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On the nature of ecodynamics

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Abstract

Conventional physics is of little help in describing how ecosystems develop. Imbalances in material and energy usually equilibrate at rates that are much faster than changes in the internal structural constraints occur. Quantifying and following these internal constraints, therefore, constitutes the primary task for those who would describe ecodynamics. Many of the internal constraints link the biotic elements that constitute the ecosystem, and such connections often form self-entailing cycles. The combination of contingent behavior with auto-referential constraints engenders decidedly non-mechanical behaviors in ecosystems. It is impossible to treat explicitly all the hidden constraints in an ecosystem, and so an implicit phenomenological approach, akin to what is done in thermodynamics is attempted. The network of material or energy exchanges in the ecosystem is used as a surrogate to record all the effects of the hidden constraints. The attributes of this network can be quantified with the help of information theory, and the ensuing measures appear to provide an adequate description of whole system development. This description of ecodynamics clashes, however, with the normal conventions on how nature is considered to operate; hence, a new ecological metaphysic is suggested.
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1. Introduction

The exact nature of ecodynamics is only rarely discussed. Dialog in ecology usually transpires under the tacit assumption that ecosystems behave like most of the rest of nature—according to the laws of conservation of material and energy and obeying a set of determinate dynamical laws, like those that govern

planetary motions. Furthermore, most appear to assume that the same mathematics that have been developed to quantify the physical world will suffice to illumine ecodynamics. The less than adequate success of this agenda, however, has given rise to what Cohen (1971) somewhat facetiously referred to as "physics envy" on the part of many ecologists.

Lest I unfairly single out ecologists for not "thinking outside the box", I should hasten to add that most of what appears in the literature under the rubric of "complexity theory" follows much the same

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agenda: Complexity is considered but an epiphenomenon of scale. Apparently complicated behavior is thought to be the result of very simple interactions at smaller levels that ramify at larger scales to yield strange and manifold behaviors. Or, complexity is business as usual, only with a few more non-linear wrinkles thrown in. Thus does Sally Goerner (1999) portray most of Complexity Theory as "21st Century science built upon 19th Century foundations." Only rarely does one encounter the opinion that complexity may require an essentially different way of apprehending how nature works (e.g., Casti, 1989; Kay and Schneider, 1994; Salthe, 1985; Li, 2000; Mickulecky, 2000).

Of course, no one is contending that ecosystems, or any other living systems for that matter, violate the laws of conservation of material and energy. Unlike the realms of relativity theory and quantum physics, there is nothing about ecodynamics that would place these dogma into question. In fact, one might even argue that ecosystems obey these dicta too well. Matter and energy in ecosystems usually return in quick order to being almost in balance and thereby render these laws of little assistance in telling us what the system is doing over the longer term. (That ecosystems are usually near balance does not contradict the common wisdom that ecosystems are far-from-equilibrium processes in the thermodynamic sense. The reason is that the thermodynamic concept of "near-equilibrium" is an infinitesimal one. Unless one is extremely close to equilibrium, the near-equilibrium dynamics will not hold. It is possible for a system to be sufficiently out of balance to qualify as far-from-equilibrium, yet insufficiently so as to control the observed dynamics).

At this point the evolutionary theorist might respond that those points are well-taken, but the controlling dynamics have already been sufficiently articulated under the "Grand Synthesis" of Fisher, Sewall and Wright. In their opinion it is the information encoded in the genome of organisms that directs the behavior of living entities, and by aggregative induction, those of the whole ecosystem. Of course, there remains a problem in that the evolutionary perspective forces the observer constantly to switch back and forth in almost schizoid manner between the contingencies of genomic reproductions and the presumably lawful behavior

of the phenome in its environment. It is sufficient, however, to note that the induction from organism to ecosystem simply does not accord with observation and intuition. As Guenther Stent (1981) put it,

"Consider the establishment of ecological communities upon colonization of islands or the growth of secondary forests. Both of these examples are regular phenomena in the sense that a more or less predictable ecological structure arises via a stereotypic pattern of intermediate steps, in which the relative abundances of various types of flora and fauna follow a well-defined sequence. The regularity of these phenomena is obviously not the consequence of an ecological program encoded in the genomes of the participating taxa" (Lewin, 1984).

Nor has elucidating the ontogenetic mapping from genome to phenome been a raging success. Efforts by Sidney Brenner et al. (ibid.) to identify the connections, together with recent results from the Human Genome Project (Strohman, 2001) reveal that a full mapping is likely a chimera. As Brenner bravely suggested, what we have to do is "try to discover the principles of organization, how lots of things are put together in the same place" (Lewin, 1984). This is a task tailor-made for the ecologist.

In exactly what ways does the task Brenner has set for ecology differ from problems as they are normally posed in physics? In that epitome of the hard sciences problems are usually parsed into what are called the field equations and the boundary conditions. Although one usually wishes to study a phenomenon over a given domain (field) of space and time, it is assumed that one need not measure the magnitude of the phenomenon at all points of the field. Rather, a particular law expresses in a very compact way how the attribute will vary from point to point within the field. It becomes necessary, therefore, to specify only the magnitude of the phenomenon at the peripheries of the field (and at the initial time.) Important here is the fact that all the known laws of physics are entirely symmetrical with respect to time. They cannot impart any asymmetry to the field by which the observer may differentiate the resulting field from an adirectional background (Steven, 1995). That is, uniqueness and direction can enter the system only via the imposed boundary constraints.

We turn our attention now to complex biotic systems that have been parsed into a number of essential components. To some degree these components respond, like physical systems, to conditions established outside the ensemble. Those exogenous constraints, however, are insufficient to drive the behavior of the component, because the components themselves interact with one another. That is, each component is constrained by, and in its own turn constrains, other compartments. (This is most unlike the systems that Boltzmann or Fischer studied, which were collections of many non-interacting elements.) In ecosystems and other biotic communities the boundary constraints on any element are set in part by other proximate elements.

