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# A Phenomenological Perspective of Ecological Development

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**ABSTRACT:** The most direct and realistic approach to quantifying ecosystems is to measure their supporting networks of flows of materials and energy. The growth and development of such networks may be quantified by applying information theory to the data on flows. Once development has been formalized, other heretofore subjective notions, such as "eutrophication" and ecosystem "health," take on more precise, quantitative significance.

**KEY WORDS:** aquatic toxicology, ecosystem theory, food webs, information theory, thermodynamics, self-organization, eutrophication, ecosystem health, networks

Ecology, like economics, anthropology, and sociology, is still considered by many to be a "soft" science. In contrast to physics, where the world is usually quantifiable and predictable, ecology remains largely descriptive and incapable of accurately forecasting events. Disdain from several quarters is only heightened by talk about an ecosystem behaving as an organic unit, or by concern for the "health" of a particular ecological community—popular idioms that have found their way into environmental legislation.

One antidote, it would seem, would be to set about placing ecology on a sound physical basis—rationally deducing macrobiological phenomena from their constitutive physical and chemical processes. Thus would one exorcise the "myths" of organic behavior and of autonomous growth and development in ecosystems. Indeed, the stunning discoveries of molecular biology have taken us some distance along this pathway.

However, it is becoming increasingly clear that reductionistic descriptions

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are insufficient narratives of events in the ecological world [*1-3*]. Models with many components seem inherently incapable of predicting circumstances very far into the future [*4,5*]. Influence over longer intervals of time appears to be directed down as well as up the hierarchy of things and events. Myths quite often entail a kernel of solid truth, and, in the zeal to "demythologize" ecology, there is the risk of neglecting what could become the keystone of ecological science.

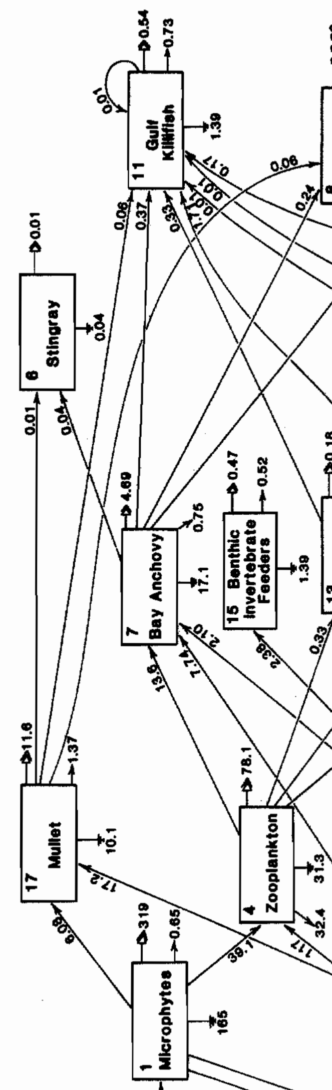
Now, I am not about to suggest to so practical a society as the ASTM that we begin to count angels on pinheads! Quite the opposite, I am urging that we confront the reality of ecosystems on the level at which they exist, and that we speak only in quantitative terms about measurable entities. I am advocating a largely phenomenological approach to the issue of whether ecosystems grow and develop. The major benefit from this endeavor should be a more profound and direct understanding of what an ecosystem is and of how it functions. In a more practical vein, the measurements should allow one to weigh whether a pond has become eutrophic or if the "health" of a lotic community has been adversely impacted and to provide quantitative, defensible judgements on these issues.

Ecology is the study of the relationships of organisms with one another and with their nonliving environment. The reader will notice that the primary reality of an ecosystem resides in the relationships among its organisms and environment, not in the organisms *per se*. The most palpable and universal way of representing the relationship between any two populations is to measure the amount of material or energy that flows from one species to the other. The underlying networks of flows of media thus serve as the concrete, material realization of an incredibly complex suite of phenomena that may be observed when the ecosystem is viewed in other contexts (see Fig. 1). The remaining question is whether the process of growth and development can be said to occur in this condensed representation of an ecosystem.

