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On Quantifying the Effects of Formal and Final Causes in Ecosystem Development

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Abstract

In physics and in traditional biology it has sufficed until now to describe phenomena as the results of purely material or efficient causes. However, a growing number of biologists and philosophers think that a satisfactory description of biological development must also include reference to what Aristotle labeled formal and final (or teleonomic, sensu Mayr) causation. A measure called the network ascendency has been defined to track the changes in the system that result from positive feedback acting as an endogenous formal cause of system development. In turn, positive feedback appears to exert a selection pressure reminiscent of teleonomic final cause upon each of its constituent elements.

Associating development with the increase of network ascendency permits the modelling of final cause using the powerful modern tools of mathematical optimization. Cheung and Goldman have developed an algorithm to find a reconfiguration of any given starting network that locally optimizes its network ascendency. Typically, the optimal configuration, as demonstrated by two simple examples, is a "one-tree", that is, a single, directed cycle adjoined to a tree. Studying the differences between the observed and the optimal networks yields insights into the particular constraints acting on the system and reveals the most efficient pathways through the network.

Introduction

Ecodynamics, as conceived by Kenneth Boulding (1978), is a highly complex subject involving numerous new and unique features. But the name itself is not evocative of just how different ecological phenomena are from those included in classical dynamics. However, such inadequacy of name is quite understandable. As the late media analyst Marshall McLuhan (1973) was wont to point out, when faced with the radically new, we are often numbed into seeing the new in the guise of the familiar. For example, the name "quantum

mechanics" stresses the formal, almost superficial connections of that field to its precursor, classical mechanics. The title tends to obscure the fact that the actual phenomena treated in both fields radically differ in qualitative and fundamental ways.

Exactly how does ecodynamics differ from the more familiar realm of classical dynamics? After all, is not significant effort now being expended in creating models of ecosystem behavior consisting of sets of coupled first-order differential equations—much as one would simulate chemical kinetics? Why is there any reason not to believe that such "mechanical" portrayals of ecodynamics will eventually predict ecosystem changes?

The answers to these questions are largely matters of experience. The recent observation is that such mechanical treatments of ecodynamics simply don't work very well, if at all. While there have been moderate successes in treating single ecological processes or populations in this manner, most projects seeking to simulate numerous coupled processes (such as comprise full ecosystems) have left much to be desired (Platt et al., 1981). It is tempting to ascribe the deficiencies of mechanical models to inadequate precision in the mathematical specifications of component processes. However, recent advances in classical mechanics (see Schaffer, this volume) indicate that ever-greater precision may not be the panacea for conventional modelling.

The reason why mechanical models remain inadequate for portraying ecodynamics may be that ecological succession and evolution are the results of causes that are not wholly mechanical in nature. It behooves us, therefore, to re-examine the nature of causality in scientific description.

The strictly mechanical, or newtonian view of the world identifies only material and proximate, or efficient causes. (Newton himself maintained a world-view that was quite unorthodox by the standards of his intellectual heirs, but that is another story.) During the Enlightenment, when the idea of the universe as a "cosmological clockwork" was at its zenith, to call someone a mechanic was one of the highest accolades one could bestow. Society, organisms and governments were perceived as machines, and one finds a substantial influence of this metaphor upon the leaders of the American Revolution (Wills, 1978).

Erosion of the clockwork image began early in the nineteenth century with the formulation of the second law of thermodynamics, i.e., the quantification of irreversibility in nature. The development of quantum mechanics later served to encourage a stochastic picture of the microscopic world. One is tempted to add the accidental to the list of natural causes, were it not for the fact that any particular manifestation of an accident can be described in

terms of its material and efficient agents. Early attempts by the philosophers of biology to amend the clockwork image as it pertained to living organisms met with disaster. Vitalism and teleology, two patently non-mechanical views of the living world, were soundly rejected--in part for their lack of supporting evidence but also because of the distaste that contemporary biologists then bore for the theological extrapolations many drew from these theories. Darwin's exposition of evolutionary change survived for numerous reasons, not the least among them his determination to remain within the bounds of proximate causality. The physicist's awakening to stochastic influence passed without much resistance into biology, and the final piece of the neo-Darwinian synthesis appeared less than 40 years ago with the identification of the material locus (cause) of heredity at the biomolecular level. Thus, the entire framework of the accepted view of evolution rests within the confines of mechanical causality, and reverberations from the earlier rejections of non-mechanical hypotheses still pose substantial professional risks to anyone who would venture beyond those limits.

