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ECOSYSTEM INTEGRITY AND NETWORK THEORY

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ABSTRACT. The observed structure of the interactions among ecosystem components results in autocatalytic feedback that occurs within the network of such exchanges. This feedback sets not only the overall rates at which the system functions but also engenders competition and selection for the more effective pathways. As a system grows more highly defined and better articulated, it also becomes more vulnerable to surprise perturbations, i.e. the integrity and reliability of a system are, to a large degree, mutually exclusive. The system integrity and the complementary capacity to adapt to perturbation can both be assessed from the network of material or energetic exchanges using information theory.

Estimating the networks of exchanges within a system provides the manager with one of the most versatile and reliable diagnostic tools available today. For example, with such information one can, in turn, assay all indirect bilateral influences between any components, elucidate the underlying trophic structure, make explicit the routes and magnitudes of recycling, and quantify the status of overall system functioning.

INTRODUCTION

There is a major difficulty in applying the word integrity to any living, non-cognitive system. In one sense, the term conveys the idea of wholeness, completeness, and coherency. At the same time, the noun also connotes soundness and incorruptibility (Webster's New Collegiate Dictionary, 1981). Unfortunately, when describing living, evolving systems, the first set of attributes is incompatible with the latter. For the sake of argument, I will take completeness as being representative of the first set of properties and incorruptibility to characterize the second. Below, I will consider the causal agencies behind completeness on one hand and incorruptibility on the other. I will argue that these underlying causes are distinct and bear a dialectic relationship to one another. Although most of my exposition will be highly abstract in nature, I believe that the exercise nonetheless will lend significant insight into how systems evolve and should interest anyone seeking to manage ecosystems.

To say that something is complete is to infer that the final state is known, can be described, and is the result of some process that transformed it from a disorganized or inchoate state toward its final, ordered form. Unlike machines, or to a lesser extent organisms, ecosystems never can be considered complete in any absolute sense of the word. The result of succession usually is either unknown or cannot be agreed upon. However, ecosystems are observed to undergo a regular series of transitions called succession resulting in more mature configurations (Odum 1969). Therefore, it makes some sense to speak of the completeness of an ecosystem in the relative sense of the configuration of an ecosystem at a particular time being more mature or complete than its predecessor states. The description of this tendency toward more complete forms has been a fundamental goal of ecosystem theory and, more generally, of biology and philosophy.

The difficulties these disciplines encounter in describing the development of living systems stem from a consensus among modern scientists to limit the designation of causes of phenomena to strictly material and mechanical agents. While this structure has contributed significantly to the rigor of physical and chemical explanations, I submit that an overly zealous adherence to minimalism could blind us to a very natural rational and highly useful description of evolving systems.

In contrast to the modern tendency to restrict the nature of causality stand the ancient writings of Aristotle, who suggested that causes in nature are almost never simple. A single event may have several simultaneous causes and Aristotle taught that any cause could be assigned to one of four categories: material, efficient, formal, or final. For example, in building a house the material cause resides in the bricks, lumber, and other tangible elements that go into its structure. The efficient cause is provided by the laborers who actually assemble these materials. The design or blueprints are usually taken as the formal cause;[1] and the need for shelter on the part of those who contracted for the construction is considered to be the final agent.

I am suggesting that autocatalytic feedback is an example of formal cause at work in living systems. By autocatalysis is meant a cyclical configuration of two or more processes or entities wherein the activity of each member positively catalyses the activity of the next element in one direction around the loop.[2] At first glance, it might appear that autocatalysis can be readily decomposed into its material and efficient mechanical components, but further reflection reveals otherwise.

Autocatalysis (AC) possesses at least six properties that reveal its stature as a formal agency:

1) As the prefix auto- suggests, AC is to at least some degree autonomous of its composite parts. Whenever the network of causal influences can be mapped, it becomes feasible to identify and enumerate all the circular causal routes. Furthermore, if the individual links can be somehow quantified, it is then possible to separate abstractly the autocatalytic nexus from the supporting tree of causal events upon which it remains contingent (Ulanowicz 1983).

2) If one observes only a subset of the elements in an autocatalytic cycle, these components form a distinctly non-autonomous chain. However, if one increases the scale of observation to include all the members of the cycle, AC is seen to emerge as a phenomenon.

3) By its very nature, AC serves to accelerate the activities of its constituents, i.e. it is growth enhancing.

