Chapter 7

The Complex Nature of Ecodynamics

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7.1. Introduction

The specific nature of ecodynamics is rarely discussed. The tacit assumption usually is 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 -- much like those that govern planetary motions. Furthermore, most continue to assume that the same mathematics that so aptly quantifies the physical world is sufficient to illumine ecodynamics. Unfortunately, precious few results have been achieved to date under this agenda, but ecologists continue nonetheless to exhibit what Cohen has somewhat facetiously referred to as "physics envy".[1]
It would be unfair to accuse only ecologists of outmoded thinking. Much of what has appeared in the literature under the rubric of "complexity theory" has proceeded along those same lines:

Complexity is considered but an epiphenomenon of scale. Complicated behavior is still thought by many to be the result of very simple interactions at smaller levels that ramify at larger scales to yield strange and manifold behaviors, such as are described by the use of fractal theory. Such "thin" complexity remains business as usual,[2] only with a few non- linear wrinkles thrown in. Whence, Sally Goerner[3] portrays most of Complexity Theory as "21st Century science built upon 19th Century foundations."

The opinion is beginning to emerge, however, that complexity may require an essentially different way of viewing how nature works (e.g., Casti,[4] Kay and Schneider,[5] Salthe,[6] Rosen,[7] Mikulecky[8].) Fortunately, those who see complexity in this new guise are usually not reticent about expressing their dissent. The mathematician, John Casti,[9] for example, builds upon a children's story, "Little Bear", by Else Minarik[10] wherein the principal character tries to get to the moon by climbing a tree. Casti contends that using the conventional methods of physics to improve one's understanding of complex systems is akin merely to climbing a taller tree. He cites how, when complex systems are approached using conventional tools, they almost invariably give qualitatively *contradictory* prognoses (and not ones that are merely quantitatively inaccurate.)

Of course, none of the dissenters 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 those dogmas into question. In fact, one might even argue that ecosystems obey these dicta too well. Matter and energy in ecosystems usually return in very quick order to being almost in balance and thereby render these laws of little assistance in revealing what the system is doing over the longer term.

The evolutionary theorist might respond that what is missing from the methods of physics is the historical approach initiated by Darwin in his theory of descent by natural selection. They would indeed be correct in crediting Darwin with the introduction of history into science. In fact, Darwin had a healthy respect for the complex nature of evolution.[11] Unfortunately, most of Darwin's nuances were ignored during the formulation of the "Grand Synthesis" by Fisher and Sewall Wright, who precipitated what now is called "neo-Darwinism". In this contemporary wisdom, 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. Those who view evolution in such simplistic fashion conveniently ignore the problem of how it forces the observer constantly to switch back and forth in almost schizoid manner between the contingencies in genomic reproduction and the presumably lawful behavior of the resulting phenome in its environment. It will suffice here, however, simply to note that the neo-Darwinian approach does not seem to be applicable to ecosystems. As Guenther Stent[12] so aptly 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." [13]

Neither has elucidating the ontogenetic mapping from genome to phenome been any raging success. Efforts by Sidney Brenner et al. (ibid.) to identify the connections, together with recent

results from the Human Genome Project[14] reveal that the full mapping is very likely a chimera. As Brenner bravely suggested, it becomes necessary to "try to discover the principles of organization, how lots of things are put together in the same place".[13] It happens that Brenner's is a relational task that is tailor-made for the ecologist.

The reader would be justified in asking how Brenner's suggested approach differs from how problems 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 needn't measure the magnitude of the phenomenon at all points of the field. Rather, a particular law expresses in a very compact way how the given 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.[15] They cannot impart any asymmetry to the field with which the observer may distinguish it from an adirectional background.[16] In other words, uniqueness and direction enter the system *only* via the imposed boundary constraints.

Turning now to complex biotic systems that can be parsed into a number of essential components, these elements respond to some degree (like physical systems) to constraints arising *outside* the ensemble. Those exogenous constraints, however, are insufficient to determine 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 arise in part *within* the system itself as engendered by other proximate elements.