Such considerations notwithstanding, the modern synthesis of evolution presumes that the dynamics of heredity and change occur against a backdrop called the environment, which for explanatory purposes is taken as given and, once specified, remains outside the scope of discussion. Several decades ago, when the neo-Darwinian synthesis precipitated, insufficient mathematical and descriptive tools were available to address adequately the context within which the evolutionary game was played. There was then little reason to question the adumbrated role assigned to the environment. But today, with recent advances in the theories of cybernetics, hierarchies, information and networks, little excuse remains not to consider the interplay between organism and environment, and the study of that interrelationship is called "ecology". However, in the process of fully incorporating the environment into discussion, it becomes difficult to describe reality in strictly mechanical terms.

Aristotlean Causalities

Rather than engage in radical speculation concerning the nature of non-mechanical causality, it is useful first to reconsider older models of how events occur. In particular, Aristotle's organismic view of nature seems appropriate to the subject of evolutionary change (Rosen, 1985). Aristotle recognized that the causes of a phenomenon were not always simple, and he proposed four types of cause that potentially could contribute to a single event: (1) material, (2) efficient, (3) formal and (4) final. The textbook

example of an event is the building of a house. The material cause is obviously the bricks, mortar, lumber, etc. that go into the structure. The laborers who assemble the materials act as the efficient cause. The formal cause is usually taken to be the blueprints, or bauplan used by the laborers, and the final cause resides in the need for shelter by its eventual occupants.

With the overwhelming emphasis that newtonian science has placed upon the first two categories of causation, the perceived significance of the latter pair has atrophied. However, with the narrative powers afforded by modern cybernetics and hierarchy theory, it is now possible to entertain formal cause in a natural and rational manner. Even more importantly, recent progress in network analysis and information theory now encourages attempts to quantify and measure at least the effects of formal and final causality in evolving systems.

Formal Cause

A significant (but not exclusive) example of formal cause is the positive feedback loop. In its ideal form one can imagine positive feedback as a ring of processes or entities wherein the activity of each member positively catalyzes the activity of the next element in one direction around the loop until the last member catalyzes the first. Thus, each member in the loop engages in some degree of autocatalysis. It is not widely appreciated that positive feedback possesses at least six important characteristics:

In the ideal case, when the only causal links are those which form the chain, the system appears as a wholly (1) autonomous structure. Of course, no real causal structure is wholly autonomous, and any actual feedback loop always appears as a substructure embedded within a larger network of causalities, at least some of which must relate to the external world (cf, Goedel, 1931). Although this contingent nature of feedback serves to diminish its autonomy, it cannot be said to eliminate it. As any student of non-linear systems will recognize, systems with internal feedback are often less responsive to changes in their boundary conditions. Some particular nonlinear systems are even capable of generating output with no given input. In order to better identify the automonous elements in a causal network, it is helpful if the linkages can be quantified in some way (see below). Then algorithms exist that can separate the feedback loops from their associated tree of unidirectional causalities (Ulanowicz, 1983).

It is not difficult to explain how one can perceive the autonomy of positive feedback as an (2) emergent property of a system. If one defines the system so that only some of the elements of a particular loop are included,

then that subset of elements will appear to function in strictly non-autonomous fashion at the behest of the boundary conditions driving them. However, once the system boundary is enlarged to include all the members of the feedback cycle, autonomy then "emerges" as a new attribute of the expanded system.

In response to stochastic influences on a system, positive feedback can serve to generate (3) selection pressure upon its composite members. This is because any accidental change in the properties of a loop element that abets its action upon the next member will be reflected positively upon itself (rewarded). Conversely, stochastic changes which diminish catalytic activity are self-inhibiting. Such selection pressure can act not only to change the attributes of a component, but it can also replace members by others that contribute more effectively to the positive feedback. For example, if a more efficient catalytic element should accidentally appear connecting any two nonsequential components, it will reinforce its own activity to the eventual exclusion of those less effective loop members it bypasses. This potential ability to replace components creates an extremely intriguing possibility. By induction, one can imagine a situation where all the original members of a loop have been replaced in turn by a new suite of elements. That is, the functional loop is seen to persist beyond the durations of all its individual components. One often observes, for example, that the cellular and material constituents of a complex organism are totally replaced over the lifetime of the organism, which nonetheless maintains its same basic structure over the longer interval. It is important to note that the context provided by the feedback cycle at any instant plays an active role in influencing what any next replacement parts might be. Not every arbitrary change is incorporated into the developing structure.

