

A UNIFIED THEORY OF SELF-ORGANIZATION¹

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ABSTRACT. Growth and development associated with a network of material or energy exchanges can be combined using information theory into a single measure, the ascendancy. Increases in ascendancy are constrained by the availability of matter or energy, dissipation, heirarchical considerations and environmental perturbations.

INTRODUCTION

Physicists are astir these days in anticipation of a breakthrough in the search for a unified force theory. Since the turn of the century the Holy Grail of physics has been the reconciliation of gravitational, electromagnetic, and (later) the two intranuclear forces as manifestations of a single, universal phenomenon. Events on a cosmic scale or those confined within a baryon are thought to derive from the same essence.

How different the outlook of most biologists today! The cause for any event is usually assumed to lie in a mechanism evident only at a smaller scale of observation. The search for explanation cascades down a heirarchy of categories until one arrives in the domain of molecular biology. It is almost as if (1814) divining angel had been rediscovered so that, knowing the sequences of nucleic acids in the gene pool of an ecosystem, the angel could tell the ecologist everything he need know about the system. Of course, in the Neo-Darwinian scenario chance can alter the course of biological events. But it appears the significant role of chance has also been relegated to the molecular level.

I submit that this wholly reductionistic attitude among many biologists is more an accident of history than an accurate perception of the nature of biological phenomena. To be sure, the advances in micro and molecular biology have immensely improved scientific understanding and human well being. In contrast, to say that

teleology, Vitalism and Lamarckism have not fared well is to speak charitably. Yet, despite this background, there appears to be no logical, apriori proscription to the existence of a principle of organization operating at, say, the level of the whole ecosystem. What does seem to be missing is a perspective of community-level phenomena which allows the articulation of development as a process which universally can be subjected to measurement.

I wish to suggest that flow analysis, the study of the network of exchanges among the components of a system, provides just such a perspective from which a useful definition of self-organization can be made. Furthermore, the key to the way in which one goes about combining flow measurements into an ensemble property reflecting the dual attributes of growth and development is to be found in the theory of quantification of knowledge, i.e., information theory.

DEVELOPMENT OF THE HYPOTHESIS

I begin the description of self-organization by modifying to the efforts of MacArthur (1955) to quantify the diversity of pathways in a flow network. If T_i is the quantity of any medium (energy, material, capital, etc.) flowing through compartment i , and T is the total system throughput of the network ($T = \sum T_i$), then $Q_i = T_i/T$ is an estimator of the probability that at any time we shall find a given quantum of medium passing through compartment i . Using the information measure of entropy, or uncertainty, we may define the diversity of throughputs in the system as

$$C = -K \sum_i Q_i \log Q_i \quad (1)$$

where K is an arbitrary constant.

Apter and Wolpert (1965) correctly criticized the use of information measures such as C to describe biological systems, saying that these indices both failed to quantify the extent, or size, of the system and did not

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convey any sense of how well the compartments were related one to another. To rephrase their critique, C as stated in equation (1) does not assess the attributes of network growth and development. This is a serious deficiency indeed, as we intuitively sense that, for an entity to survive vis-a-vis another system (real or putative), it requires some advantageous combination of both size and coherent structure.

Fortunately, it is possible to overcome these deficiencies in C without abandoning the use of either the flow description or information theory. For example, the lack of scale can be rectified by equating the oft-neglected constant K to the total systems throughput T. Lest this equivalence seem arbitrary or simplistic, Tribus and McIrvine (1971) note how the thermodynamic entropy function has been scaled in a similar manner since before the time of Shannon.

To assess the degree of network coherence it becomes necessary to know more than just the apportionment of throughputs. One further needs to know the probability that a quantum of throughput T_i will flow directly as input to another member j of the community. Call the estimator of this probability f_{ij} . Rutledge et al. (1976) show how these conditional probabilities reduce the uncertainty about flow partitioning by an amount equivalent to what is known in information theory as the average mutual information,

$$A = T \sum_i \sum_j f_{ij} Q_i \log [f_{ij} / (\sum_k f_{ik} Q_k)], \quad (2)$$

where I have again chosen to scale the information measure by T. McEliece (1977) shows how information measures can be superior to covariance indices in quantifying relationships. Thus, one may look upon the average mutual information as being the best available assessment of the internal coherence of the flow network. The index A, therefore, embodies the notions of both growth and development. One might speculate that A quantifies the extent to which a given network is ascendent over similar real or putative networks. I, therefore, refer to A as the network ascendancy.

