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Short communication

Exergy, information and aggradation: An ecosystems reconciliation

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ABSTRACT

Ecosystems have been hypothesized to develop according to increases in four separate system attributes: (1) ascendency, (2) storage of exergy, (3) the ability to dissipate external gradients in exergy and (4) network aggradation. Analysis of the formal descriptions of these attributes reveals a theoretical consistency among the four trends. The treatment also points to the attribute of autocatalytic configurations called "centripetality" as the core unitary agency responsible for all four separate descriptions.

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1. Introduction

During the last two decades several statements attempting to describe tendencies that orient developing ecosystems have appeared (Mueller and Leupelt, 1998). Notable among them are those that deal with exergy, a measure of the potential for a given amount of energy to perform work. Perhaps one of the earliest hypotheses is that of Jørgensen and Mejer (1977), who suggested that, all other things being equal, an ecosystem will take on that configuration that maximizes its storage of exergy.

Exergy, when used in an ecological context is denoted "eco-exergy". It is a measure of the distance from thermodynamic equilibrium, because it is defined as the capacity a system has for performing work over and above what the same system would possess at thermodynamic equilibrium (when the system consists only of inorganic matter in its highest possible oxidation state and contains no gradients). It can be shown (Jørgensen and Svirezhev, 2004) that eco-exergy according to this definition is equal to $BRTK$, where B is the biomass, R the gas constant, T the absolute temperature and K Kullback's measure of information. (See below.)

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Not long thereafter, Schneider and Kay (1994a,b) proposed a seemingly contradictory direction that favors the configuration that degrades available gradients in exergy at the fastest possible rate. The two observations are not necessarily mutually exclusive. For example, Fath et al. (2001) showed how exergy storage (Total System Storage—TSS) and dissipation (Total System Export—TSE) can occur in tandem and are consistent with a third tendency, the minimization of specific dissipation (Total System Export/Total System Storage). That is, while both TSE and TSS may increase simultaneously, TSS increases more rapidly than expected from power scaling of respiration rates to organism size, $R \sim B^{3/4}$ (Von Bertalanffy, 1957). Furthermore, ecosystems can utilize energy input to grow and develop in three stages: (1) in physical structure, (2) in network configuration and (3) in information (Jørgensen et al., 2000). Fath et al. (2004) showed that both exergy degradation and exergy storage can increase with the first growth form (physical structure), but that only an increase in exergy storage is commensurate with the other two growth forms. Hence, TSE is a good descriptor during early stages, and TSS during all stages, but particularly during later ones after limits on imports constrain further dissipation.

At about the same time as Jørgensen and Mejer (1981) were studying the role of exergy in ecosystems, Ulanowicz (1980) was experimenting with the use of information theory to describe developing ecosystems. Ulanowicz, taking a lead from Rutledge et al.'s (1976) application of conditional information indices to weighted digraphs of ecosystem flows, identified the average mutual information (AMI) of the trophic flow structure as a surrogate for the degree of organization inherent in the ecosystem. He scaled the AMI by the total system activity (the total system throughput [TST], which is equal simply to the sum of all transfers occurring in the system) to yield a quantity he called the ascendency. Ulanowicz (1986) hypothesized that, in the absence of major perturbations, ecosystems had an inherent tendency to increase in ascendency with time.

It happens that there is a fundamental link between mutual information and exergy in that in statistical mechanics exergy is defined in terms of the "cross-information" between energies within a system (Kay, 1984; Jørgensen and Svirezhev, 2004). Cross-information is related to mutual information, which prompts the question whether a deep relationship might exist between the ascendency and ecosystem exergy that would reveal all three hypotheses as facets of a single, unifying principle?

Yet a fourth trend, that of network aggradation, or the movement away from thermodynamic equilibrium, occurs when the throughflow (Total System Throughflow) and throughflow derived storage (TSS) exceed the steady-state input (Patten and Fath, 1998; Fath and Patten, 2001). Throughflow is the sum of flows into or out of each internal system compartment, and can be partitioned into five different classes: boundary input, first passage flow, cycled flow, node-specific dissipation, and boundary export (Fath et al., 2001). Aggradation starts with an external gradient generating input across a system boundary and is augmented within the system by connectivity and feedback. Due to aggradation, a certain quantity of steady-state input supports a greater (often significantly) quantity of system throughflow or storage, because that resource can be retained and cycled throughout a sequence of pathways having multiple impacts in the system. Aggradation shows the degree to which a certain quantity of export (which is equal to import at steady-state) can maintain a higher level of internal throughflow and storage.