## Quantifying Growth and Development

I submit that the evolution of a flow network is readily quantifiable. Furthermore, when the ecological ensemble is viewed solely in terms of flows, the growth and development of the system come to appear as two aspects of a unitary process. To see why this is so, it is helpful to distinguish various types of flow using an appropriate nomenclature. I choose to differentiate four categories of flows that can occur in a system (see Fig. 2): (*a*) the flow from any Compartment *i* to any other Compartment *j* within an *n*-compartment system is designated by $T_{ij}$; (*b*) the inputs to Compartment *i* coming from outside the ensemble boundaries become $T_{oi}$; (*c*) the exports of still-usable medium from *i* out of the system are $T_{i,\,n+1}$; (*d*) finally, the amount of medium that is dissipated (that is, becomes unusable by any other compartment) by *i* is $T_{i,\,n+2}$.

Now, growth may be thought of as an increase in size. As the discussion is



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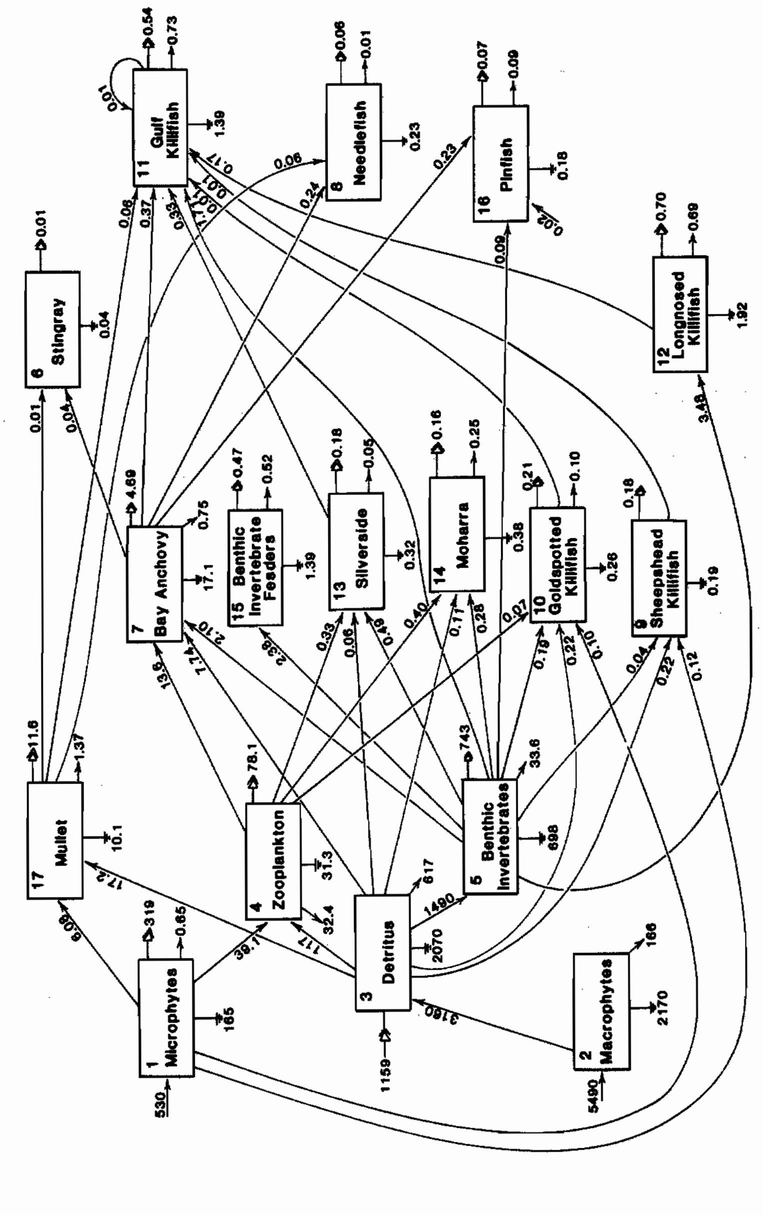