In particular, one of the attributes of a loop element subject to positive selection is its ability to bring external resources into the cycle. Hence, one effect of positive feedback can be to draw progressively more medium into the loop. In a system with fixed or diminishing resources available, this self-aggrandizing tendency will have the unavoidable consequence of (4) inducing competition among the various loops present in the system. The net effect of such competition is the tendency during the latter stages of system development towards a more highly articulated topology of network flows, wherein those pathways and loops with more efficient overall transfers would grow at the expense of less effective routes. The ultimate outcome of progressive articulation, if it were allowed to persist without mitigation, would be for a single loop to win out; that is, the resulting

network configuration would be a "one-tree",or a causal tree with but a single cycle.

A typical extensive effect of feedback self-aggrandizement, and of positive feedback more generally, is to increase the level of total system activity, i.e., (5) growth enhancement.

Finally, it should be noted that positive feedback is inherently (6) formal in nature in that it is defined as a relational structure of the processes comprising it.

System Ascendency

Properties 1, 3, 4 and 5 enumerated above strongly suggest that positive feedback possesses agency. More specifically, it is a formal agent working at the level of the whole system to augment system activity and to streamline and make more efficient the associated network topology. With the qualitative nature of positive feedback as a formal agent now evident, it becomes fruitful to shift attention to quantifying its effects on the process of the "growth and development" of an evolving system.

In order to keep the discussion focused upon palpable entities, it is useful at this point to confine further discussion of species interactions to material causalities, i.e., the exchanges of materials or energy that transpire within an ecosystem. One must decide upon a particular medium to follow (e.g., energy, carbon, nitrogen, etc.);this restriction to a single medium is an artifact of the present stage of the research being reported. After numbering the elements of the system in some fashion, the flow of medium from species i to population j (if possible) can be denoted as T_{ij}, with i and j taking on values from 1 to n, the number of nodes in the network. Exogenous inputs will be presumed to flow from a fictitious compartment 0 (zero), so that T_{oi} will represent the external input to compartment i. Likewise, the fictitious compartments n+1 and n+2 will be assumed to receive the usable exports and the products of dissipation, respectively.

The level of activity in each compartment can be measured either by the total amount flowing out of it,

$$T_i = \sum_{j=0}^{n} T_{ij} , \qquad (1)$$

or by the aggregate entering it,

$$T_i' = \sum_{j=1}^{n+2} T_{ji} . \qquad (2)$$

These two measures are equivalent only when the system is at steady-state. Even if the system is not in balance, its unique measure of total activity is

$$T = \sum_{i=0}^{n} T_i = \sum_{i=1}^{n+2} T_i' , \qquad (3)$$

and is referred to as the total systems throughput. Growth in its purely extensive manifestation would translate as an increase in T.

"Development" refers predominantly to intensive characteristics of the network and will be taken here to mean an increase in articulation, or organization of the flow structure. The more articulated a network becomes, the less uncertain one is about the destination of a quantum leaving a particular compartment. Information theory provides the appropriate calculus to quantify uncertainty. The apriori uncertainty about the direction of a quantum leaving a particular compartment, when averaged over all compartments in the system, is captured by the Shannon-Wiener index of uncertainty

$$H = -K \sum_{i=0}^{n} p_i \log p_i, \qquad (4)$$

where p_i is the probability that the quantum is leaving compartment i.

Knowing the (conditional) probabilities of which compartment will receive the flow from i reduces one's initial uncertainty by an amount known in information theory as the "average mutual information" (McElice, 1977),

$$AMI = K \sum_{i=0}^{n} \sum_{j=1}^{n+2} p_{ij} \log [p_{ij}/p_i p_j'], \qquad (5)$$

where p_{ij} represents the joint probability that a quantum both leaves i and enters j, and p_j' is the probability that a quantum enters compartment j.

