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A Phenomenology of Evolving Networks

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Key words—Causality; formal cause; autocatalysis; network analysis; information theory; ascendency; ecosystems; growth and development; system overhead.

Abstract—A significant characteristic of post-Newtonian science is its exclusion of all but material and mechanical causalities. There is reason to question whether such minimalism is sufficient to describe living processes. Paradoxically, a strict material/mechanical stance may engender unnecessary anthropomorphism. By admitting autopoiesis as an example of formal cause at work in living system, a more sufficient and natural description of biological phenomena results. Furthermore, recent advances in the analysis of networks provide a quantitative framework for identifying the effects of formal causes at the system level.

INTRODUCTION

RECENTLY, Roger Lewin [7] posed the question in *Science* magazine, 'Why is development so illogical?' Levin's concern was that developmental biology wasn't acting according to the script that molecular biologists had written. If the sequence of an organism's genes determines its physical characteristics, then it should be possible to map from the coded material elements in the genome into the facets of the somatic structure. But after over two decades of trying to trace the consequences of known substitutions in the genome of a very elementary multi-cellular nematode, Sidney Brenner and colleagues [7] have been unable to elucidate how specific genes relate to the process by which cells assemble into an organism. Brenner concludes that 'The molecular mechanisms look boringly simple, and they do not tell us what we want to know'. With cogent insight he goes on to say 'We have to try to discover the principles of organization, how lots of things are put together in the same place.'

In the opinion of this writer, development will remain illogical and mysterious so long as a Newtonian description of biology is the only legitimate narrative. Paradoxically, the strictures introduced after Newton to obviate mystery from the physical realm guarantee that a Newtonian view of the biological world will remain mysterious and obscure. To be more specific, causality in a Newtonian world is limited to the material or mechanical. However complex the neo-Darwinian picture of evolution may become, one may be assured that it will remain an intricate juxtaposition of material and mechanical elements—intentionally nothing more. But other agencies are at work in developing systems, and one need not make recourse to teleology, vitalism or Lamarckism to describe them.

AUTOCATALYSIS AS FORMAL AGENCY

The notion that scientific descriptions should include only material and mechanical agents is decidedly modern and dates from the late 18th century. Even Newton himself envisioned other agencies behind natural phenomena. Under extreme pressure to finish *Principia* before his perceived arch-competitor Benjamin Hook could explain planetary motion, Newton had to forego the elaboration of his full beliefs and wrote only a minimalist description of the causes behind physical motions.* For philosophical and political reasons this suited many of his contemporaries just fine; and Newton, thanks in part to his economy of description, became a legend in his own time. As his fame grew, he found little motivation to publish the text of a complete world-view that he had written in the interim since *Principia* [24].

Newton's vision encompassed theology and alchemy, subjects which obviously should remain beyond the scope of this journal. However, there are ancient ideas about natural causality that do bear consideration here. Prominent among them was Aristotle's notion that a single event often has multiple causes. Furthermore, he reasoned that all causes were of four types: (1) material, (2) efficient, (3) formal and (4) final. The textbook example of an event with multiple causes is the building of a

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* R. Artigiani, personal communication.

house. Its material causes are evident in the bricks, mortar and other physical elements that go into construction. The laborers who put the materials together constitute the efficient cause. The blueprints outlining the shape and structural details are usually cited as the formal cause, and the need or desire for housing on the part of the eventual occupants comprise the final cause. The first two categories have fared well since Newton's time, but the latter have atrophied.

The exclusion of formal agency as a type of natural cause is unfortunate. There are sound reasons to consider autocatalysis, and in particular autopoiesis, as agents akin to Aristotle's formal causation that are capable of influencing the life process. Autocatalysis is a particular form of positive feedback wherein the activity of an object or a process augments itself, usually via the mediation of some other object or process. For example, if the activity of A catalyzes the activity of B, which goes on to accelerate C, and C in turn accelerates A; then A, B and C are elements of a three-member autocatalytic loop.