If one considers the constraint exerted by one compartment upon another as a directed link, then these links are wont to combine with one another into chains of constraints, which in some instances can fold back upon themselves and form cycles. When this latter circumstance occurs, the participating elements exert a degree of constraint upon themselves that traces back to no external source (Hutchinson, 1948). Rosen (1991) defined organisms as systems that were self-entailing with respect to efficient causes. That is, the agencies behind repair, growth and metabolism are all elicited by each other and do not derive from any external source. (Certainly, the material for such interaction derives from outside these open systems, but material cause is traditionally separated from efficient cause, which can remain within the community.) Similarly, closed cycles of constraints set the stage for some internal (partially) autonomous control of biotic systems.

The controlling nexus of ecodynamics now begins to emerge. It is not the field equations of conservation of mass and energy that are of greatest interest. These are nearly satisfied in relatively short order. Nor need we feel compelled to believe that some energetic variational constraints (e.g., ecosystems develop so as to store the maximal amount of exergy possible (Joergensen and Mejer, 1979)) will fully dictate the final outcome (although such global constraints most probably do affect the endpoint.) Rather, the paramount focus concerning transitional dynamics should be upon the interactions among the (mostly hidden) internal constraints, which change more slowly with time. That is, the controlling nexus of ecodynamics

appears to be relational in nature: how much any change in one constraint affects others with which it is linked. As Stent suggested, changes in genomic constraints remain hidden to this perspective; and, furthermore, there seems to be no obvious reason to suspect that they are cryptically directing matters. In fact, it would appear more plausible that the internally closed loops of constraints serve over the longer run to sift among genetic variations and to select for those which accord better with their own agencies, as will be explained presently.

2. Measuring the effects of incorporated constraints

Our musings on ecodynamics have thus far remained entirely conceptual—perhaps it is an intriguing story to some, but it remains an irritating repetition of the theme of circular causality that has long been eschewed by others. It helps to tell a plausible story, but science requires measurement and quantification as well. Any well-posed theory must have the potential to become operational. Herein lies a possible difficulty, as there is simply no hope of making explicit, much less measuring, every item of internal constraint in any living system. But science has faced this quandary before, most notably in the arena of thermodynamics and statistical mechanics. There one was faced with effects stemming from an unmanageable number of atomic entities, and it was impossible to follow the actions of each actor in detail. What physicists did was to retreat and measure only some overall consequences of the individual agencies. Rather than attempt to quantify the trajectories of each individual actor, physical attributes of the entire (macroscopic) ensemble were measured. Whole system properties, such as pressure, temperature and volume, were assumed to be common attributes upon which implicitly were written the contributions of each microscopic event.

This same stratagem can be applied to ecosystems as well. We acknowledge the importance of each internal constraint, such as prey escape tactics, mating displays, or visual cues, etc. We elect, however, to focus upon and measure (or otherwise estimate) more aggregated processes, such as how much material and/

or energy passes from one system element to another over a given interval of time. All such estimated transfers can then be arrayed as a network of ecosystem material and/or energy linkages – diagrams of ''who eats whom, and at what rates?'' (Ulanowicz, 1986). This ''brutish'' description (Engleberg and Boyarsky, 1979) of ecosystem behavior ostensibly ignores most of what interests individual autecologists and what imparts pattern to the ecosystem, but in the spirit of thermodynamics, those vital elements are assumed to write their effects upon this ''macroscopic'' quantification of ecosystem behavior. Change any one of the hidden constraints, and its consequence(s) will be observed, at least incrementally, upon the network of system flows.

Just as the aggregated effects of individual agents are captured by the macroscopic variables of thermodynamics, so does an ecosystem flow network embody all the consequences of the hidden constraints. It remains, however, to quantify the effects of existing embodied constraints upon this pattern over and against other confounding factors that may affect the network structure of the system. Before doing so, however, we first need to address the significant temptation to assume that closed circuits of concatenated constraints are merely another mechanical ensemble. That we are dealing rather with an essentially different dynamics becomes apparent once we appreciate two significant points: (1) Constraints in living systems are not rigidly mechanical in nature, but incorporate contingency in a necessary but limited way. (2) Cyclical relationships among some constraints, due to their contingent natures, give rise to categorically non-mechanical behaviors.

3. Ecosystems and contingency

First we turn our attention to the nature of contingency in ecodynamics. That living systems are not fully constrained, that is that they retain sufficient flexibility to adapt to changing circumstances, is (along with self-entailment) another necessary attribute of living systems. We will see, furthermore, that the tension between constraint and its complement, flexibility is probably easier to discern in ecosystems than in organisms, where the constraints are more prevalent and rigid.

Reconciling chance with deterministic constraint is no easy task, and this problem has occupied some of the best minds over the past two centuries (Ulanowicz, 2000). Ludwig von Boltzmann and Josiah Gibbs dominated the effort during latter 19th Century to construct a statistical mechanics that would salvage the mechanical view of nature from the challenge posed by the irreversibility inherent in thermodynamics. Then, as mentioned above, early in the 20th century Ronald Fisher used almost identical mathematics to join the gradualist narrative of Darwin with the discrete phenomena observed by Mendel, into what came to be known as ''The Grand Synthesis''. Both these attempts at reconciliation are relevant only to systems of many components that are largely decoupled from one another—hardly the description of an ecosystem with its complement of internal constraints.