FIG. 1—*A schematic of carbon flows among the taxa of a marsh gut ecosystem. Crystal River, FL. All flows are in (mg carbon)/m² per day. The ground symbols represent respiratory losses. The linked arrows depict returns to the detritus (figure from Ulanowicz [2], data from M. Homer and W. M. Kemp, unpublished manuscript).*

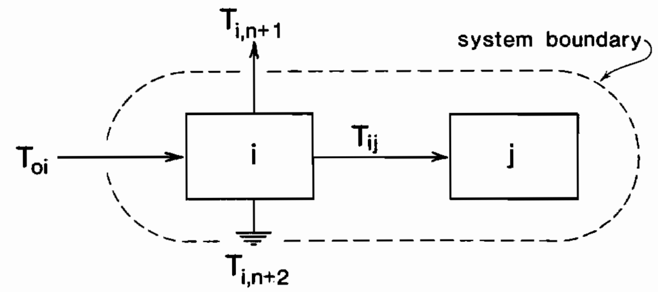


FIG. 2—*Representations of the four categories of flow that may occur in an* n*-compartment ecosystem. Flows between arbitrary Compartments* i *and* j *within the system are labeled* $T_{ij}$. *Inputs to the system are treated as coming from a virtual Compartment O. Exports of useable medium are assumed to flow to hypothetical Compartment* n + 1, *and dissipation of medium to* n + 2.

now limited to speaking in terms of flows, the most natural way to gage the size of a particular compartment is to measure the total amount of flow through that node. In general, one may either sum all the inputs[2]

$$T_i' = \sum_{j=0}^{n} T_{ji}, \; i = 1,2, \ldots, n + 2,$$

or collect all the outputs

$$T_i = \sum_{j=1}^{n+2} T_{ij}, \; i = 0,1,2, \ldots, n$$

Either way, the unique size of the entire system becomes the sum of the individual compartmental throughputs

$$T = \sum_{i=1}^{n+2} T_i' = \sum_{i=0}^{n} T_i$$

Growth is thereby represented as an increase in the total system throughput, $T$. Lest anyone feel this is a strange way to identify system size, it should be noted that the familiar gross natural product (GNP) in economics is calculated in virtually this same manner.

On the other side of the coin, development may be taken as an increase in organization. Quantifying the factor of organization is a more complicated task, and space does not permit a full derivation here [7,8]. Suffice it to say

[2]If more than one commodity is being circulated, one cannot add inputs expressed in different units without first "pricing" these flows in terms of a single reference medium [6].



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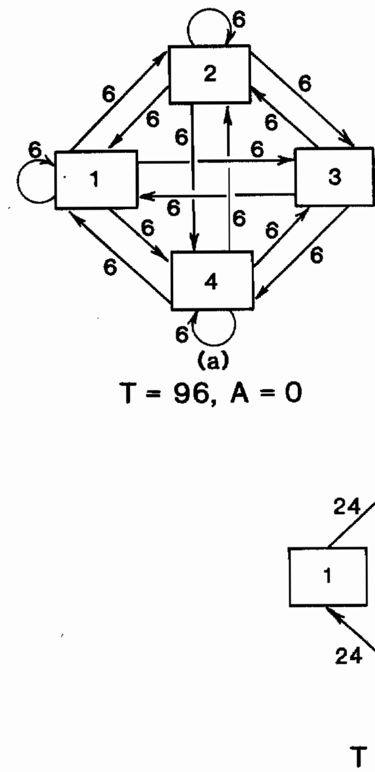


FIG. 3—*Three hypothetical, closed net*
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that an organized system is assumed to be highly articulated in the sense that a flow issuing from any given compartment will engender flow only in a narrow subset of other *loci*. By contrast, in a disorganized system there is great uncertainty as to where the effects of any particular flow will be realized.