Some may object that autocatalysis is itself mechanistic, a subclass of the oft-cited 'feedback mechanisms' that populate descriptions of developing systems. But autocatalysis is mechanistic in at most a metaphorical sense. The late media theorist, Marshall McLuhan, was wont to emphasize how narrators were often numbed by the still unfamiliar nature of newly observed phenomena and by default tend to cast descriptions in more familiar, but usually less-than-adequate terms [9]. His favorite example was how IBM burgeoned as a corporation only after it realized that its real product was information processing, not simply the manufacture of business hardware. Similarly, new scientific endeavors sometimes carry labels born of antecedent disciplines to which they are later seen to bear only the faintest semblance. For example, the link between quantum theory and classical mechanics is tenuous at best, and consists of a formal similarity in the mathematics used to quantify quite disparate phenomena in the two realms. Yet the term 'quantum mechanics' persists. In similar manner 'autocatalytic mechanisms' is a misnomer of observed phenomena.

However, autocatalysis is not a formal cause in the strict sense of Aristotle. To him the cause behind embryonic development was a form immanent in the juvenile stages that eventually was manifested by the mature individual. The hidden form drove the organism towards its final configuration in a way that remotely prefigures neo-Darwinism. In this discourse formal cause is considered to be that agency which issues from the particular juxtaposition of system elements or processes and which is capable of affecting the system at some later time.

Autocatalysis as a formal entity possesses seven additional attributes that together qualify it as an active agency. To begin with, it is by definition *growth enhancing*. An increment in the activity of any element in the loop engenders greater activity in all the other elements, thereby stimulating the aggregate activity of the cycle.

An autocatalytic configuration exerts *selection pressure* upon the properties of all its constituents. If a random change occurs in one member, and furthermore if that change accelerates the catalytic effect of the compartment upon the next element, then (assuming the phasing is right) the initial change will be rewarded in its own turn. Similarly, any change in the character of a compartment that decrements its catalytic effect upon the next element will propagate around the loop in negative fashion to result in decreased catalysis of the starting node by its upstream neighbor. Selection pressure is thus a *symmetry-breaking* agent, always ratcheting the configuration toward ever higher performance.

Selection pressure acts not only upon characteristics of the components, but upon their persistence as well. For example, if A, B and C are three sequential elements in an autocatalytic loop, and (1) element X appears suddenly by happenstance, (2) is more sensitive than B to catalysis by A and (3) provides greater enhancement to C than does B, then X will grow eventually to dominate B, or even to displace B altogether. Hence, the entire configuration helps to establish what replacement components are possible. One can further imagine the stepwise replacement of all initial elements in a loop, so that the configuration itself may endure well beyond the lifetimes of its component parts. The reader's corporeal body is both materially and cellularly different than it was seven years ago, yet the reader maintains a distinct physical identity. Autocatalytic cycles exhibiting such ability to replace its parts are called autopoietic loops [23].

A particular property of a loop member is its ability to capture the resources necessary for its own activity. One can argue that any accidental fortification of this capacity will enhance the member's own activity and thereby be self-rewarding. This *central tendency* of the autocatalytic cycle to appropriate increasing amounts of resources for its own use has been called 'chemical imperialism' [4]. It follows that if a system possesses more than one feedback loop, and the same resources are required by each cycle, then *competition* among autocatalytic pathways should ensue. The result of such competition among loops is that certain pathways will become more dominant, while less effective routes will wane. Therefore, the network of interactions likely will develop into one consisting of progressively fewer pathways along which increasingly stronger interactions occur. That is, the selection pressure exerted by autocatalysis drives the interaction network toward what variously might be called more highly contrasting, sharply defined, or narrowly articulated configurations.

Regardless of where in the hierarchy inputs may issue, autocatalytic subsystems do not react just passively to incoming signals. The facts that autocatalytic configurations have characteristic lifetimes longer than their constituent parts and that overall structures actively influence the nature of allowable replacements both imply that autocatalytic behaviour cannot be regarded in reductionistic fashion as the superposition of component events at lower levels. Furthermore, the central tendency imparts an active identity to the loop (they name hurricanes!). In short, autocatalytic structures exhibit a degree of *autonomy* from their surroundings. That is not to say that such feedback systems can ever be fully autonomous either of their infrastructures or their environments. Total independence would violate the second law of thermodynamics and/or Goedel's theorem. Real systems always remain contingent upon events lower down the hierarchy and constrained by influences from outside the system boundary. But a palpable agency engendered by autocatalysis does originate at the focal level. Hence, a full description of developing systems is possible only in the context of what Salthe calls the triadic system, wherein causes originate at, above and below the given hierarchical level [14].