The above speculation is reinforced when it is noticed that the ascendancy is usually augmented by such network attributes as the tendency to internalize flows, the amount of cybernetic feedback, the degree of specialization of compartmental outputs and the number of compartments (Ulanowicz, 1980). These properties encompass all the factors which Eugene Odum (1969) cited as being typical of mature ecosystems.

If growth and development are to be identified with the optimization of network ascendancy, the question immediately arises as to what, at the macroscopic level, constrains any increase in A. Here it is useful to note the inequality (McEliece, 1977),

$$C \geq A \geq 0, \quad (3)$$

that is, C serves as an upper bound on ascendancy. For this reason I refer to C as the development capacity of the network.

Factors which limit the increase in capacity also place a bound on the ascendancy. Two constraints on capacity seem immediately apparent. First, the total systems throughput should be constrained by the total input flows available to the system. Second, increases in the throughput diversity will be limited by how finely the total throughput can be partitioned. Extremely small compartments will be liable to chance extinctions due to arbitrary perturbations. Hence, the rigor of the environment in which the network exists also limits the degree of partitioning possible, and thereby the development capacity.

In addition to the limits on the increase in capacity one must also study the positive difference between capacity and ascendancy; or, if you will, the network overhead. Overhead can be decomposed into three components. Suppose it is determined that the fraction r_i of the throughput of compartment i is dissipated, as required by the Second Law of Thermodynamics, into a form which cannot be used by any member of the community, or another similar community. Likewise, e_i is identified as the fraction of throughput exported from component i as useful medium to another community. Then the overhead can be shown algebraically to equal the sum of three non-negative quantities:

$$S = -T \sum_i r_i Q_i \log Q_i > 0, \quad (4)$$

$$E = -T \sum_i e_i Q_i \log Q_i \geq 0, \quad (5)$$

$$\text{and } R = -T \sum_i \sum_j f_{ij} Q_i \log [f_{ij} Q_i / (\sum_k f_{ik} Q_k)] \geq 0. \quad (6)$$

The dissipation, S, is the net encumbrance of the thermodynamic losses on each pass through a compartment. Odum and Pinkerton (1955) infer that r_i increases monotonically with T_i . This would make it impossible to cycle medium at an arbitrarily high rate. Thus, an upper bound would exist on how much a given amount of input flow could be translated into total systems throughput.

The export fraction, E, I have called tribute. One might expect that development would proceed in a direction so as to minimize tribute. But if exports and inputs are coupled within the context of a higher hierarchical network, it may be detrimental to the ascendancy of the larger system (and hence to the original system's inputs) to reduce exports below some critical level.

The remaining fraction, R, or redundancy, was first shown by Rutledge et al. (1976) to be related to the multiplicity of pathways between

two arbitrary components of the network. Again, one might expect feedback loops of greater efficiency to begin to dominate during the course of development, causing ascendancy to grow at the expense of redundancy. However, chance perturbations could retard or reverse this tendency, and we thus anticipate that the redundancy would reflect the variety and magnitude of the perturbations to which a climax community is subject. Because perturbations are never absent from the real world, actual ecosystems should always possess refractory amounts of redundancy characteristic of their environments.

All of the previous speculations can be summarized by a single hypothesis: A self-organizing community flow network evolves over an adequate interval of time so as to optimize its ascendancy subject to thermodynamic, hierarchical and environmental constraints. In symbols one may write

$$A = C - (S + E + R), \quad (7)$$

noting that the development capacity of a network is characterized by the intensity and diversity of its constituent flows, and that not all of this capacity can appear as coherent structure — a necessary amount is always encumbered for thermodynamic, hierarchical or environmental reasons. Not only does (7) bear marked similarity to the definition of Gibbs' free energy, but when combined with the inequality $S > 0$ they together subsume the two laws of thermodynamics.

