulated by Casey (1992) and quoted in Pahl-Wostl and Ulanowicz (1993), as

$$\frac{\delta A}{\delta T_{pq}} = \log \left(\frac{T_{pq} T}{T_p \cdot T_q} \right) \quad (10)$$

where

$$\begin{aligned}
 T_{p..} &= \sum_q T_{pq}; T_{..q} = \sum_p T_{pq}; T_{..} = T = \sum_p T_{p..} = \sum_q T_{..q} \\
 &= \sum_p \sum_q T_{pq} \quad (11)
 \end{aligned}$$

We see how the sensitivity of the ascendancy to single fluxes takes on a surprisingly simple form, whereby the sensitivity consists of a part of the ascendancy itself. Eq. (10) makes it possible to investigate the development of the system in response to changes in flows crossing the boundaries. Other related investigations can be found in Ulanowicz (1995), Ulanowicz and Wolff (1991), Ulanowicz and Arbarca-Arenas (1997), and Ulanowicz and Baird (1999).

6.1. Sensitivity to dissipative outputs

Looking only at the respiratory or dissipative outputs of the system it follows that:

$$\frac{\delta A}{\delta T_{p,n+2}} = \log \frac{T_{p,n+2} T_{..}}{T_{..n+2} T_p} \quad (12)$$

where the right side is equivalent to the expression

$$\log \frac{T_{p,n+2}}{T_p} - \log \frac{T_{..n+2}}{T_{..}} \quad (13)$$

Eq. (10) means that any compartment having a dissipation that is higher than the overall rate of system dissipation will make a positive contribution to the ascendancy, i.e.

$$\frac{T_{..n+2}}{T_{..}} < \frac{T_{i,n+2}}{T_i} \Rightarrow \frac{\delta A}{\delta T_{i,n+2}} > 0 \quad (14)$$

6.2. Sensitivity to inputs to the system

Concentrating on the inputs leads to analogous arguments:

$$\frac{\delta A}{\delta T_{0q}} = \log \left(\frac{T_{0,q} T_{..}}{T_{..q} T_{0..}} \right) \quad (15)$$

The right side of this equation may be rewritten as

$$\log \frac{T_{0,q}}{T_{..q}} - \log \frac{T_{0..}}{T_{..}} \quad (16)$$

so that

$$\frac{T_{0..}}{T_{..}} < \frac{T_{0i}}{T_{..i}} \Rightarrow \frac{\delta A}{\delta T_{i,n+2}} > 0 \quad (17)$$

The last formula implies that any compartment importing more than the average import of the system is contributing positively to the ascendancy!

7. The biological interpretation

This analysis of the sensitivity of the ascendancy to external fluxes leads to some surprising conclusions. First, it was found that the compartments performing highly dissipative processes, can contribute to increasing the ascendancy. At first glance, this seems to contradict the above statements that systems should minimize their losses and/or dissipations. However, it should be noted that this conclusion was deduced at the level of subsystem.

Any compartment that increases its own respiratory coefficient more than the average must have at least one counterpart elsewhere. That is, an increase in dissipation/respiration at one trophic level must be accompanied by a corresponding decrease in the respiration at another level of the system.

One's attention thus falls on the organisms that have relatively high respirations. Bacteria, especially, have higher than average respiration. The implication is that by shunting most of its dissipation out of a single compartment the system ascendancy is abetted. Regarding Fig. 3, this makes perfect sense. The biggest difference between Figs. 2 and 3 is the introduction of detrital and bacterial links, which permits a lot of cycling to ensue. Cycling and autocatalysis serve to retain matter in the system, allowing it to build up more structure. The focus of dissipation into a few compartments such as bacteria, implies that its dissipation will be balanced out by that of many other compartments that attempt to save as much as possible, thereby minimizing their maintenance costs. In those other systems components' relative dissipation will decrease and storage will be favoured. Those compartments that squeeze the final exergy out of the system release compounds to be utilized again. This perspective stresses the roles of the

detrital and bacterial links of the system as being non-limiting in that they return matter for reuse.

Looking at the inputs, one's attention is drawn to the autotrophic compartments of the system. Those are the only compartments drawing directly from the outside in the form of the high quality energy input of solar radiation, or indirectly from the soluble pool of nutrients, part of which was in fact returned by the detrital-bacterial food chain. Thus, from a thermodynamical point of view, ecosystem development seems to be regulated from the bottom up (Nielsen, 1992), as nutrients and solar energy are the only forms of exergy that cross the boundary. They are, therefore, the driving inputs of the system.

8. Conclusion

There appears to be a high concordance between the network formulation of ecosystem ascendancy and the thermodynamical concept of exergy. This may help to explain the high correlations often observed between the two indices when calculated on the same systems (Christensen, 1992; Salomonsen, 1992; Jørgensen, 1994). The result of the analysis places emphasis upon the compartments responsible for (1) the inputs of energy or matter, and (2) cycling and retention of energy and matter in the system.

Acknowledgements

This study was in part made possible by a grant from the European Union under the MAST II Programme, MAS2-CT-920036. We are indebted to Dr S.E. Jørgensen and Dr B.C. Patten for their helpful comments, and to critics of the manuscript.

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