If one focuses too narrowly upon a subsystem of an autocatalytic loop, that fragment probably will not exhibit most of the attributes just discussed. The strictures that accompany the neo-Darwinian world-view guarantee that nature will be observed in such an adumbrated fashion that formal cause is unlikely to be noticed. Conversely, by expanding the scope of observation one increases the probability that entire feedback loops will be encompassed by the system boundary. That is, the system attributes deriving from autocatalysis *emerge* as the scale of observation increases.

Rigid adherence to mechanical reductionism often forces an advocate into making statements that paradoxically are more metaphysical than the claims that materialism were invoked to avoid. For example, the DNA molecule was said to direct the assembly of the organism. Elsewhere, Dawkins [3] writes about genes as though they were selfish entities. It seems more natural and less anthropomorphic to admit formal cause as the origin of much that transpires in living systems. Doing so requires that the Darwinian paradigm be shifted only slightly to focus on autocatalytic ensembles of populations as the natural units of selection [25, 26].

QUANTIFYING THE INFLUENCE OF AUTOCATALYSIS

It is exciting to consider autocatalysis as a manifestation of formal cause in developing systems. However, one might as well debate the number of angels that can fit on a pinhead, unless it becomes possible to quantify and monitor the effects of this formal agency.

As a prelude to such quantification, it is useful to note two ways in which the influence of autocatalysis is exhibited. Firstly, the positive feedback that supports autocatalysis always works to increase the dimensions of the system. By 'dimension' here is meant more the total activity level rather than the actual spatial extent. Autocatalysis causes the level of aggregate activity to rise. In thermodynamic parlance such increase constitutes an *extensive* aspect of the system. However, it has just been argued that autocatalysis also affects the configuration of the interactions. The web of influences becomes progressively more articulated, having fewer pathways of more intense interactions. Insofar as the latter relational matters are independent of physical scale, they are said to be *intensive* in the thermodynamic sense of the word.

Although the word 'growth' has multiple intricate definitions, perhaps the closest association it sparks in the minds of most readers will be with an increase in system dimensions. Growth is fundamentally an extensive property. In contrast, the term 'development' most immediately connotes a refinement in configuration (see also 'differentiation' [14]). Development more closely resembles a dimensionless or intensive process. The single agent, autocatalysis, simultaneously manifests both extensive and intensive aspects. Growth and development, therefore, should be regarded as two facets of a single, unitary process [17, 19].

Growth and development occurs among a multitude of processes. It spans the hierarchy of living forms from ontogeny through ecology and on into economic and social structures. If one wishes to concentrate on the formal agency *per se*, then in ontogeny one's attention is distracted by the overwhelming influence of the genome and its mechanical programmatic actions. At larger scales, economics and sociology are confounded by the ubiquity of conscious decisions (which are expressed in more of a distributed fashion than most investigators care to admit). That leaves ecology as the most propitious arena in which to study growth and development, as such. (There are purely physical manifestations of growth and development, such as hurricanes, but oddly enough these phenomena seem even less well understood than is the case with ecosystem development [5]). Doctrinaire sociobiologists to the contrary, over the long term the genomes exert only secondary influence upon ecosystem development. Some have argued how ecosystems predate genes in the evolutionary sequence [2, 11]. Others have remarked how it is the ecosystem that creates species [14]. From the other direction, despite the severity of anthropogenic stresses on many of the world's ecosystems, conscious human decisions are only indirectly involved in ecosystem development, which in any event antedates the appearance of humankind on the planet.

That ecosystems are complex is indisputable. Opinions do vary, however, on how best to represent the myriad of interactions that occur in ecological communities. One abstraction having a long tradition in American ecology is to quantify ecological interactions solely in terms of the palpable transfers of material and energy that transpire within the ecosystem [8, 10]. By excluding nonmaterial interactions (e.g. behavior, interference, etc.) one forfeits any hope of achieving a reductionistic or mechanistic explanation of development, but such is not the present goal. Although development is the result of causes arising at all hierarchical levels, the intention in this paper is to emphasize those effects of the formal agency that appear at the focal level. For this limited purpose, a network of physical exchanges should be quite adequate.