There exist, in fact, empirical data to support the notion that all four hypotheses are consistent with each other (Jørgensen et al., 2000.) In what follows a theoretical approach to exploring such unity will be pursued. In particular, we show how increasing exergy storage and dissipation can also arise from the application of information theory to ecosystem networks and how all three contribute to the property of network aggradation.

2. Exergy as medium of exchange

In order to quantify networks of exchange, one must decide upon the medium to be used in the bookkeeping. Usually, the medium is either energy (the generic sense) or some specific chemical element, such as carbon, nitrogen or phosphorus. Nothing, however, prohibits the choice of a medium that might serve a particular purpose, such as the attempt here to highlight connections between exergy and network information. Whence, the medium for the remainder of this essay is chosen to be the exergy, as described by Jørgensen et al. (1995) and Jørgensen (1992, 2002). Accordingly, the following terms will be defined: let X_i represent the amount of exergy stored in the ith compartment of the ecosystem. Similarly, let T_{ij} be the amount of exergy that is transferred from compartment i to compartment j within a unit of time.

Now, information is the measure of change in a probability assignment (Tribus and McIrvine, 1971). Usually, the two distributions in question are the a priori and a posteriori versions of a given probability—in this case the probability that a quantum of exergy will flow from i to j. As the a priori estimate that a quantum of exergy will leave i during a given interval of time, one may use the analogy from the theory of mass-action that this probability can be estimated as $(X_i/X.)$, where $X.$ represents the sum of all the X_i. In strictly similar manner, the probability that a quantum enters some other compartment j should be proportional to the quotient $(X_j/X.)$. If these two probabilities were completely independent, the a priori joint probability that a quantum flows from i to j would become proportional to the product $(X_iX_j/X.^2)$.

Of course, the exit and entrance probabilities are usually coupled and not entirely independent. In such case the a posteriori probability could be estimated by empirical means in terms of the T_{ij}. That is the quotient $(T_{ij}/T..)$ would be an estimate of the a posteriori joint probability that a quantum leaves i and enters j.

Kullback (1959) provides a measure of information that is revealed in passing from the a priori to the a posteriori. It is called the Kullback–Leibler information measure and takes the form:

$$I = \sum_i p(a_i) \log \left\{ \frac{p(a_i)}{p(b_i)} \right\},$$

where $p(a_i)$ and $p(b_i)$ are the a posteriori and a priori probabilities of the ith event, respectively. Substituting the probabilities as estimated in the preceding paragraphs, one obtains the form for the Kullback–Leibler information of exergy flow in a network as

$$I = \sum_{i,j} \frac{T_{ij}}{T_{..}} \log\left(\frac{T_{ij}X_{.}^{2}}{T_{..}X_i X_j}\right).$$

Following the lead of Tribus and McIrvine (1971), as in Ulanowicz (1980), one may scale this information measure by the total activity ($T_{..}$) to yield the storage-inclusive ascendency (Ulanowicz and Abarca-Arenas, 1997) as

$$A = \sum_{i,j} T_{ij} \log\left(\frac{T_{ij}X_{.}^{2}}{T_{..}X_i X_j}\right).$$

3. Exergy storage

Odum (1969) proposed 24 properties as indicators of maturity in ecosystems. These could be grouped under increases in species richness, trophic specificity, cycling and containment. It happens that, other things being equal, an increase in any of these attributes will result in an increase of systems ascendency. As a result, Ulanowicz (1980, 1986) proposed as a phenomenological principle describing ecosystem development that "in the absence of major perturbations, ecosystems exhibit a tendency to increase in ascendency." Similarly, it may be shown that the 24 properties of Odum (1969) are consistent with the four growth forms that again all yield increasing eco-exergy (Fath et al., 2004). Those factors which lend to an increasing ascendency, therefore, should be considered as significant contributors to ecosystem development.