Rutledge et al. [9], while addressing other issues, quantified such articulation of a flow network by equating it to the average mutual information defined by information theory

$$A = K \sum_{i=1}^{n} \sum_{j=1}^{n} (T_{ji}/T) \log (T_{ji}T/T_jT_i')$$

where $K$ is a scalar constant of proportionality. In Fig. 3*a*, each node exchanges medium equally with all other nodes, and articulation is minimal. In Fig. 3*b*, transfers are slightly more decisive, and in Fig. 3*c*, the network is

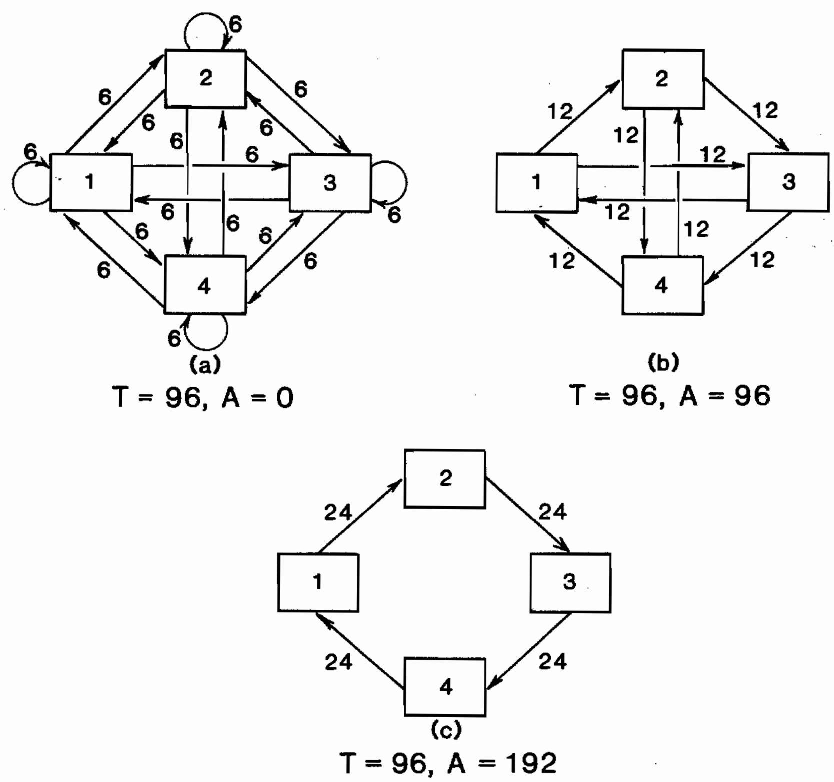


FIG. 3—*Three hypothetical, closed networks with increasing degrees of articulation. All three systems have identical total systems throughputs (*T = 96 *units):* (a) *the maximally connected and minimally articulated configuration,* (b) *the same compartments with an intermediate level of articulation, and* (c) *the maximally articulated configuration of flows.*

maximally articulated. The average mutual information of the network flows increases as they become more highly organized.

The scale factor, $K$, is often ignored by those who apply information theory, but here it becomes of paramount importance in establishing the size of a system. The most natural choice for $K$ is to equate it to the total system throughput, $T$. Then, the quantity, $A$, becomes the product of a factor of size and an index of organization. This product is given the name "ascendency," and I submit that growth and development are cogently quantified by any increase in system ascendency.

Ascendency was not originally developed in epistemological fashion [10]. Rather, its roots were phenomenological. Odum [11] presented a summary of some 24 attributes thought to characterize mature ecosystems. They may be further aggregated under four headings as the tendencies: (1) to internalize flows, (2) to increase cybernetic feedback, (3) to augment the degree of specialization of compartments, and (4) to add new compartments. Under appropriate conditions, all four trends may contribute to a higher network ascendency. Whence, ecosystems appear to evolve so as to optimize the ascendency of their underlying network of transformations.

## Limits to Growth and Development

The full interplay of factors affecting the network ascendency may be illustrated and the limits to increasing $A$ are readily shown by decomposing $A$ into four terms