The first step in systems analysis is to decide what the important elements of the system are. Ecosystems can be resolved according to species, deme, habitat, trophic level, etc. It is unlikely that any two observers of the same ecosystem would spontaneously choose exactly the same list of components. Such arbitrariness in the lexical phase of system representation leads many to question the value of all quantitative theories that might ensue. The challenge is to build a theory that yields qualitative pronouncements that are reasonably independent of the exact choice of system components.

Once the investigator has defined the n elements that comprise the ecosystem, it is necessary to investigate which of the n^2 possible transfers among them are both feasible and significant. In practice the fraction of possible flows that is seen to occur is usually less than 20%. The amount of chosen medium (e.g. carbon, energy, nitrogen, etc.) that passes from some donor (usually a prey) i to a recipient (predator or abiotic pool) j is designated here by T_{ij}. Estimating the internal exchanges does not complete the picture, however. No living system is isolated, and one must also account for exchanges with the environment. To accommodate exogenous transfers within the chosen nomenclature it becomes necessary to define three virtual compartments to serve as sources and sinks of medium. Thus, T_{0i} will represent all external inputs of medium into i. For hierarchical reasons (that will become evident later), it is useful to distinguish between two types of flows leaving the system. Some exports from i, such as cropping or advection of organisms or detritus out of the given system, can still be used by systems of equivalent scale and will be denoted by $T_{i,n+1}$. Other losses are dissipated entirely (either as unusable heat or in the form of some low-energy chemical ground state) and will be labeled $T_{i,n+2}$. An example of the annual flows of carbon among 36 significant taxa of the mesohaline Chesapeake Bay ecosystem is depicted in Fig. 1. All four types of flow are represented in the diagram.

Given the framework of flow measurements just sketched, quantifying what is meant by the growth of the ecosystem becomes an easy task. The reader will recall that the activity level of each component is taken to be its most significant dimension. Hence, each element or node can be characterized either by the total amount flowing out of it,

$$T_i = \sum_{k=1}^{n+2} T_{ik},$$

or by the sum of all the inputs into it,

$$T_i' = \sum_{m=0}^{n} T_{mi}.$$

T_i and T_i' will be unequal whenever i is not in steady-state, however, at all times the dimension of the entire system can be defined uniquely by the sum of all the compartmental throughputs, otherwise known as T, the total system throughput, where

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

The extensive aspect to growth can thereby be characterized as any increase in T. It may at first seem strange to speak of growth as a rise in activity level, until one realizes that growth in economic systems has long been measured in precisely this way (e.g. the Gross National Product).

To quantify the development of a network, i.e. its progression toward ever more articulated configurations, requires some deliberation. The situation, as described earlier, is that some of the T_{ij} are growing at the expense of others. Those flows that rise into prominence remain connected with each other in nearly concatenated fashion. The key to quantifying the degree of articulation, or concatenation is to note that with progressively fewer flows into and out of each node, any uncertainty