From the observed flows and their aggregates one can construct convenient estimators for the various probabilities in equations 4 and 5. The estimate for the probability that a quantum leaves node i (p_i) is T_i/T; that it enters j (p_j'), T_j'/T; that it both leaves i and enters j (p_{ij}), T_{ij}. As for the unspecified scalar, K, Tribus and McIrvine (1971) suggest that it be used to impart physical dimensions to the information measures, i.e., to scale it in the literal sense of the word. The appropriate size of a flow network is its total activity, T. Making these various substitutions into equation (5) yields a scaled quantity called the network ascendency (Ulanowicz, 1980),

$$A = T \sum_{i=0}^{n} \sum_{j=1}^{n+2} (T_{ij}/T) \log [T_{ij}T/T_i T_j'] \qquad (6)$$

The ascendency has the dimensions of the constituent flows multiplied by the informational units specified by the base used to calculate the logarithms. For example, if the medium in question is energy and the base of the logarithms is 2, the ascendency has the units "power-bits". Ascendency is the product of an extensive factor (the "size", T) times an intensive factor that gauges the articulation of the network (the double summand). Figure 1 shows how the latter factor expresses the network articulation. All three hypothetical networks shown have the same total throughput (96 units) and differ only in their visible degrees of articulation, which are reflected in their respective values of ascendency.

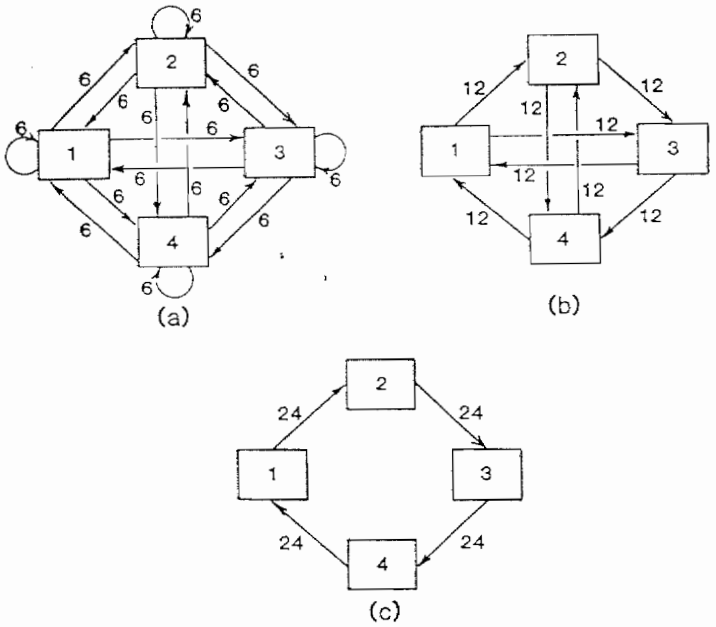

Figure 1: Three hypothetical configurations of 96 arbitrary units of flow among 4 compartments. (a) No articulation—ascendency is identically zero. (b) Moderate articulation—A=96 bits. (c) Maximal articulation—A=192 bits.

Because positive feedback tends to increase both factors in the ascendency, a rise in that measure can be said to quantify the effects of feedback as a formal agent imparting structure to evolving systems. Of course, other agents or accidental influences might also contribute to a rise in the observed ascendency, which serves as a phenomenological indicator in its own right. In fact, ascendency first appeared as a purely phenomenological quantity that unified most of Eugene Odum's (1969) 24 characteristics of "mature" ecosystems (Ulanowicz, 1980). The unifying power of this variable suggests the following ecological principle: *In the absence of major disturbances ecosystems naturally tend in the direction of increasing network ascendency.* Because this principle has been formulated from only the most general properties of ecosystems, it is likely to be applicable also to other evolving systems, such as one encounters in economics, sociology, and developmental biology.

Limits to Development

The proclivity of living systems to increase their ascendencies is only one half of the development story. Opposing this drive towards organization and efficiency is a host of countervailing entropic, or disorganizing effects.

Fortunately, these effects can be quantified in much the same way as was the ascendency. When the same probability estimators that were used to derive equation (6) are substituted into equation (4), another attribute called the development capacity,

$$C = -T \sum_{i=0}^{n} (T_i/T)\log(T_i/T), \qquad (7)$$

results. It can be readily demonstrated that this capacity always serves as an upper bound on the ascendency, that is,

$$C \geqslant A \geqslant 0. \qquad (8)$$

Therefore, specifying the limits on C will simultaneously elucidate some of the constraints on increasing A.

Equation (7) reveals that, like the ascendency, the capacity also consists of the product of an extensive factor (T) times an intensive index (the Shannon-Wiener index of uncertainty calculated using the of flow outputs). Now, the total systems throughput is limited by the rates at which resources are made available to the system. Although a given rate of supply can underwrite progressively more activity, as medium is more tightly retained and recycled within the system, the second law of thermodynamics still extracts a loss from each successive transfer, thus guaranteeing that the increase in T will have a finite limit. Despite the limit on T, the system capacity might still rise by dividing into ever-finer and more numerous compartments, which process drives up the second factor in the capacity (the Shannon-Wiener index). But the partition of a finite activity into sufficiently many components insures that eventually some of those components will become vanishingly small and subject to chance extinction by prevailing perturbations.