The Grand Synthesis was formulated using classical probability theory—the study of random events that occur again and again. We emphasize in passing, however, how under the rubric of chance must also be included those ubiquitous and ever-present singular events that occur once and never again. For in a truly complex world it becomes imperative to consider events that are made up of numerous distinct, independent entities. Once the number of distinguishable components rises, so does the improbability that they could possibly recur. Elsasser (1981), for example, estimated the number of simple particles in the known universe at 10^{85}. He noted as well that 10^{25} ns have transpired since the Big Bang. Whence, his estimate for the number of simple events that could possibly have occurred during the course of known time was about 10^{110}. Elementary combinatorics reveals, however, that whenever the number of distinguishable entities involved in an event is greater than about 75, there is simply no physical chance that it will ever recur again (i.e., its probability of recurrence is less that one in 10^{110}.) As simple ecosystems consist of hundreds or thousands or more distinguishable organisms, we ecologists must reconcile ourselves with the circumstance that we are surrounded by a legion of singular events happening everywhere, all the time.

Furthermore, evolutionary narrative is constantly switching back and forth between the realms of strict determinism and pure stochasticity, as if no middle

ground existed. In referring to this regrettable situation, Popper (1990) remarked that it still remains for us to achieved a truly "evolutionary theory of knowledge", and we will not do so until we reconsider our fundamental attitudes toward the nature of causality. True reconciliation, Popper suggested, lies in envisioning an intermediate to stochasticity and determinism. To meet this challenge, he proposed a generalization of the Newtonian notion of "force". Forces, he posited, are idealizations that exist as such only in perfect isolation. The objective of experimentation is to approximate isolation from interfering factors as best possible. In the real world, however, where components are loosely, but definitely coupled, one should speak rather of "propensities". A propensity is the tendency for a certain event to occur in a particular context. It is related to, but not identical to, conditional probabilities.

Consider, for example, the hypothetical "table of events" depicted in Table 1, which arrays five possible outcomes, b_1–b_5, according to four possible eliciting causes, a_1–a_4. For example, the outcomes might be several types of cancer, such as those affecting the lung, stomach, pancreas or kidney, while the potential causes might represent various forms of behavior, such as running, smoking, eating fats, etc. In an ecological context, the b's might represent predation by predator j, while the a's could represent donations of material or energy by host i.

We notice from the table that whenever condition a_1 prevails, there is a propensity for b_2 to occur. Whenever a_2 prevails, b_5 is the most likely outcome. The situation is a bit more ambiguous when a_3 prevails, but b_1 and b_4 are more likely to occur in that situation, etc. Events that occur with smaller frequencies, e.g., $[a_1,b_3]$ or $[a_1,b_4]$ result from what Popper calls "interferences".

Table 1
Frequency table of the hypothetical number of joint occurrences that four "causes" (a_1–a_4) were followed by five "effects" (b_1–b_5)

	b1	b2	b3	b4	b5	Sum
a1	40	193	16	11	9	269
a2	18	7	0	27	175	227
a3	104	0	38	118	3	263
a4	4	6	161	20	50	241
Sum	166	206	215	176	237	1000

Table 2
Frequency table as in Table 1, except that care was taken to isolate causes from each other

	b1	b2	b3	b4	b5	Sum
a1	0	269	0	0	0	269
a2	0	0	0	0	227	227
a3	263	0	0	0	0	263
a4	0	0	241	0	0	241
Sum	263	269	241	0	227	1000

We now ask how might the table of events appear, were it possible to isolate phenomena completely, that is, were it possible to impose further constraints that would keep both other propensities and the arbitrary effects of the surroundings from influencing a given particular constraint? Probably, the result would look something like Table 2, where every time a_1 occurs, it is followed by b_2; every time a_2 appears, it is followed by b_5, etc. That is, under isolation, propensities degenerate into mechanical-like forces. It is interesting to note that b_4 never appears under any of the isolated circumstances. Presumably, it arose purely as a result of interferences among propensities. Thus, the propensity for b_4 to occur whenever a_3 happens is an illustration of Popper's assertion that propensities, unlike forces, never occur in isolation, nor are they inherent in any object. They always arise out of a context, which invariably includes other propensities.

In light of our discussion on constraint, we might want to view Popper's propensity as a constraint that is unable to perform unerringly in the face of confounding contingencies. Propensity encompasses both chance and law-like behavior under a single rubric. We note also that the transition depicted from Tables 1 and 2 was accompanied by the addition of constraints, and it is the appearance of such progressive constraints that we infer when we use the term "development". We now turn our attention to the second point mentioned above and ask ourselves how the incorporation of chance moves the ensuing dynamics out of the realm of the purely mechanical?

4. Autocatalysis and non-mechanical behavior

It was mentioned above how constraints can be concatonated and in some cases joined back upon themselves (form cyclical configurations.) It has not

yet been mentioned that constraints of one process upon another can be either excitatory (+) or inhibitory (−). It happens that the configuration of reciprocal excitation, or mutualism (+,+) can exhibit some very interesting behaviors that on balance qualify its action as a non-mechanical causal agency. Investigators such as Eigen (1971), Haken (1988), Maturana and Varela (1980), Kauffman (1995), Li (2002) and DeAngelis et al. (1986) have all contributed to the growing consensus that some form of positive feedback is responsible for most of the order we perceive in organic systems. It is useful now to focus attention upon a particular form of positive feedback, autocatalysis.

Autocatalysis is positive feedback across multiple links wherein the effect of each and every link in the feedback loop upon the next remains positive. To be more precise about what form of autocatalysis I am considering, I direct the reader's attention to the three-component interaction depicted in Fig. 1. We assume that the action of process A has a propensity to augment a second process B. I wish to emphasize my use of the word "propensity" to mean that the excitatory constraint that A exerts upon B is not wholly obligatory, or mechanical. Rather, when process A increases in magnitude, most (but not all) of the time, B also will increase. B tends to accelerate C in similar fashion, and C has the same effect upon A.