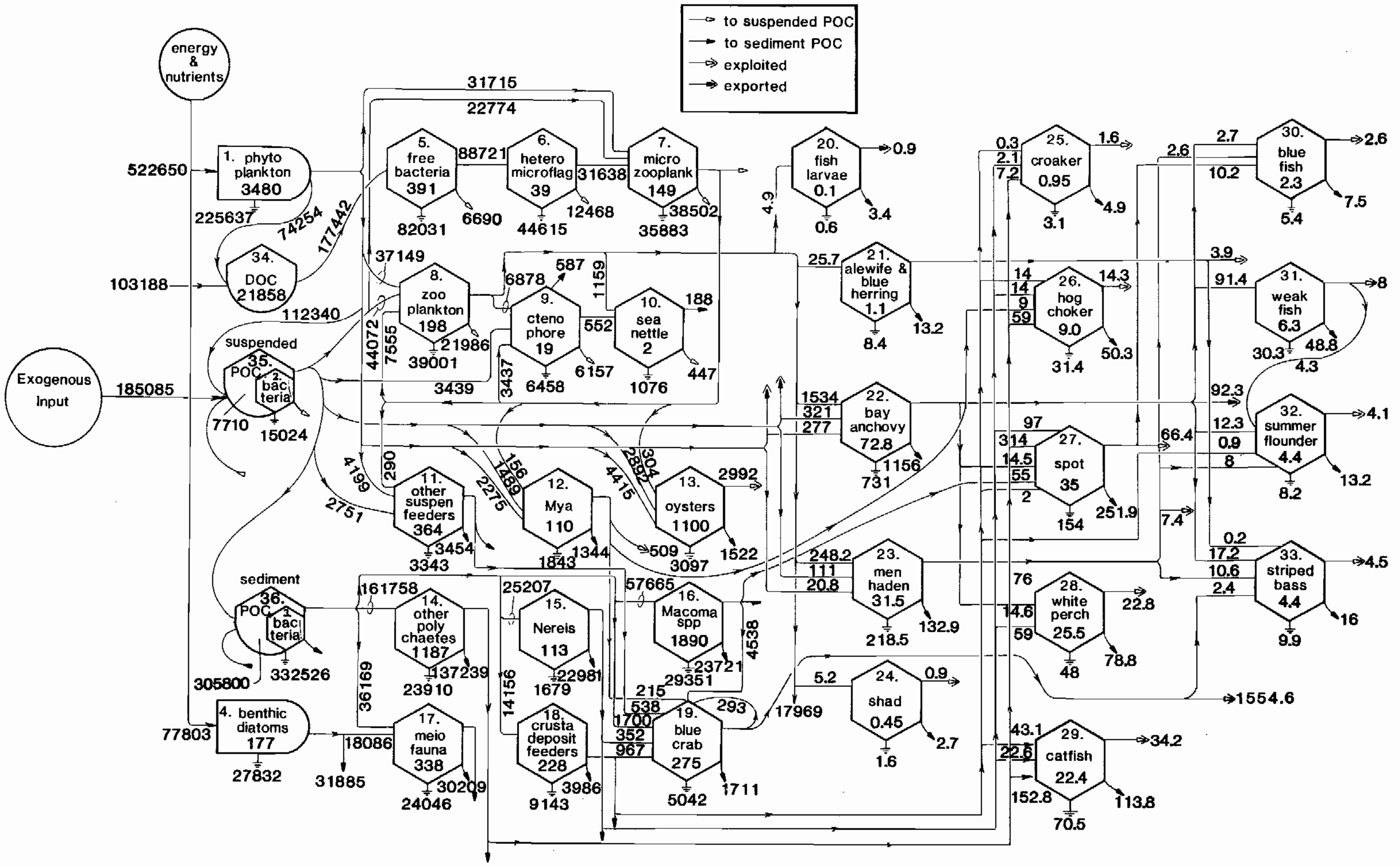

Fig. 1. Schematic representation of the annual carbon flows among the principal components of the Chesapeake mesohaline ecosystem. Standing crops are indicated within the compartments in mgCarbon m^{-2}, and the flows are shown in mgCarbon m^{-2} y^{-1}.

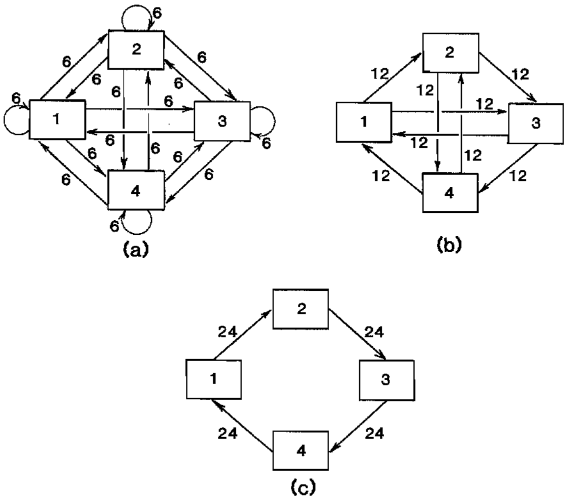

Fig. 2. Three hypothetical, closed networks having identical total system throughputs but differing degrees of articulation. (a) The maximally connected and minimally articulated configuration. (b) An intermediate level of articulation. (c) The maximally articulated configuration.

about whither a quantum of medium will next flow is bound to decrease. Any relative decrease in uncertainty suggests that information theory should provide a useful tool with which to quantify network structure [13].