Even after the rise in C has somehow been arrested, the ascendency may still continue to increase by minimizing the difference between itself and its limit, C. This amount, C-A, is called the system overhead, and may be algebraically decomposed into 4 separate terms. Three of the overhead elements are generated by the exogenous transfers, while the remaining term represents the average redundancy in the number of pathways connecting any two arbitrary nodes. Not all of the overhead can be expended to create ascendency, however. Much of it stands as the system's "strength-in-reserve" with which to maintain structure in the face of unexpected perturbations. The hierarchical, thermodynamic and environmental interplay between ascendency and overhead is a long and interesting story that is developed more fully in Ulanowicz (1986).

Ascendency and Final Cause

Little mention has been made thus far of final cause. But the distinction between final, formal and efficient causes is sometimes mostly a matter of scale. For example, it has been argued earlier how a feedback loop visible at the system level (i.e., identifiable in the representative network) can act as a formal cause. However, another loop acting at a much smaller scale (i.e., incorporated into a single node) would probably be classified as an efficient cause. Conversely, if some of the pathways in the observed system constitute links in a feedback loop that lies partially outside the given system (that is, the entire loop exists only at a higher level), then its agency will be exercised upon the system in question via the driving boundary conditions. It appears as an agent exerting its influence in the guise of a final cause acting on the object being studied from above and beyond.

In particular, a population within an ecosystem interacts with its environment. The biotic portion of that interaction is expressed in terms of its connections with the other members of the system. But we have already suggested that this biotic context seen by the population is itself evolving at the level of the whole system according to the principle of increasing ascendency. Therefore, one may interpret the agency behind increasing ascendency as a final cause affecting the given population. This is not a trivial shift in perspective. Heretofore, any processes inherent in the development of a population or a species have, by default, always been referred towards events and mechanisms at lower levels of the hierarchy. But now the possibility also exists to interpret evolutionary developments as responses to active agencies existing at higher hierarchical levels. Some will immediately object to this last statement as being rife with teleology and goal-seeking. However, those who object to teleological overtones are encouraged to read Mayr's (1974) apology for "teleonomic" behavior as a legitimate concern of biology. Furthermore, as shall presently become clear, any goal that might serve as an attractor for system ascendency is hardly immutable, but rather is nonunique, transitory and constantly changing as the system develops (see Allen, this volume).

The mathematical tools with which one studies how systems approach goals constitute the realm of optimization theory. In this discipline one typically begins with a mathematical description of the system under study and then uses elements of this description to define some quantitative system attribute to be optimized (the objective function.) A state of the system is sought that

optimizes the value of the objective function subject to a specified set of constraints on the system variables. The actual mechanics of how to find the optimal states are manifold. If both the objective function and the system constraints are all linear in nature, then the global optimum can be determined in routine algorithmic fashion. The introduction of nonlinearities anywhere into the problem can seriously confound the solution. Sometimes when the nonlinear objective function possesses "regularizing" (smooth) properties, such as uniform concavity or convexity, analytical techniques (or at least efficient numerical techniques) can be applied.

In this paper ecosystems are quantified in terms of their intercompartmental transfers. The system ascendency serves as the nonlinear objective function, and mass balances around each species compartment, along with nonnegativity requirements on the flows, comprise the constraint set. Optimizing such systems is problematical on several fronts. Firstly, the ascendency is neither uniformly concave nor convex over the entire range of allowed flows. The situation is not hopeless, however, in that it is possible to hierarchically decompose the ascendency into three terms, each of which behaves uniformly in either convex or concave fashion (Cheung, 1985a). In general, even the mass balance constraints are nonlinear without the rather restrictive assumption that dissipations and exports remain fixed fractions of their corresponding throughputs (T_i's), as will be assumed here. To deal with these difficulties Cheung (1985b) and Goldman have written an algorithm that proceeds by successive linear approximations, adapting generalized network techniques (Kennington and Helgason, 1980) to solve at each stage the resulting "minimum-cost flow in a network with gains" problem.