My favorite ecological example of autocatalysis is the community that centers around the aquatic macrophyte, Utricularia, or bladderworts (Ulanowicz, 1995a). All members of the genus *Utricularia* are carnivorous plants. Scattered along its feather-like stems and leaves are small bladders, called utricles (Fig. 2a). Each utricle has a few hair-like triggers at its
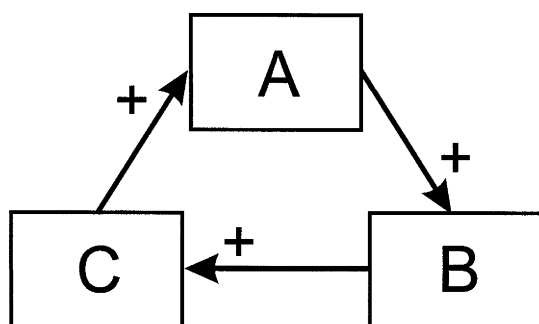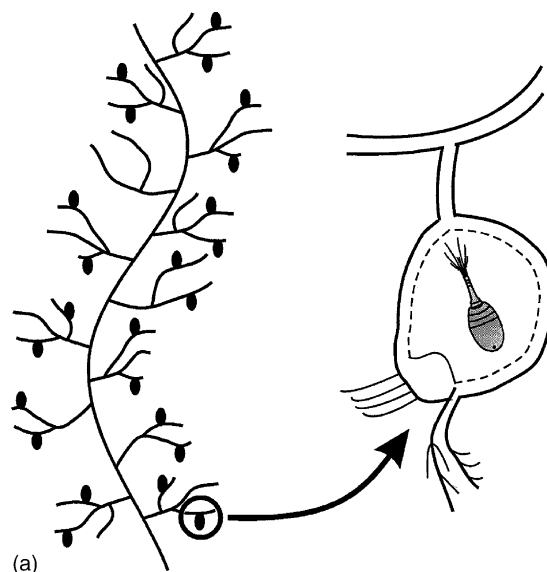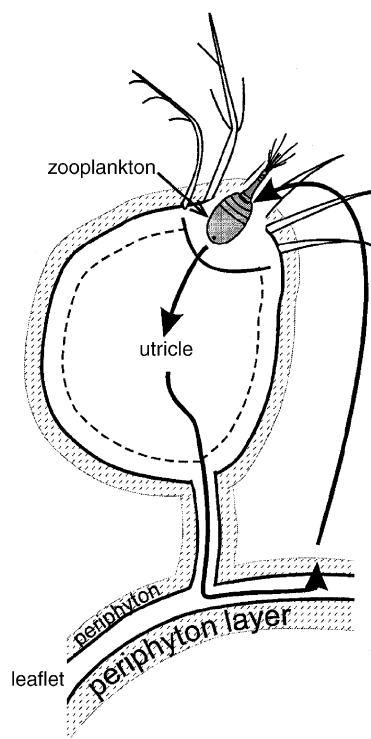

(a)

(b)

Fig. 2. (a) Sketch of a typical "leaf" of *Utricularia floridana*, with detail of the interior of a utricle containing a captured invertebrate. (b) Schematic of the autocatalytic loop in the *Utricularia* system. Macrophyte provides necessary surface upon which periphyton (striped area) can grow. Zooplankton consumes periphyton, and is itself trapped in bladder and absorbed in turn by the *Utricularia*.

Fig. 1. Schematic of a hypothetical three-component autocatalytic cycle.

terminal end, which, when touched by a feeding zooplankter opens the end of the bladder and the animal is sucked into the utricle by a negative osmotic pressure that the plant had maintained inside the bladder. In the field *Utricularia* plants always support a film of algal growth known as periphyton (Fig. 2b). This periphyton in turn serves as food for any number of species of small zooplankton. The catalytic cycle is completed when the *Utricularia* captures and absorbs many of the zooplankton. Hence, looking in the positive direction, one observes only excitatory constraints: Although the periphyton is constrained to grow upon the surface of the *Utricularia*, once it has made the attachment, it can grow at amazingly rapid rates per unit of biomass and is especially effective at incorporating nutrients in resource-poor environments. The effect of host periphyton upon zooplankton is salutary, and likewise that of the captured zooplankton upon the *Utricularia*. Looking in the reverse direction, however, one discovers the inhibitory constraints that keep the positive feedback from growing arbitrarily large in magnitude: Periphyton shades its host plant; *Utricularia* diminishes the zooplankton numbers and zooplankton clean periphytion from the supporting matrix of bladderwort.

Autocatalysis among propensities gives rise to at least eight system attributes, which, taken as a whole, comprise a distinctly non-mechanical dynamic. We begin by noting that by our definition autocatalysis is explicitly growth-enhancing. Furthermore, autocatalysis exists as a relational or *formal* structure of kinetic elements. Far more interesting is the observation alluded to earlier that autocatalysis is capable of exerting *selection* pressure upon all characteristics of its ever-changing constituents. To see this, let us suppose that some small chance alteration occurs spontaneously in process B. If that change either makes B more sensitive to A or a more effective catalyst of C, then the change will receive enhanced stimulus from A. Conversely, if the change in B either makes it less sensitive to the effects of A or a weaker catalyst of C, then that change will likely receive diminished support from A. We note that such selection works on the processes or mechanisms as well as on the elements themselves. Hence, any effort to simulate development in terms of a fixed set of mechanisms is doomed ultimately to fail.

It should be noted in particular that any change in B is likely to involve a change in the amounts of material and energy that flow to sustain B. Whence, as a corollary of selection pressure, we recognize the tendency to reward and support changes that bring ever more resources into B. As this circumstance pertains to all the other members of the feedback loop as well, any autocatalytic cycle becomes the center of a *centripetal* vortex, pulling as many resources as possible into its domain.