4) Chance perturbations in any element of a loop that enhance AC are themselves enhanced and vice versa. That is, AC exerts selection pressure upon deviations in the loop to foster only those characteristics which contribute to the ensemble behavior. It is a short step from selection for character traits to selection among possible replacement components.

   Once one recognizes that the ensemble exerts selection upon its replacement parts, it becomes clear that the characteristic lifetime of the configuration exceeds that of any of its parts and selection becomes a key element of the autonomy mentioned in (1) above. In particular, changes in any element that result in its drawing increased resources into the loop will be rewarded, giving rise to a central tendency, or, as Denbigh put it, a form of chemical imperialism.

5) Both selection and central tendency result inevitably in competition for resources among multiple AC loops. The result is an ever more

streamlined or articulated topology (network structure) of interactions.

6) Finally, AC is manifestly the result of a dynamical structure, thereby making it formal in nature.

The six properties of AC constitute a strong case for it to be considered a formal agent. In the absence of major destructive perturbation, AC serves to increase the level of activity of the system (an extensive, or size-dependent, effect) while at the same time it prunes the less effective pathways from the causal network (an intensive, or size-independent, effect). The system at any time can be said to be more complete than in its earlier forms. It remains to quantify the dual (i.e. extensive and intensive) effects of the unitary agency (AC) behind this tendency. Toward this end, it is useful to turn to networks of material or energy transfer as they occur in ecological communities. Thus, the activity level of the ecosystem becomes synonymous with the magnitude of the aggregate transfers occurring in its underlying network. This latter sum is known in economic theory as the total system throughput (TST), a term which has carried over into ecology (Hannon 1973). In the early stages of development, when only the extensive properties of AC are manifest, rampant expansionism (or growth as sheer increase in system size) is adequately gauged by the rise in total system throughput.

Quantifying the tendency toward an ever more articulated network topology of fewer but stronger connections is a slightly more difficult proposition. Suffice it here to note that in more articulated or highly defined networks, there is less uncertainty as to whether medium at any given mode will flow next. Less uncertainty implies more information, and Rutledge et al. (1976) have shown how the average mutual information, as estimated from the relative magnitudes of the flows, captures the degree of articulation inherent in the flow topology.

However, the average mutual information, being an intensive attribute, lacks physical dimensions. It is, nonetheless, multiplied by a scalar constant which can be used to give dimensions to the measure (Tribus and McIrvine 1971). Thus, scaling the average mutual information by the total system throughput gives rise to a quantity known as the network ascendancy--a surrogate for the efficiency with which the system processes the medium in question. Because any increase in the level of activity can be characterized as growth (e.g., the increase in the gross national product of a country's economy) and because the augmented definition (or completeness) of its topology may be termed development, any increase in the product of the total system throughput by the average mutual information (the ascendancy) serves to measure the unitary process of growth and development (Ulanowicz 1986a).

Of course growth and development can never continue unabated, and it is in the discussion of the limits to increasing ascendancy that one discovers the basic incompatibility between completeness and incorruptibility. To begin with, average mutual information is bounded from above by the Shannon-Wiener index of uncertainty. Scaling this latter measure by the total system throughput yields a quantity called the development capacity--a measure of the size and complexity of the network. The limits to rising development capacity (and also to ascendancy) are recognizable from the mathematical form of the development capacity. One constraint is the finitude of each external source available to the system. A second limitation exists in the number of compartments. Disaggregation cannot continue beyond a point where the finite resources become spread over too large a number of categories. Otherwise, some compartments would come to possess so few resources that they would be highly vulnerable to chance extinction by the inevitable perturbations to which any real system is always subjected.

Even if the development capacity has leveled off, the ascendancy may continue to increase by diminishing the amount by which it falls short of the capacity, a difference called the overhead. The overhead, in turn, can be traced to four sources:

1) the multiplicity of external inputs,

2) the exports of usable medium from the system,

3) the dissipations inherent in the activities at each node, and

4) the average redundancy among various pathways joining any two arbitrary compartments.