As is often the case with nonlinear optimizations, the solution process does not necessarily converge upon a global optimum. Instead, the process takes the system to a local optimum relatively nearby the starting configuration. Beginning with a different network configuration will often result in the system approaching another local optimum. Although the existence of multiple local optima tends to detract from the definitiveness of the optimization, it adds realism to this mathematical representation of the development process. As Holling (1973) pointed out, ecosystems are unlikely to possess a single climax state, but rather are characterized by a multiplicity of adjoining domains of local attraction. It was noted earlier how the increase in system ascendency can result through the progressive dominance of one or a few feedback loops, and it seems a plausible speculation that each of the local regions of attraction corresponds to an ascendant loop. This identification accords with the observation of Richardson (1984), that in

economic and social systems "'structural change' is usually little more than a term used to cover unexplainable behavior... We might better speak of shifting loop dominance,...the process by which control of a system moves from one set of feedback loops to another set, often with dramatic changes in behavior."

Two examples of the application of the optimal ascendency algorithm are presented here. The first involves the familiar Cone Spring network (Tilly, 1968). As shown in Figure 2a, this simple lotic system is depicted as a simple network of transfers among 5 functional compartments. The key element is the detritus, which allows for five separate pathways of recycle (Ulanowicz, 1983). All flows are in Kcal $m^{-2}y^{-1}$, and the ascendency of this configuration is 56,725 kcal-bits $m^{-2}y^{-1}$. The nearby local optimum is the one-tree shown in Figure 2b, and it possesses an ascendency of 64,291 kcal-bits $m^{-2}y^{-1}$. One is immediately faced with the question of how to interpret the local optimum. Invariably, the optima resulting from maximizing the ascendency will possess unrealistic features. For example, it is clearly impossible for detritivores to consume only bacteria, as shown in the figure.

Configurations of maximal ascendency are virtually never realized, because well before the system can reach such a state, perturbations or other constraints intervene to slow or rescind progress towards higher efficiencies. In fact, Figure 2a was already the result of a natural standoff between those tendencies towards efficiency and those in the direction of chaos. Unless the algorithm leaves such a climax input unchanged, the result is bound to deviate from reality, because the set of mathematical constraints used is always a gross simplification of those actually limiting the system.

Further steps in this program will, of course, include refining and expanding the constraints to better approximate the real system limits. (We emphasize that such normal scientific steps, of successive testing and improving the theory, are made possible here only through the embodiment of each stage of that theory in an explicit mathematical model with an operational optimization algorithm to generate its "predictions".) Such a project would significantly deepen one's understanding of the community dynamics. However, even before going to such lengths it is possible to gain useful insights into the particular system dynamics (and sometimes to learn about ecosystems in general) by carefully studying how the local optimum differs from the observed network. One need only remember that a nearby optimum represents how the system might reconfigure if many of its natural constraints were released. The optimum emphasizes the most efficient pathways available among the components, assuming that each element maintains a constant rate of respiratory loss for each unit of throughput.