It follows that, whenever two or more autocatalyic loops draw from the same pool of resources, autocatalysis will *induce competition*. In particular, we notice that whenever two loops partially overlap, the outcome could be the exclusion of one of the loops. In Fig. 3, for example, element D is assumed to appear spontaneously in conjunction with A and C. If D is more sensitive to A and/or a better catalyst of C, then there is a likelihood that the ensuing dynamics will so favor D over B, that B will either fade into the background or disappear altogether. That is, selection pressure and centripetality can guide the replacement of elements. Of course, if B can be replaced by D, there remains no reason why C cannot be replaced by E or A by F, so that the cycle A, B, C could eventually transform into D, E, F. One concludes that the characteristic lifetime of the autocatalytic form usually exceeds that of most of its constituents. This is not as strange as it may first seem. With the exception of our neurons, virtually none of the cells that composed our bodies seven years ago remain as parts of us today. Very few of the atoms in our body were parts of us eighteen months ago. Yet if a close friend were to see us for the first time in 10 years, chances are he/she would recognize us immediately.

Autocatalytic selection pressure and the competition it engenders define a preferred direction for the system—that of ever-more effective autocatalysis. In
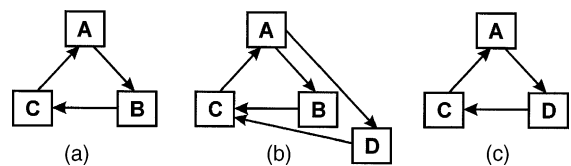

Fig. 3. (a) Original configuration. (b) Competition between component B and a new component D, which is either more sensitive to catalysis by A or a better catalyst of C. (c) B is replaced by D, and the loop section A–B–C by that of A–D–C.

the terminology of physics, autocatalysis, predicated as it is upon eliciting internal constraints, each of which can be asymmetric, is itself, therefore, *symmetry-breaking*. One should not confuse this rudimentary directionality with full-blown teleology, however. It is not necessary, for example, that there exist a pre-ordained endpoint towards which the system strives. The direction of the system at any one instant is defined by its state at that time, and the state changes as the system develops. I use the term ''telos'' to denote this weaker form of directionality and to distinguish it from the far rarer and more complex behavior known as teleology.

Taken together, selection pressure, centripetality and a longer characteristic lifetime all speak to the existence of a degree of *autonomy* of the larger structure from its constituents. Again, attempts at reducing the workings of the system to the properties of its composite elements will remain futile over the long run.

In epistemological terms, the dynamics I have just described can be considered *emergent*. In Fig. 4, for example, if one should consider only those elements in the lower right-hand corner (as enclosed by the solid line), then one can identify an initial cause and a final effect. If, however, one expands the scope of observation to include a full autocatalyic cycle of processes (as enclosed by the dotted line), then the system properties I have just described appear to emerge spontaneously.

5. Causality reconsidered

Autocatalysis is thus seen to behave in ways quite uncharacteristic of machines. It is important also to note that the causal agency of autocatalysis appears in a form that is foreign to conventional mechanical analysis. In particular, the selection pressure that arises from autocatalysis acts from higher scales downwards. Conventional wisdom allows only influences originating at lower realms of time and space to exert their effects at larger and longer scales (reductionism.) This convention is a legacy of the Newtonian worldview and the ensuing Enlightenment. Prior to Newton, however, the prevailing view on natural causalities had been formulated by Aristotle,

enlarged system boundary
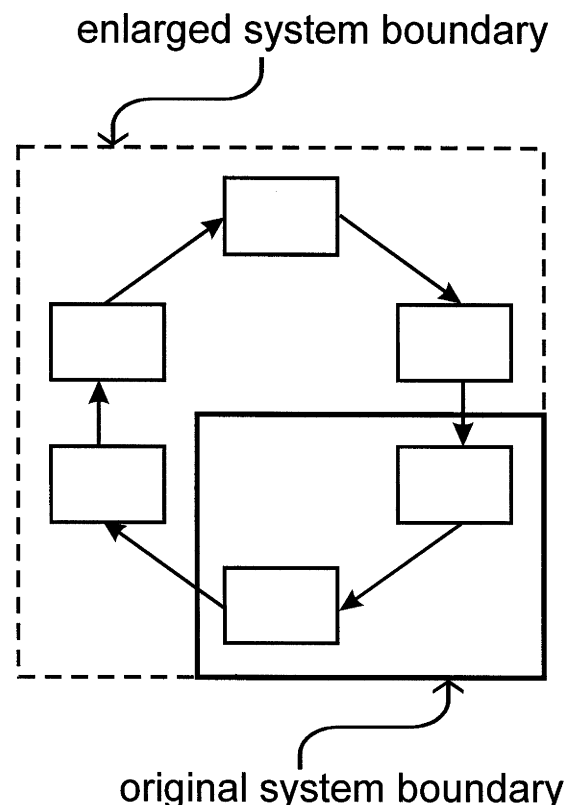
original system boundary

Fig. 4. Two hierarchical views of an autocatalytic loop. The original perspective (solid line) includes only part of the loop, which therefore appears to function quite mechanically. A broader vision encompasses the entire loop, and with it several non-mechanical attributes.

who explicitly recognized the existence of downward causation.

Aristotle identified four categories of cause: (1) material, (2) efficient (or mechanical), (3) formal and (4) final. An effective, albeit unsavory, example of an event wherein all four causes are at work is a military battle (Ulanowicz, 1995b). The swords, guns, rockets and other weapons comprise the material causes of the battle. The soldiers who use those weapons to inflict unspeakable harm on each other become the efficient agents. The topography of the battlefield and the changing positions of the troops on the battlefield with respect to each other and with respect to natural factors, such as sun angle and wind, constitute the formal cause. Final cause originates mostly beyond the battlefield and consists of the social, economic and

political factors that brought the armies to face each other.