Rather than being an unmitigated encumbrance upon the system's performance, the overhead is seen at times to be essential for system persistence. That is, diminishing any term in the overhead beyond some unspecified point will eventually place the given system at risk. For example, relying completely upon a single external source of medium makes the system highly vulnerable to chance disruptions in that source. Similarly, it would be counterproductive to cut back on exports which might be coupled autocatalytically to the system's inputs at the next higher hierarchical level. Furthermore, the resources that are dissipated at each node often underwrite structural maintenance at a lower level of the hierarchy. It would be detrimental to decrease such support to very low levels, even if such arbitrary cutbacks were thermodynamically feasible (which they are not). Finally, a channel of flow between two nodes or species having no redundant backup is susceptible to disruption by exogenous perturbation in the same way as discussed above for the external sources[3].

In an abstract but cogent way, overhead represents the system's incompleteness. At the same time it embodies the ecosystem's strength-in-reserve, soundness, and potential to resist corruption. Therefore, the dialectic nature of the two aforementioned connotations of integrity becomes manifest. The eventual stasis and possible breakdown of the drive toward completeness (or higher ascendancy as driven by AC) is inevitable. The only uncertainty is how or when such limits will be encountered. In very regular, stable, physical environments, such as occur in many tropical rain forests, the balance between ascendancy and overhead appears rather quiescent.

At higher latitudes, however, there appears to be a tendency for the ecosystem ascendancy to overshoot its virtual balance point with the overhead. In such systems, there is more uncertainty (and hence, potential for surprise) concerning when the particular external perturbation will occur that will send the system ascendancy plummeting below its average value. From its underdeveloped status after the crash, the system gradually builds toward another overshoot. Such cyclic behavior has been well-described by Holling (1986) and it is characteristic of boreal and cold temperature ecosystems.

It should be evident that in order to evaluate the organizational status of an ecosystem and to follow its system level dynamics, it is necessary first to quantify at least one of the networks of material and energy flows. Once all the flows of a particular medium are known, it is a routine matter to calculate the information indices that characterize each of the properties mentioned above. One can then determine with some quantitative confidence when a system retrogresses as the result of some environmental insult or when it goes eutrophic in response to elevated inputs of nutrients (Ulanowicz 1986b). The reader is cautioned that any prediction that whole system indices might provide will be valid only at the level of the entire system. Statements about the behaviors of system ascendancy, capacity, or overhead do not translate into prognostications about the future dynamics of particular ecosystem elements of interest; e.g., favorite sport or commercial fishes.

If one wishes to go beyond keeping an eye on the pulse of the whole ecosystem, the data assembled to quantify the network of ecosystem exchanges can either be applied to conventional simulation modeling or be subjected to additional network analyses. For example, one may assess all the bilateral indirect influences occurring in the system; i.e. how each species contributes to or depends upon any other species over all indirect pathways that connect them (Patten et al. 1976). One may construct a picture of the underlying trophic structure and efficiencies (Ulanowicz 1988). All of the pathways for recycling of the given medium can be identified and quantified (Ulanowicz 1983). Finally, the data in the networks can be used, if one desires, to construct a conventional simulation model of the system. (One should remember, however, that such models by their limited nature usually exclude the actions of formal agencies.)

The measurement of ecological networks should provide the background that will allow ecologists better to understand and to evaluate the integrity of ecosystems. It is hoped that from a deeper understanding of ecodynamics will follow the capability to keep the magnitudes of ecological surprises within reasonable bounds.

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NOTES

1. Aristotle actually believed that the final form of any developing object is imminent in its inchoate stages and drives the system towards completion. In every blastula resides the mature form striving to express itself. The neo-Darwinian notion of genome portrays such formal agency as residing in the material locus of the DNA molecule. However, only the most recalcitrant of sociobiologists are willing to accept such a reduction as sufficient. In ecology, one is unhampered by either final forms or material loci. Here it is sufficient to regard formal cause as the effect that the present juxtaposition of component processes has on the system at a later time. Why such identification need be made at all should become clear presently.

2. The details of positive feedback are complex. No attempt is made here to discuss such matters as time delays and phasing as they affect autocatalysis, in the belief that such digression would detract from the treatment of the attributes presented here. Similarly, there are other ramifications of positive feedback, such as the cross-catalysis inherent in nucleotide synthesis and transfer-RNA dynamics, which provide variations on the theme discussed in this paper (Joel Fischer).

3. As the system achieves network states of higher mutual information, it becomes internally more self-consistent. In a sense, one might say that mature systems are less likely to collapse because of indigenous disharmonies; e.g., astatic fish communities (R. Ryder). However, this increasing resistance to disruption by internal dissonance belies an enhanced vulnerability to external disruptions towards which the system is unadapted.

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