IMPLICATIONS OF THE HYPOTHESIS

There are certain to be some who will look upon this hypothesis as nothing more than an exercise in epistemology (or perhaps tautology!). I would respond by noting that the theory is quantitative and can be tested. What scant data are available to test the hypothesis tend to support it (Ulanowicz 1980). Although there remain lexical problems in comparing networks of radically different ecosystems (e.g. tundra with coral reef), consistent choices for compartments should allow one to use the information variables for comparative purposes.

One exciting possibility afforded by the network variables is to give quantitative definitions to certain hitherto subjective abstractions. The common notion of a "desirable" ecosystem, for example, usually is applied to a community which is "highly-developed". Does not the network coherence (A/T) assign a number to the degree of development? "Eutrophic" systems sometimes displace more "desirable" communities. Eutrophication is seen here as an increase in ascendancy corresponding to an increase in input flows. This augmented ascendancy, however, is due to a disproportionate increase in total systems throughput outweighing a concomitant decrease in network

coherence. Even the "fitness" of a species vis-a-vis the community should be related to the contribution of that species to the ascendancy of the ensemble... The possibilities are numerous.

Furthermore, the community variables help to resolve the conflict surrounding the earlier "diversity implies stability" hypothesis. May's (1973) remark that a benign environment allows a greater diversity to exist was echoed in my earlier statements about the limits to development capacity. At the same time a given component of this capacity, the redundancy, quantifies Odum's (1953) idea that multiple pathways buffer the system against small perturbations.

If the medium of exchange is taken to be energy, the ascendancy takes on the dimensions of power. The hypothesis of maximal ascendancy can then be viewed as a generalization of the Lotka maximum power principle applicable to the community as a whole (Odum and Pinkerton, 1955). If t_{kj} represents the flow of energy from k to j , the ascendancy (eqn. 2) can be rewritten as

$$A = \sum_k \sum_j t_{kj} \log \left[\frac{f_{kj}}{\sum_i f_{ij} Q_i} \right]. \quad (8)$$

That is, A can be regarded as the weighted sum of all the intramural energy exchanges. Could each weighting factor possibly be identified with the quality of its associated flow? I am not aware of any successful methodology for measuring the entropy of a living organism. Perhaps we could circumvent this difficulty by regarding bioenergetic quality as a relativistic notion. Rather than look upon quality as an intrinsic property of the medium being exchanged, might we not infer that the quality of the flowing medium is determined by the particular network of exchanges in which it is imbedded?

If future empirical evidence should lend further credence to the development hypothesis, then perhaps we need to rethink the current emphasis on reductionism in biology. Leaving aside Neo-Darwinism, we find examples of whole-ecosystem models which are implicitly reductionistic: The system is broken into compartments, and bilateral interactions between compartments are studied in isolation and given mathematical expression. These expressions are collected (usually as a set of coupled differential equations) and the behavior of the whole system is believed to correspond to the behavior of the mathematical ensemble. But, if the ecosystem is following some variational law at the community level, then who is to say that bilateral functionalities cannot change and undergo selection during community development in the same sense that genotypes are assumed to undergo selection?

Finally, and most importantly, I would hope that debate over this hypothesis will rekindle optimism concerning the search for unifying principles in biology. As this exercise demon-

strates, by examining different perspectives upon the same natural phenomena, it may be possible to choose a frame of reference wherein diverse living phenomena at different temporal and spatial scales can be adequately described by a single principle. This principle might even transcend the living domain and find application wherever highly dissipative phenomena occur, e.g. economic development (E. P. Odum 1977) and meteorological systems (H. T. Odum 1971). One thing is certain, however, if we allow ourselves to be persuaded that such unity of description cannot exist, we will surely never discover it. But, if we are willing to risk the rigors and frustration of a search, there is no telling what scientific and philosophical achievements might await us!

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