Information theory deals with changes in probability assignments [16]. The probability that a given quantum of total activity participates in the flow from i to j will be called the joint probability of i and j and is estimated by the quotient T_{ij}/T. The average uncertainty about both the origin and the destination of any arbitrary quantum is then given by the Shannon–Wiener index of uncertainty,

$$H = -K \sum_{i=0}^{n} \sum_{j=1}^{n+2} (T_{ij}/T)\log(T_{ij}/T),$$

where H is called the joint uncertainty,* and K is an unspecified scalar constant.

If the origin of a particular quantum is known, this knowledge reduces the uncertainty about where it will next flow by an amount known as the average mutual information (AMI). It also happens that the drop in uncertainty about the origin of a quantum once its destination is known is identical to the AMI [1]. In either case, the information that accrues from knowing the network topology is given by

$$\mathrm{AMI} = K \sum_{i=0}^{n} \sum_{j=1}^{n+2} (T_{ij}/T)\log[T_{ij}T/(T_iT_j)].$$

That AMI indeed measures the degree of articulation is shown in Fig. 2. All three hypothetical networks exhibit the same amount of total activity ($T = 96$ units in all three cases). Figure 2a shows a minimally articulated network, where knowing the node of origin reveals nothing new (does not decrease the uncertainty) about where any particular quantum will next flow. The associated AMI is identically zero. In Fig. 2b, if the origin of a quantum is known, exactly half of the transition possibilities have been eliminated. (For example, if the particle issues from 2, it can flow to either 3 or 4, but not to 1 or back into 2.) Finally, in the maximally articulated network shown in Fig. 2c, once a quantum's origin is known, its destination is determined. In the last instance, the AMI reaches its maximum theoretical value of $2K$ bits of information. Hence, network development, or an increase in articulation, is characterized by an increase in AMI.

As regards the constant K, the usual practice is to choose a base for the logarithms and set $K = 1$. The resulting measure will have mathematical dimensions such as bits, nats or hartleys, but will not possess physical dimensions. Tribus and McIrvine [16] have suggested that K also be used to impart physical dimensions to the information measure of a system. As the flow networks discussed here are gauged by their total system throughputs, that means setting $K = T$. The resulting index is the product of the system's extent times its organizational status. The name 'ascendency' has been given to the scaled quantity, henceforth denoted by A and calculated as

$$A = \sum_{i=0}^{n} \sum_{j=1}^{n+2} T_{ij} \log[T_{ij}T/(T_iT_j)].$$

Any increase in ascendency indicates that the unitary process of growth and development has occurred. Autocatalysis is the major, but not exclusive agent behind a rising ascendency.

Ascendency was not derived in deductive fashion. Rather, it was discovered phenomenologically as an index that characterizes most of the attributes observed in more mature systems. Eugene Odum [10] outlined 24 properties that differentiated mature ecosystems from their earlier, more inchoate antecedents. Each of Odum's characteristics that somehow could be related to flow networks was seen to contribute (in isolation) to an elevated ascendency. The central (and originally the starting) point of this thesis is the principle that 'in the absence of major perturbations, ecosystems tend naturally towards flow configurations of higher ascendency' [17, 19].

Thus, it becomes feasible to attach a value for ascendency to any fully quantified network of ecosystems transfers. It is then possible to compare the maturational status of a given system to any of its

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* A common, but inadvisable practice is to call H the joint *entropy*; however, the term 'entropy' is best left to the realm of thermodynamics.

earlier states in order to draw conclusions about succession or retrogression. Comparisons between different ecosystems are more problematical, but can yield much valuable comparative information [27]. Maturation, however, is not fully described by A alone, and one should resist the temptation to ascribe normative significance to the ascendency. A higher ascendency is not necessarily better, either for the welfare of the ecosystem itself or for those who exploit its natural resources. To achieve a fuller insight into what constitutes a robust ecosystem, it is necessary first to describe the limits to increasing ascendency, i.e. to ecological succession.