Encouraged by the simplicity of Newton's *Principia* and perhaps influenced by the politics of the time, early Enlightenment thinkers acted decisively to excise formal and final causalities from all scientific description. We are urged, however, by contemporary thinkers, such as Rosen (1985) to reconsider how appropriately these discarded categories might serve for the interpretation of complex phenomena. Indeed, there appear to be especial reasons why Aristotle's schema provides a more satisfactory description of ecological dynamics, and those reasons center around the observation that efficient, formal and final causes are hierarchically ordered—as becomes obvious when we notice that the domains of influence by soldier, officer and prime minister extend over progressively larger and longer scales. We now see how the loops of constraints that we identify as autocatalysis are acting in the sense of formal agency (much like the ever-shifting juxtaposition of troops on the battlefield), selecting for changes among the participating ecosystem components.

The Achilles heel of Newtonian-like dynamics is that it cannot in general accommodate true chance or indeterminacy (whence the "schizophrenia" in contemporary biology.) Should a truly chance event happen at any level of a strictly mechanical hierarchy, all order at higher levels would be doomed eventually to unravel. The Aristotelian hierarchy, however, is far more accommodating of chance. Any spontaneous efficient agency at any hierarchical level would be subject to selection pressures from formal autocatalytic configurations above. These configurations in turn experience selection from still larger constellations in the guise of final cause, etc. One may conclude, thereby, that the influence of most irregularities remains circumscribed. Unless the larger structure is particularly vulnerable to a certain type of perturbation (and this happens relatively rarely), the effects of most perturbations are quickly damped.

One might even generalize from this "finite radius of effect" that the very laws of nature might be considered to have finite, rather than universal, domain (Allen and Starr, 1982; Salthe, 1993). That is, each law is formulated within a particular domain of time and space. The farther removed an observed event is from that domain, the weaker becomes the

explanatory power of that law, because chance occurrences and selection pressures arise among the intervening scales to interfere with the given effect. To the ecologist, therefore, the world appears as granular, rather than universal.

6. Quantifying constraint in ecosystems

With this background on contingency, autocatalysis and causality, we are finally ready to embark upon quantifying the overall degree of constraint in an ecosystem as manifested by its network of material/energy flows. We begin by abstracting from our discussion two major facets pertaining to the action of autocatalysis: (a) it serves to increase the activities of all its constituents, and (b) it prunes the network of interactions so that those links that most effectively participate in autocatalysis become dominant. Schematically this transition is depicted in Fig. 5. The upper figure represents a hypothetical, inchoate four-component network before autocatalysis has developed, and the lower one, the same system after autocatalysis has matured. The magnitudes of the flows are represented by the thicknesses of the arrows.
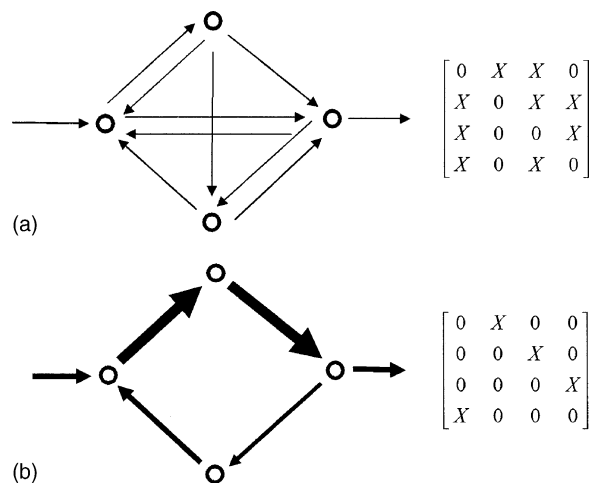

Fig. 5. Schematic representation of the major effects that autocatalysis exerts upon a system. (a) Original system configuration with numerous equiponderant interactions. (b) Same system after autocatalysis has pruned some interactions, strengthened others, and increased the overall level of system activity (indicated by the thickening of the arrows). Corresponding matrices of topological connections indicated to the right.

To the right appear the matrices that correspond to the pattern of flows. One recognizes that the transition resembles that between Tables 1 and 2 presented earlier in connection with Popper's propensities.

We begin by defining the transfer of material or energy from prey (or donor) i to predator (or receptor) j as T_{ij}, where i and j range over all members of a system with n elements. The total activity of the system can be measured simply as the sum of all system processes, $T = \sum_{i,j} T_{ij}$, or what is called the "total system throughput". We can then represent the first aspect of autocatalysis as any increase in the total system throughput, much as economic growth is reckoned by any increase in Gross Domestic Product.

It is the second aspect that bears upon constraint, because the "pruning" referred to can be regarded as the appearance of additional constraints that channel flow ever more narrowly along efficient pathways— "efficient" here meaning those pathways that most effectively participate in the autocatalytic process. Another way of looking at pruning is to consider that constraints cause certain flow events to occur more frequently than others. We begin the quantification of constraint by estimating the joint probability that a quantum of medium is constrained both to leave i and enter j by the quotient T_{ij}/T. We then note that the unconstrained probability that a quantum has left i can be acquired from the joint probability merely by summing the joint probability over all possible destinations. The estimator of this unconstrained probability thus becomes $\sum_q T_{iq}/T$. Similarly, the unconstrained probability that a quantum enters j becomes $\sum_k T_{kj}/T$. Finally, we remark how the probability that the quantum could make its way by pure chance from i to j, without the action of any constraint, would vary jointly as the product of the latter two frequencies, or $\sum_q T_{iq} \sum_k T_{kj}/T^2$.