$$A = C - (E + S + R)$$

where

$$C = -T\sum_{i=1}^{n} (T_i/T) \log (T_i/T),$$

$$E = -\sum_{i=1}^{n} T_{i,\,n+1} \log (T_i/T),$$

$$S = -\sum_{i=1}^{n} T_{i,\,n+2} \log (T_i/T), \text{ and}$$

$$R = -\sum_{i=1}^{n} \sum_{j=1}^{n} T_{ji} \log (T_{ji}/T_i').$$

In this form, the ascendency may be increased by maximizing $C$ or by minimizing any or all of the three terms in parentheses or both. The $C$ has the mathematical form of an informational "entropy." It serves as an upper bound on $A$, and for that reason is called the development capacity. One way $C$ may increase is for the total system throughput, $T$, to rise. This will occur when species are maximizing their power throughput, a non-conservative strategy for survival similar, but not identical, to one first advocated by A. J. Lotka and later by H. T. Odum and Pinkerton [*12*]. However, the combination of finite input flows and mandatory dissipation at each node serves ultimately to limit the rise of $T$.

Of course, $C$ also may be augmented by maximizing the informational entropy factor, as has been proposed by Jaynes [*13*]. Network entropy is increased by ever-finer partitioning among an increasing number of nodes. However, the finite availability of resources implies that some finely-partitioned nodes inevitably will become too small to persist in the face of chance environmental perturbations.

The three terms in parentheses comprise a conditional entropy, referred to here as the systems' overhead. The first overhead term, $E$, is generated by transfers to higher hierarchical levels. Minimizing $E$ fosters internalization, but there usually are limits on the degree to which $E$ may be reduced. For, if the exports and imports of a given system both happen to be elements in a positive cybernetic loop at some higher level, then decreasing the exports from the given system might eventually diminish its own sustenance.

Minimizing the dissipation term, $S$, is an obvious analog to the Prigogine entropy minimization principle [*14*]. So long as resources are abundant, $A$ is more readily increased by a growing $T$ and a widening gap between capacity and overhead. Minimizing $S$ under such conditions (for example, embryonic growth) would be counter-productive. Later, however, after limitations become severe, minimizing $S$ becomes an appropriate strategy to increasing $A$ in mature systems.

The final term, $R$, rises with the number of redundant or parallel pathways in the network. Decreasing $R$ results in a more streamlined and efficient network topology. However, it can also make for a more fragile structure. In systems with insufficient $R$, perturbations at any point are likely to have disastrous consequences on downstream nodes, whereas a modicum of redundant pathways will allow for compensatory flows to the affected compartments along the less impacted lines of communication [*15*].

**Implications for Ecosystem Management**

In trying to apply ascendency and related measures to the management of ecosystems, it is a temptation to identify $A$ with the "health" and "desirability" of the underlying community. However, a little reflection shows that such correspondence is not complete. For example, the Lotka hypothesis infers that a system may grow in response to the availability of new resources (inputs) by rapidly increasing its total system throughput. At the same time the organization factor might decrease due to the extinction of species and other effects. Thus, it may happen that a system gains in robustness (ascendency) despite diminishing in structural attributes. This possibility suggests the following formal definition.

> *Eutrophication*—any increase in system ascendency due to a rise in total system throughput that more than compensates for a concomitant fall in the mutual information of the flow network.

Thus, although $A$ captures the combination of size and organization that confers reality upon a given system in the place of other virtual configurations, it is not always a good indicator of the level of maturity (and in the opinion of many, the "desirability") of an ecosystem. Ulanowicz and Mann [*16*] have argued that these traits are better represented by the unscaled ascendency, $A/T$. Any decrement in this organizational factor is a cause for concern and further investigation by the system manager.

A high value of $A/T$ is a necessary but unfortunately not a sufficient indicator of a "healthy" system. Communities with very high values of $A$ may nonetheless be very "brittle," or fragile. As was implied earlier, the system overhead, $C$-$A$, serves to quantify the reservoir of adaptability upon which the system can draw to meet unexpected emergencies [*17*]. The upshot is that a healthy system is one with a high capacity, $C$, or diversity, $C/T$, high enough to reflect a richness in structure ($A/T$), while at the same time exceeding the ascendency by an amount sufficient to allow for adaptable responses to unexpected perturbations.

At present, it is probably best not to specify the definition of a "healthy" ecosystem any further. Much more data on flow networks of various systems need to be amassed before any numbers can be attached to the words "high" and "sufficient" in the preceding description. Also, the values of $C$ and $A$ should be normalized to account for different preferences in identifying the system components. Nevertheless, there is good cause to hope that quantitative measures of ecosystem status are in the offing. It is also satisfying to see some rationale given to the solid intuition that diversity is a desirable attribute of ecosystems.