CONSTRAINTS ON GROWTH AND DEVELOPMENT

The reasons why ascendency cannot increase without bound become evident when one studies the algebraic properties of the joint uncertainty and the average mutual information. Because the logarithmic function is convex, both of these variables can be proved to be intrinsically non-negative. Furthermore, the joint uncertainty serves as an upper bound on the mutual information [1]. To see what these inequalities imply about growth and development, it is useful to scale the joint uncertainty by T. The scaled uncertainty is thereafter called the 'development capacity', C,

$$C = -T\sum_{i=0}^{n}\sum_{j=1}^{n+2}(T_{ij}/T)\log(T_{ij}/T),$$

and the following inequalities prevail:

$$C \geqslant A \geqslant 0.$$

Because the development capacity serves as an upper bound on the ascendency, any limits to the increase of C apply *a fortiori* to A. The development capacity may be regarded as the product of the total system throughput multiplied by the diversity of the individual flows. Thus, the limits on the product can be viewed in terms of the limits on each factor. Because the exogenous inputs to the system must remain finite, the total system throughput has to converge to a finite value. Although T can be inflated through the recycling of medium, the gain achieved by this route is limited by thermodynamics. Each pass through a node extracts an obligate loss of dissipation. Therefore, the amount remaining in circulation after each transit of the loop must become progressively smaller, and the accumulated flow when summed over the infinite series of cycle passes always converges to a finite limit.

As to the multiplicand in the development capacity, the diversity of a finite total flow can increase either through greater evenness among the individual flows or by finer partitioning into an ever larger number of constituent flows. The diversity of q flows has an absolute upper bound, $\log(q)$, which implies that any gains made by homogenizing the magnitudes of a fixed number of flows remains bounded [1]. However, the second factor could increase without limit if it were possible to partition the total flow ever more finely into an always increasing number of flows, q. As q approaches n^2 this would require that the system compartments likewise be divided into a larger number of nodes. At some point (usually well before q approaches n^2) many of the flows (and compartments), growing ever-smaller by successive divisions, will become vulnerable to chance extinction by the always-present exogenous perturbations. Thus, one concludes that the ultimate limits to increasing C reside in the finitude of resource inputs and the rigors of the environment.

Even if C should come to stasis, the ascendency could temporarily continue to increase as it closes upon its upper limit C. The non-negative difference, $C-A$, is called the 'systems overhead' and is represented here by θ. The development capacity represents an upper potential, but not all of that potential can be manifested as coherent, articulated structure (as measured by A). Real systems are always restrained from reaching their full potential by a variety of encumbering causes that are represented by the overhead, θ.

Overhead can be decomposed into four terms, each of which corresponds to a source of encumbrance:

$$\theta_0 = -\sum_{j=1}^{n} T_{0j}\log[T_{0j}^2/T_0T'_j]$$

$$\theta_E = -\sum_{i=1}^{n} T_{i,n+1}\log[T_{i,n+1}^2/T_iT'_{n+1}]$$

$$\theta_s = -\sum_{i=1}^{n} T_{i,n+2}\log[T_{i,n+2}^2/T_iT'_{n+2}]$$

$$\theta_I = -\sum_{i=1}^{n}\sum_{j=1}^{n} T_{ij}\log[T_{ij}^2/T_iT'_j].$$

By describing anything that might prevent each term from reaching zero, one is thereby evaluating the nature of the constraints on increasing growth and development.

The first term is said to be generated by the exogenous inputs in the sense that these flows multiply each logarithmic term in the summation. That is, should the T_{0i} be zero, θ_0 would vanish. θ_0 could be minimized either by decreasing the magnitudes of the inputs, or by consolidating the same amount of input into fewer sources. Decreasing the magnitudes of the inputs pointedly jeopardizes the system, however decreasing the relative amounts that each component receives from the outside is feasible to a degree. Systems are often observed to develop ways that minimize their dependence upon imported resources. Developing communities also tend to focus upon those sources that are most accessible or least costly. The danger in relying on too few sources is that the system becomes increasingly vulnerable to disruptions in those remaining. There is reliability in redundancy, but there is also cost for multiplicity. The evolution of developing systems naturally involves balancing the costs against the risks.