From a mathematical point of view, one can elucidate how a system gains in ascendency by calculating what contributes to positive gradients of that measure. So, for example, if one wishes to know what changes in the X_k foster increases in ascendency, one would want to study the partial derivatives ($\partial A/\partial X_k$). After rather tedious algebraic manipulation, the results reduce to

$$\frac{\partial A}{\partial X_k} = 2\left(\frac{T_{..}}{X_{.}} - \frac{1}{2}\frac{T_{k.} + T_{.k}}{X_k}\right).$$

This formula has a straightforward meaning. The first term in parentheses is the overall throughput rate. The second quotient is the average throughput rate for compartment k. That is, the sensitivity of the exergy-ascendency is proportional to the amount by which the overall throughput rate exceeds that of the compartment in question. If the throughput of compartment is smaller than the overall rate, then ascendency is abetted. In other words, increasing ascendency is favored by slower passage (longer storage) of exergy through compartment k. That is, exergy storage favors increased ascendency.

4. Exergy usage

One can also investigate how ascendency changes in response to changing system flows by calculating the sensitivities ($\partial A/\partial T_{pq}$). Because A is a first-order homogeneous function in T_{ij}, one may invoke Euler's result (Courant, 1936) to yield:

$$\frac{\partial A}{\partial T_{pq}} = \log\left(\frac{T_{pq}X_{.}^{2}}{T_{..}X_p X_q}\right).$$

In particular, one wishes to explore how A changes in response to increased depletion of external gradients of exergy, T_{oq}. The relevant derivative would be

$$\frac{\partial A}{\partial T_{oq}} = \log\left(\frac{T_{oq}X_{.}^{2}}{T_{..}X_o X_q}\right).$$

The problem with interpreting this last derivative is that it is unclear what X_o would mean, as the compartment o is a virtual one representing the source of all inputs. Ulanowicz and Abarca-Arenas (1997) showed that one may choose a value for the virtual sources and sinks that will not otherwise bias the results. In the case of X_o, this becomes:

$$X_o = \left(\frac{\left[T_{o.}\sum_{k=1}^{n} X_k\right]}{T_{..} - T_{o.}}\right),$$

and for $X_.$ it is

$$X_{.} = \left(\frac{\left[T_{..}\sum_{k=1}^{n} X_k\right]}{T_{..} - T_{o.}}\right).$$

Substituting these in the sensitivity gives

$$\frac{\partial A}{\partial T_{oq}} = \log\left(\left\{\frac{T_{oq}}{T_{o.}}\right\}\left\{\frac{T_{..}}{T_{..} - T_{o.}}\right\}\left\{\frac{\sum_{k=1}^{n} X_k}{X_q}\right\}\right).$$

Now, it is evident that

$$\frac{T_{oq}}{T_{o.}} \le 1, \qquad \frac{T_{..}}{T_{..} - T_{o.}} \ge 1, \qquad \frac{\sum_{k=1}^{n} X_k}{X_q} \ge 1.$$

So that whenever $T_{oq}/T_{o.} \ge X_q/\sum_k X_k$, the sensitivity is guaranteed to be positive. In words, whenever a primary producer brings in disproportionately more of total primary production than its biomass fraction of the whole system, further increases in production by that compartment are favored. This inequality is satisfied in immature systems. If higher heterotrophs come to store large amounts of exergy (as in the later stages of development), then the value of the sensitivity coefficient will diminish. In other words, in systems with abundant resources, the premium on bringing in further resources is higher than in more mature systems, where the storage of exergy becomes proportionately greater.

The importation of exergy comes at the expense of external gradients in exergy. That is, systems develop in the direction of greater dissipation of external gradients in exergy, as proposed by Schneider and Kay (1994a,b). This is especially true in the early stage of development when growth form 1 (biomass) dominantes. Later, however, as the storage of exergy increases, further destruction of exergy will wane in its benefits, because the amount of exergy available per unit of time will not be able to increase beyond the amount supplied by solar radiation. Beyond that point, the growth of the network structure and information will predominate (see also Fath et al., 2004; Jørgensen and Fath, 2004; Jørgensen, 2002).