This last probability obviously is not equal to the constrained joint probability, T_{ij}/T. Recalling that Tribus and McIrvine (1971) defined information as "anything that causes a change in probability assignment", we conclude that Tribus essentially equated information to constraint. We look, therefore, to information theory for clues as to how to quantify constraint. Information theory, however, does not address information (constraint) directly. Rather it uses as its starting point a measure of the rareness of an event, first defined by Boltzmann (1872) as $(-k \log p)$, where p is the probability $(0 \le p \le 1)$ of the given event happening and k is a scalar constant that imparts dimensions to the measure. One notices that for rare events $(p \approx 0)$, this measure is very large and for very common events $(p \approx 1)$, it is diminishingly small.

Because constraint usually acts to make things happen more frequently in a particular way, one expects that, on average, an unconstrained probability would be rarer than a corresponding constrained event. The more rare (unconstrained) circumstance that a quantum leaves i and accidentally makes its way to j can be quantified by applying the Bolzmann formula to the probability just defined, i.e., $-k \log\left(\sum_k T_{kj} \sum_q T_{iq}/T^2\right)$, and the correspondingly less rare condition that the quantum is constrained both to leave i and enter j becomes $-k \log(T_{ij}/T)$. Subtracting the latter from the former and combining the logarithms yields a measure of the hidden constraints that channel the flow from i to j as $k \log\left(T_{ij}T / \sum_k T_{kj} \sum_q T_{iq}\right)$. (I note in passing that this quantity also measures the propensity for flow from i to j (Ulanowicz, 1996).)

Finally, to estimate the average constraint at work in the system as a whole, one weights each individual propensity by the joint probability of constrained flow from i to j and sums over all combinations of i and j. That is,

$$\text{AMC} = k \sum_{i,j} \left(\frac{T_{ij}}{T}\right) \log\left(\frac{T_{ij}T}{\sum_k T_{kj} \sum_q T_{iq}}\right)$$

where AMC is the "average mutual constraint" (known in information theory as the average mutual information (Rutledge et al., 1976)).

To illustrate how an increase in AMC actually tracks the "pruning" process, I refer the reader to the three hypothetical configurations in Fig. 6. In configuration (a) where medium from any one compartment will next flow is maximally indeterminate. AMC is identically zero. The possibilities in network (b) are somewhat more constrained. Flow exiting any compartment can proceed to only two other compartments, and the AMC rises accordingly. Finally, flow in schema (c) is maximally constrained,
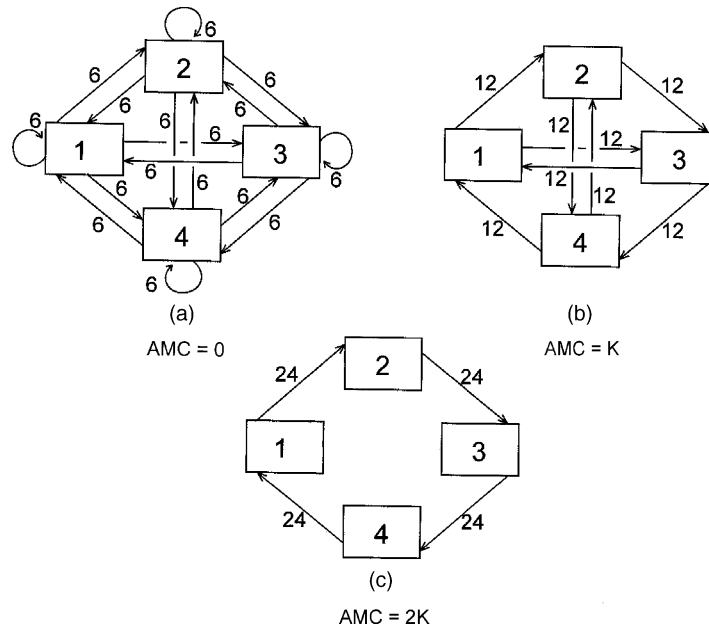
Fig. 6. (a) The most equivocal distribution of 96 units of transfer among four system components. (b) A more constrained distribution of the same total flow. (c) The maximally constrained pattern of 96 units of transfer involving all four components.

and the AMC assumes its maximal value for a network of dimension 4.

One notes in the formula for AMC that the scalar constant, k, has been retained. We recall that although autocatalysis is a unitary process, we have defined separate measures for its two attributes. We can easily rectify this disparity and combine the measures of both attributes simply by making the scalar constant k represent the level of system activity, T. That is, we set $k = T$, and we name the resulting product the system ascendency, A, where

$$A = \sum_{i,j} T_{ij} \log \left(\frac{T_{ij}T}{\sum_k T_{kj} \sum_q T_{iq}} \right)$$

In his seminal paper, "The strategy of ecosystem development", Odum (1969) identified 24 attributes that characterize more mature ecosystems. These can be grouped into categories labeled species richness, dietary specificity, recycling and containment. All other things being equal, a rise in any of these four attributes also serves to augment the system ascendency (Ulanowicz, 1986). It follows as a phenomenological principle that

"in the absence of major perturbations, ecosystems have a propensity to increase in ascendency."