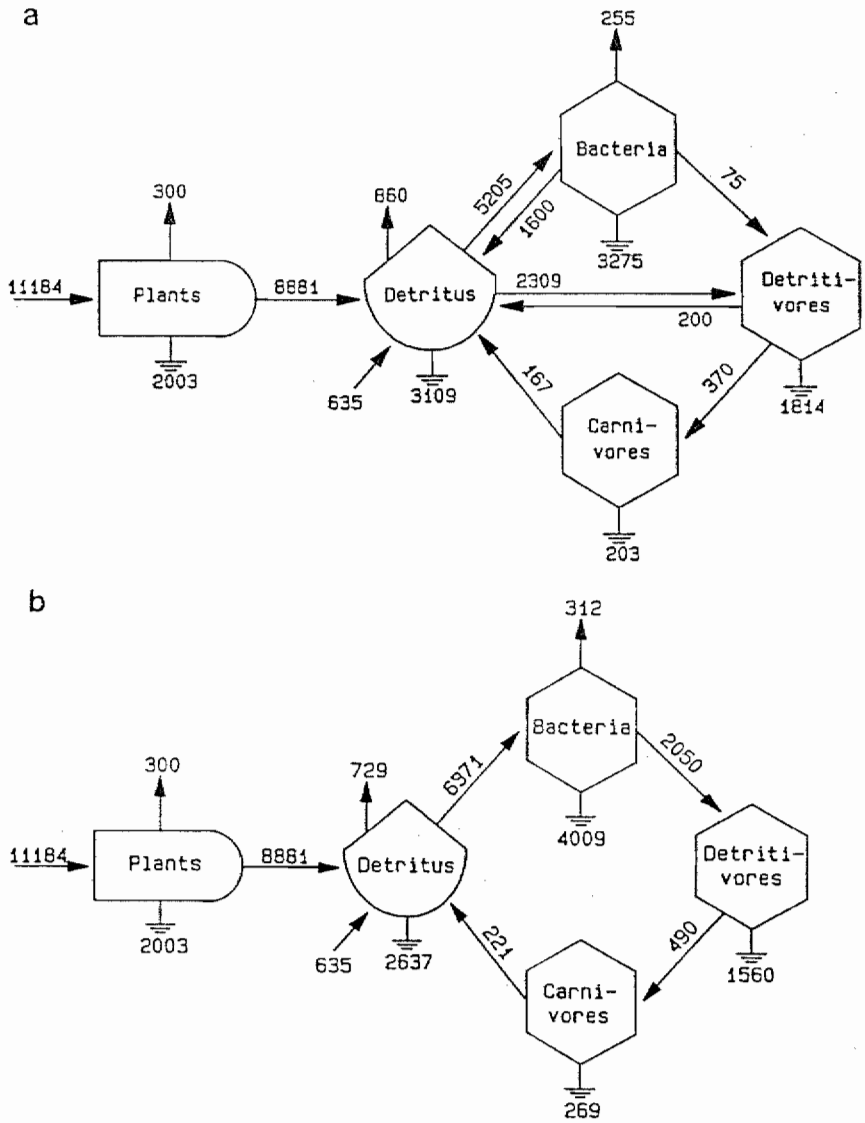

Figure 2: (a) Energy flow among the 5 functional compartments of the Cone Spring ecosystem according to Tilly (1968). Flows are in Kcal $m^{-2}y^{-1}$. A=56 725 Kcal-bits $m^{-2}y^{-1}$. (b) Optimal reconfiguration of flows in (a) maintaining constant respiration rates. A=64 291 Kcal-bits $m^{-2}y^{-1}$.

One notes that the role of the carnivores is hardly changed in the optimal configuration—save that slightly more energy passes through that component. The major difference in the optimal network is the rerouting of all the detrital carbon through the bacteria before it reaches the detritivores. Other things being equal, detritivores certainly would grow

more efficiently on a diet of pure bacteria. However, such a feeding strategy would require that the detritivores separate the bacteria from the detritus to which these microorganisms are attached. In a thermodynamic sense, this separation would entail considerable work on the part of the detritivores (Cousins, 1985), and such overhead would probably be expressed as a higher rate of dissipation by these feeders (assumed constant in this optimization). One notes secondarily that the losses to detritus from the bacteria and the detritivores have disappeared in the optimal network. All indications point towards thermodynamic limitations related to particle size, dispersal and adhesion that all converge to make detritivory a "sloppy" process in comparison to predator-prey interactions.

This conclusion is underscored by the results from a second optimization. Figure 3a shows the transfers among the seven major functional units (in mg $Cm^{-2}d^{-1}$) of a tidal marsh gut in Crystal River, Florida (Homer and Kemp, unpublished; Hirata and Ulanowicz, 1985). The adjacent optimal configuration is shown in Figure 3b. As expected, the network is a one-tree (albeit a degenerate one). The pelagic grazing chain appears to be more efficient than the parallel benthic route, dependent as the latter is upon inefficient detritivory. The relative efficiency of the grazing chain over that of the detrital pathway has also been observed by Wulff and Ulanowicz (1988), and is possibly a general feature of aquatic and marine ecosystems. In oligotrophic, or low productivity systems, the grazing chain is usually dominant; but as productivity increases beyond the capacity of the herbivores to crop the additional production, the less efficient detrital pathways become more prominent.

(The careful reader may have noticed that the link from detritus to microphytes in Figure 3b did not exist in the starting network. The appearance of this new connection was because the optimization routine allows one to specify at the outset a number of links that are not present in the initial graph but which might appear under subsequent development. If this particular and somewhat problematical process had not been included as a potential transfer, the optimal configuration would have resembled that given in Figure 3b, except that the detritus would have fed into the pelagic herbivores.)

Thus, an optimal network can be considered as a virtual state towards which the observed system would tend, if existing, but unspecified constraints were relaxed. Conversely, those pathways present in the observed system but missing from the optimal configuration are those less efficient processes likely to diminish if the environment should become less erratic.