Many investigators have been discouraged from studying entire ecosystems as a behavioral unit either because of unnecessarily proscriptive attitudes on the part of colleagues or for the lack of an adequate conceptual basis upon which to plan measurements. Much precious time has been lost because of these unnecessary constraints. The highest priority now should be given to expanding ecosystem-level research, for we are on the brink of discoveries in macrobiology that should rival those made in molecular biology during the 1950s and 1960s for the degree to which they will change our thinking and alter how we deal with the living world around us.

## References

[*1*] Ulanowicz, R. E. in *Theoretical Systems Ecology*, Academic Press, New York, 1979, pp. 107-117.

[*2*] Ulanowicz, R. E., *Mathematical Biosciences*, Vol. 65, 1983, pp. 219-237.

[*3*] Weiss, P. A. in *Beyond Reductionism*, MacMillan, New York, 1969, pp. 3-55.



[*4*] Lorenz, E. N., *Journal of Atm*

[*5*] Platt, T., Mann, K. H., and U *ography*, UNESCO Press, Par

[*6*] Costanza, R. and Neill, C., *Jo*

[*7*] Hirata, H. and Ulanowicz, R. pp. 261-270.

[*8*] Ulanowicz, R. E., *Growth a* Verlag, New York, 1986.

[*9*] Rutledge, R. W., Basorre, B. Vol. 57, 1976, pp. 355-371.

[*10*] Ulanowicz, R. E., *Journal of T*

[*11*] Odum, E. P., *Science*, Vol. 16

[*12*] Odum, H. T. and Pinkerton, I

[*13*] Jaynes, E. T., *Physics Review*,

[*14*] Prigogine, I., *Bulletin Classe S* 600-606.

[*15*] Odum, E. P., *Fundamentals o*

[*16*] Ulanowicz, R. E. and Mann, K UNESCO Press, Paris, 1981, p

[*17*] Conrad, M., *Adaptability: Th* Plenum Press, New York, 1983

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1983, pp. 219-237.
w York, 1969, pp. 3-55.

[4] Lorenz, E. N., *Journal of Atmospheric Science*, Vol. 20, 1963, pp. 130-141.
[5] Platt, T., Mann, K. H., and Ulanowicz, R. E., *Mathematical Models in Biological Oceanography*, UNESCO Press, Paris, 1981.
[6] Costanza, R. and Neill, C., *Journal of Theoretical Biology*, Vol. 106, 1984, pp. 41-57.
[7] Hirata, H. and Ulanowicz, R. E., *International Journal of Systems Science*, Vol. 15, 1984, pp. 261-270.
[8] Ulanowicz, R. E., *Growth and Development: Ecosystems Phenomenology*, Springer-Verlag, New York, 1986.
[9] Rutledge, R. W., Basorre, B. L., and Mulholland, R. J., *Journal of Theoretical Biology*, Vol. 57, 1976, pp. 355-371.
[10] Ulanowicz, R. E., *Journal of Theoretical Biology*, Vol. 85, 1980, pp. 223-245.
[11] Odum, E. P., *Science*, Vol. 164, 1969, pp. 262-270.
[12] Odum, H. T. and Pinkerton, R. C., *American Scientist*, Vol. 43, 1955, pp. 331-343.
[13] Jaynes, E. T., *Physics Review*, Vol. 106, 1957, pp. 620-630.
[14] Prigogine, I., *Bulletin Classe Scientifique, Academie Royale Belgique*, Vol. 31, 1945, pp. 600-606.
[15] Odum, E. P., *Fundamentals of Ecology*, Saunders, Philadelphia, 1953.
[16] Ulanowicz, R. E. and Mann, K. H. in *Mathematical Models in Biological Oceanography*, UNESCO Press, Paris, 1981, pp. 133-137.
[17] Conrad, M., *Adaptability: The Significance of Variability from Molecule to Ecosystem*, Plenum Press, New York, 1983.