In Jørgensen and Svirezhev (2004) the following expression was derived for the gain in eco-exergy, Ex, as a result of the

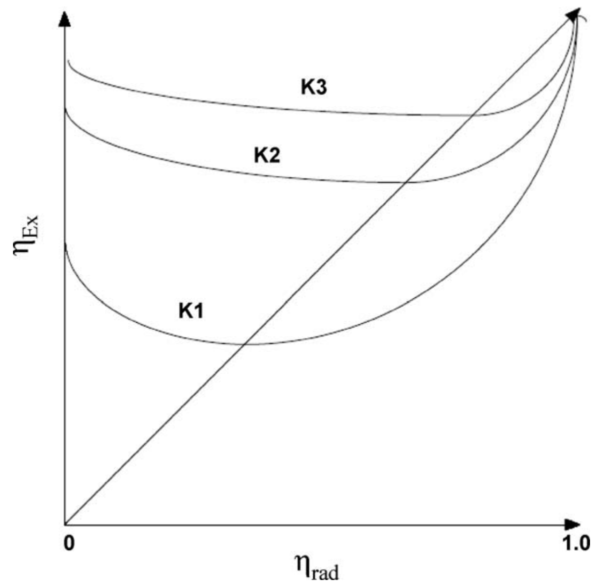

Fig. 1 – η_{Ex} is plotted vs. η_{rad} for three information levels, K3 > K2 > K1. An increasing Kullback measure of information implies that the ecosystem will continue to accrue information at progressively higher values of η_{rad}.

energy of the incoming solar radiation, E_{in}:

$$Ex = (E_{in} - R)\left[K - \ln\left(\frac{E_{in} - R}{E_{in}}\right)\right] + R,$$

where R is the difference between the total incoming and outgoing radiation and K is Kullback's measure of information. If we introduce the radiation efficiency, $\eta_{rad} = R/E_{in}$, and the exergy efficiency, $\eta_{Ex} = Ex/E_{in}$, then the equation can be reformulated as

$$\eta_{Ex} = (1 - \eta_{rad})K + (1 - \eta_{rad})\ln(1 - \eta_{rad}) + \eta_{rad},$$

η_{Ex} is therefore a function of two independent variables, η_{rad} and K, but is independent of any parameter.

Fig. 1 shows the relationship between η_{Ex} and η_{rad} for three different values of K. The active surface of an ecosystem will, as seen in the figure, perform the role of a classical thermodynamic engine in doing mechanical and chemical work whenever K is low and the radiation efficiency is high (as is the case in immature systems). The ecosystem will accrue information when K is high and η_{rad} is not too high. When a certain level of information has been obtained (the system approaches maturity), mechanical and chemical work (which imply exergy destruction) will be replaced by the accrual of information (the storage of exergy accompanied by a less than proportionate destruction of exergy). This is completely consistent with the results of the inequalities derived above, and with the dominance of growth form 1 in the immature stage and growth forms 2 and 3 in the mature stage.

5. Ecosystem aggradation

Aggradation also shows how internal storage and throughflow rise with the addition of import. The external exergy gradients, once imported into the system, increase total system throughflow and storage through the internal system connectivity. A single connection is sufficient to ensure that total system throughflow exceeds boundary flow and more complex structures add even greater amounts of first passage and cycled flow. Therefore these findings based on ascendency are also consistent with the property of network aggradation.

6. Conclusions

At the crux of ascendency lies the action of autocatalysis. One of the chief attributes of autocatalysis is what Ulanowicz and Abarca-Arenas (1997) calls "centripetality", or the tendency to draw increasing amounts of matter and energy into the orbit of the participating members. This tendency inflates ascendency both in the quantitative sense of increasing total system activity and qualitatively by accentuating the connections in the loop above and beyond pathways connecting non-participating members.

At the same time, any increasing storage of exergy is a particular manifestation of the centripetal tendency, and the dissipation of external exergy gradients to feed system autocatalysis describes centripetality in almost tautological fashion. The principle of aggradation further implicates this closure by showing that the importation, and hence dissipation, of the exergy source leads to even greater exergy storage and throughflow through internal network connections.

In retrospect, the elucidation of the connections among ascendency, exergy and aggradation has been effected by stages that are typical of theory-driven research. First, it was noted in phenomenological fashion how quantitative observations of the properties were strongly correlated. Thereafter, formal definitions were used to forge theoretical ties among the separate attributes. Finally, the perspective offered by these new theoretical connections facilitated a verbal description of the common unitary agency that gave rise to the independent trends that had been formalized as separate principles.

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