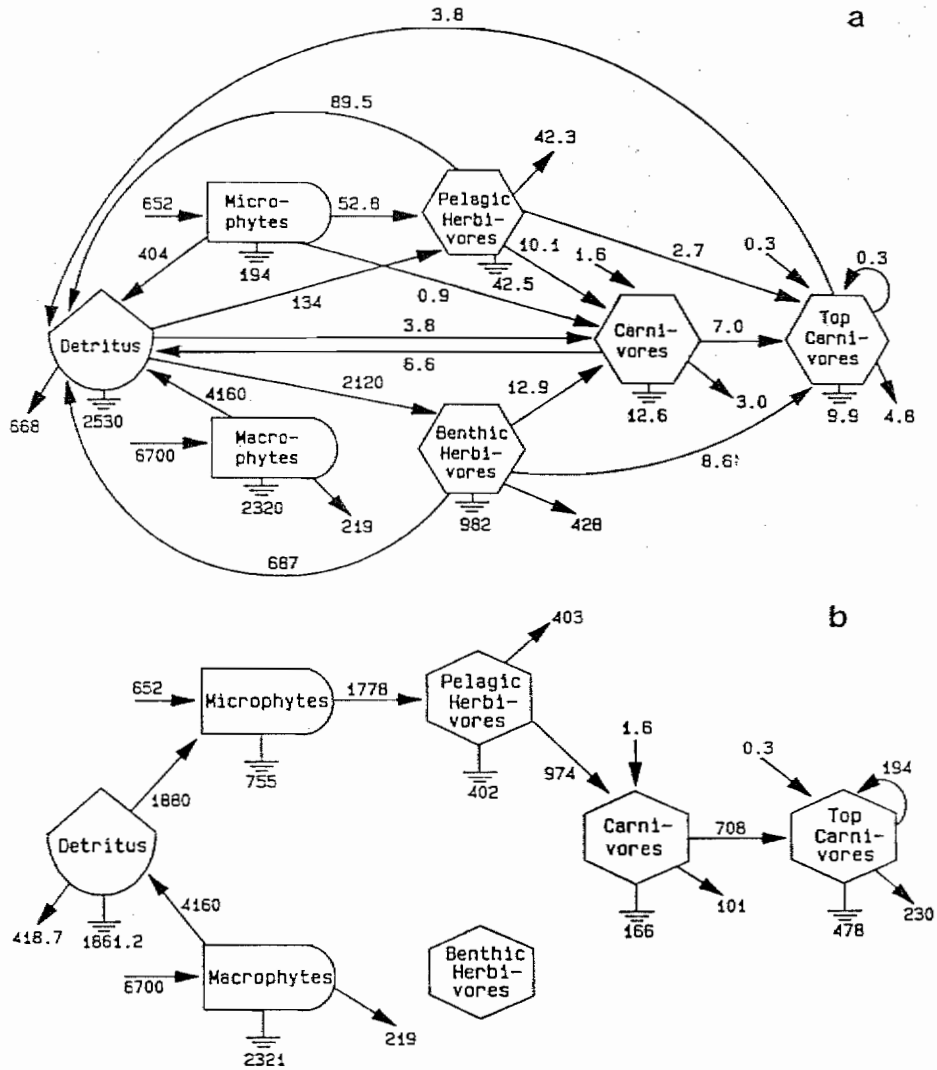

Figure 3: (a) Carbon flow among the seven major functional compartments of a Crystal River, Florida march gut according to Hirata and Ulanowicz (1985). Flows are in mg Carbon $m^{-2}d^{-1}$. A=28 279 mg C-bits $m^{-1}d^{-1}$. (b) Reconfiguration of (a) yielding locally maximal value of ascendency. A=41 163 mg C-bits $m^{-2}d^{-1}$.

Conclusions

While ecosystems remain contingent upon lower-level biological phenomena, their dynamical structures are not entirely determined by such smaller-scale events. The structure of ecosystems derives in part from formal agencies that

can be described and quantified only at larger scales. Conversely, the fate of particular ecosystem elements will be influenced by mechanisms not included in the neo-Darwinian scheme of evolutionary change. How well a particular population fares is also a matter of how well it fits into the larger context of ecosystem trophic relationships, and we can now aim to quantify the influences of the whole community upon single species through the use of network, information and optimization theories.

The realm of ecodynamics transcends the scope of classical dynamics, and a more thorough quantification of such complex behavior is almost certain to lead to a deeper understanding of the living world and possibly to significant new insights into the related fields of economics, sociology and developmental biology.

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