The next two terms are generated by export and dissipation terms, respectively. θ_E, which elsewhere has been called 'tribute' [17], can be reduced by minimizing the exports to other systems. Any export that is not connected back to the system's inputs via some autocatalytic loop at a higher hierarchical level becomes a candidate for elimination. However, if positive feedback does occur between some exports and the system imports, then reducing those exports below an unspecified non-zero threshold will become counterproductive. Some tribute may be necessary to maintain the environment (context) from which the given system derives its sustenance.

Because the second law of thermodynamics mandates a loss at each pass through a node, the dissipation from any real system, θ_s, will always exceed zero. However, not all of this cost is spent in vain, as some goes towards maintaining the structural integrity of lower hierarchical levels. For example, the metabolic heat given off by an organism results from numerous physiological processes at the cellular and organ levels that serve to keep the body in a functional state. Most of the dissipation goes to maintain the system's infrastructure.

Finally, θ_I reflects the average redundancy of pathways between any two arbitrary nodes. As argued above, development naturally favors more efficient pathways at the expense of other, less effective routes. However, just as there is danger in a system that relies upon too few imports, whenever elements become too sparsely connected with each other, their sustenance grows vulnerable to disruption along the few remaining channels. Pathway redundancy provides potentially compensating routes over which medium can flow whenever the primary, more efficient lines are disrupted. Internal redundancy affords a system-level strength-in-reserve.

It should now be clear why the effort was made to distinguish between useful and dissipative exports. The last three overhead terms are seen to represent the payments required of the system to maintain conditions propitious to itself above, below and at the focal level, respectively. The encumbrances proper to each element of Salthe's fundamental triad are thereby explicitly delimited.

ANCILLARY ANALYSES

While evidence favoring the existence of formal causality in ecosystems appears mostly in the behavior of the system-level indices just discussed, there are other analyses of ecosystem structure that help further to elucidate how the system functions as a unit. The first method was intended to quantify non-proximate causalities in economic and ecological systems. 'Input–output (I–O) analysis' employs matrix algebra to estimate both the direct and indirect influences that any member of the system exerts upon any other element over *all* existing pathways of sequential exchanges [6, 12, 15]. I–O analysis had been limited to the propagation of material causes when viewed from either the input or the output directions; however, the methods have recently been extended to encompass both positive and negative trophic impacts in either direction [22]. The expanded analysis is particularly useful for identifying autocatalytic configurations of trophic interactions.

Creating an exhaustive list of directed cycles in a network is no trivial task. It entails a systematic search procedure that can grow to exponential proportions. Fortunately, most ecological networks are sparsely coupled, so that the task remains within reasonable bounds. Elsewhere, the author has outlined a backtracking algorithm effective in identifying all the simple directed cycles in a network [18]. Furthermore, it is feasible to remove the identified recycle loops from their supporting tree-like configuration of dissipative flows. In other words, *a propos* the autonomy of autocatalytic loops, it is now possible to separate any real, weighted network of flows into an (imaginary) autonomous graph of purely recycled flows on one hand and a strictly non-autonomous acyclic tree of dissipative exchanges on the other.

Finally, a variation of I–O analysis has been developed that permits one to map a complicated web of feeding interactions into a concatenated Lindeman chain of trophic interactions [20, 21]. As Lindeman originally had intended, this chain or pyramid is co-joined with the pathways of recycle through passive abiotic (detrital) compartments. By mapping arbitrary ecosystem networks into a standard topological format it becomes possible to compare the underlying trophic-dynamics of widely disparate ecosystems.

CONCLUDING REMARKS

In response to the post-Newtonian focus in physics upon material and mechanical causalities, biologists have sought to restrict explanations of life processes to only proximate interactions. At the time these strictures on biology evolved, they were not difficult to defend, absent of any convincing framework for treating non-proximate, non-mechanical agencies. However, recent advances in systems research (by no means limited to the methods described in this paper) now provide the conceptual foundations upon which to build a new view of the natural world, and of the phenomenon of life in particular.

Excuses for continuing to restrict the narration of evolution to the interactions between individual organisms and their physical environments are becoming increasingly difficult to defend. The evolution of scientific narration, like that of the natural world itself, does not long suffer ideological barriers. Nor should the demise of long-held prohibitions necessarily be grounds for fear. Like relinquishing an axiom from Euclidian geometry, a less-rigid set of assumptions can initiate new growth and development in human thinking.

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