I should hasten to emphasize in the strongest terms possible that increasing ascendency is only half of the dynamical story. Ascendency accounts for how efficiently and coherently the system processes medium. Using the same mathematics, one can compute as well an index called the system overhead, Φ, that is complementary to the ascendency (Ulanowicz and Norden, 1990).

$$\Phi = -\sum_{i,j} T_{ij} \log \left(\frac{T_{ij}^2}{\sum_k T_{kj} \sum_q T_{iq}} \right)$$

Overhead quantifies the inefficiencies and incoherencies present in the system. Although these latter properties may encumber overall system performance at processing medium, they become absolutely essential to system survival whenever the system incurs a novel perturbation. At such time, the overhead comes to represent the degrees of freedom available to the system and the repertoire of potential tactics from which the system can draw to adapt to the new

circumstances. Without sufficient overhead, a system is unable create an effective response to the exigencies of its environment. The configurations we observe in nature, therefore, appear to be the results of a dynamical tension between two antagonistic tendencies (ascendency versus overhead).

It is perhaps worthwhile at this juncture to recapitulate what has been done: First, we have shifted our focus in ecosystem dynamics away from the normal (symmetrical) field equations of physics and concentrated instead upon the origins of asymmetry in any system—the boundary constraints. We then noted how biotic entities often serve as the origins of such constraint upon other biota, so that the kernel of ecodynamics is revealed to be the mutual (self-entailing) constraints that occur within the ecosystem itself. We then identified a palpable and measurable entity (the network of material/energy exchanges) upon which this myriad of mostly hidden constraints writes its signature. Finally, we described a calculus that could be applied to the network to quantify the effects of all the hidden constraints. Hence, by following changes in the ascendency and overhead of an ecosystem, we are focusing squarely upon that which makes ecodynamics fundamentally different from classical dynamics.

7. New constraints to help focus a new perspective

By many accounts, the Enlightenment started in earnest with Newton's publication of *Principia*, which provided a quantitative basis for classical dynamics. In the years that followed, numerous thinkers built around Newtonian dynamics a supporting metaphysic that for the last three centuries has strongly guided how we are to look at nature. It is only fair to ask how well that metaphysic supports the emerging ecodynamics that have just been described (Ulanowicz, 1999)? To provide a basis for comparison, we must first describe the Newtonian metaphysic as it appeared at its zenith.

Depew and Weber (1994) have identified four postulates under which Newtonian investigations were pursued during the early 19th century:

Newtonian systems are causally *closed*. Only mechanical or material causes are legitimate.

Newtonian systems are *deterministic*. Given precise initial conditions, the future (and past) states of a system can be specified with arbitrary precision. Newtonian systems are *reversible*. Laws governing behavior work the same in both temporal directions. Newtonian systems are *atomistic*. They are strongly decomposable into stable least units, which can be built up and taken apart again..
After consulting with these authors, I have added a fifth article of faith (Ulanowicz, 1997), namely that Physical laws are *universal*. They apply everywhere, at all times and over all scales.

Early in the 19th century, the notion of reversibility had already been challenged by Sadi Carnot's thermodynamical elaboration of irreversibility and several decades later by Darwin's historical narrative. The development of relativity and quantum theories early in the 20th century worked to subvert even further the assumptions of universality and determinism, respectively. Despite these problems, many in biology (and especially in ecology) continue to operate under the mechanistic umbrella just delimited.

In taking stock of all that has been said thus far, it becomes apparent that the Newtonian metaphysic accords rather poorly with ecodynamics and with the accompanying assumptions that allow one to follow what is controlling changes in community structure. In fact, the new dynamics appear to be dissonant with each of the five Newtonian precepts. To wit:

1. Ecosystems are not causally closed; rather they appear to be *open* to the influence of non-mechanical agency. Spontaneous events may occur at any level of the hierarchy at any time. Efficient (or mechanical) causes usually originate at scales inferior to that of observation, and their effects propagate upwards. Formal agencies appear at the focal level; and final causes exist at higher levels and propagate downwards (Salthe, 1985; Ulanowicz, 1997).
2. Ecosystems are not deterministic machines. They are *contingent* in nature. Biotic actions resemble propensities more than mechanical forces.
3. The realm of ecology is *granular*, rather than universal. Models of events at any one scale can explain matters at another scale only in inverse

proportion to the remoteness between them. On the other hand, the domain within which irregularities and perturbations can damage a system is usually circumscribed. Chance does not necessarily unravel a system.

4. Ecosystems, like other biotic systems, are not reversible, but *historical*. Irregularities often take the form of discontinuities, which degrade predictability into the future and obscure hindcasting. The effects of past discontinuities are often retained (as memories) in the material and kinetic forms that result from adaptation. Time takes a preferred direction or telos in ecosystems—that of increasing ascendency.

5. Ecosystems are not easily decomposed; they are *organic* in composition and behavior. Propensities never exist in isolation from other propensities, and communication between them fosters clusters of mutually reinforcing propensities to grow successively more interdependent. Hence, the observation of any component in isolation (if possible) reveals regressively less about how it behaves within the ensemble.

Although the ecological worldview may at first blush seem wholly revolutionary, by following Popper's evolutionary leads we have retained some connections with the orthodox and the classical. For example, because propensities are generalizations of Newtonian forces, it can be shown how the principle of increasing ascendency resembles a generalization of Newtonian law upwards into the macroscopic realm, in a way similar to how Schroedinger's wave equation is an extension of Newton's second law downwards into the netherworld of quantum phenomena (Ulanowicz, 1999).

Such continuity notwithstanding, it would be a major distortion to claim that the ecological metaphysic describes a new mechanics (in much the same manner that quantum physics is often still referred to as ''quantum mechanics'', despite the fact that there is virtually nothing mechanical about the phenomena). It is past time to make a clean break with the vision of ''*natura cum machina*'' (Dennett, 1995). If it does not look like a machine, if it does not act like a machine, if it does not smell like a machine, why then persist in calling it a machine? Such procrustean nostalgia only fosters a highly distorted vision of the world in which we are immersed. Metaphors and methods are

emerging that are far more effective and appropriate to charting the pathways our living world seems to be blazing for itself (Ulanowicz, 2001).

Acknowledgements

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