If one represents 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. Robert Rosen[7] 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. Similarly, closed cycles of constraints set the stage for some internal (partially) autonomous control of biotic systems.

The controlling nexus of ecodynamics now becomes clearer. 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 are energy-based constraints (e.g., ecosystems develop so as to store the maximal amount of exergy possible[17] alone sufficient to dictate the final outcome [although such global constraints most probably do affect the endpoint.]) It appears as concerns transitional ecodynamics that the paramount focus should be upon the interactions among the (mostly hidden) internal constraints, which change more slowly with time. That is, control 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 in this perspective; and, furthermore, there is no obvious reason to suspect that they are cryptically directing matters. In fact, it could even be argued that the internally closed loops of constraints serve, over the longer run, to sift among genetic variations and to select *for* those that accord better with their own actions, as will be developed below.

7.2. Measuring the Effects of Incorporated Constraints

Such theorizing may be all for the good, but science requires measurement and quantification as well. Any well- posed theory must have the potential to become operational. Herein lies a possible stumbling- block, because there is simply no hope of making explicit, much less measuring, every item of internal constraint in any living system (the Human Genome Project notably *notwithstanding*.) But this quandary is not unknown to those familiar with thermodynamics and statistical mechanics. There one is confronted with effects stemming from an unmanageable number of atomic entities, and it is impossible to follow the actions of each actor in detail. So, rather than attempting to quantify the trajectories of each individual actor, physical attributes of the entire (macroscopic) ensemble are measured. Whole system properties, such as pressure, temperature and volume, are assumed to be common attributes upon which have been implicitly written the contributions of each microscopic event.

This same stratagem can also be applied to ecosystems. One begins by acknowledging the importance of each internal constraint, such as prey escape tactics, mating displays, visual cues, etc. The focus, however, is upon the measurement (or at least estimation) of 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?" This "brutish" description[18] of ecosystem behavior at first glance appears to ignore most of what interests biologists 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.[19]

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, it is necessary first to avoid the significant temptation to assume that closed circuits of concatenated constraints are merely another mechanical agency. With ecosystem networks one is dealing instead with an essentially different dynamics, which is made apparent by two significant points: (1) Constraints in living systems are not rigidly mechanical in nature, but incorporate singular contingencies in a necessary but limited way. (2) Cyclical relationships among some constraints, by virtue of the singular events they incorporate, give rise to categorically non- mechanical agencies.

7.3. Ecosystems and Contingency

That living systems are not fully constrained, i.e., that they retain sufficient flexibility to adapt to changing circumstances, is (along with self- entailment) a necessary attribute of living systems. It should become apparent, 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; for every ecologist is acutely aware of the significant role that the aleatoric plays in ecology. Chance events occur everywhere in ecosystems. Stochasticity is hardly unique to ecology, however, and the entire discipline of probability theory has evolved to

cope with contingencies. Unfortunately, few stop to consider the tacit assumptions made when invoking probability theory -- namely that chance events are always simple, generic and recurrent. If an event is not simple, or if it occurs only once for all time (is truly singular), then the mathematics of probabilities will not apply.

It may surprise some, therefore, to learn that ecosystems appear to be rife with singular events.[20] To see why, it helps to recall an argument formulated by physicist Walter Elsasser.[21] Elsasser sought to delimit what he called an "enormous" number. By this he was referring to numbers so large that they should be excluded from physical consideration, because they greatly exceed the number of physical events that possibly could have occurred since the Big Bang. To estimate a threshold for enormous numbers Elsasser reckoned the number of simple protons in the known universe to be about 10^{85}. He then noted as how the number of nanoseconds that have transpired since the beginning of the universe have been about 10^{25}. Hence, a rough estimate of the upper limit on the number of conceivable events that could have occurred in the physical world is about 10^{110}. Any number of possibilities much larger than this value simply loses any meaning with respect to physical reality.

Anyone familiar with combinatorics immediately will realize that it doesn't take very many distinguishable elements or processes before the number of their possible configurations becomes enormous. One doesn't need Avagadro's Number of particles (10^{23}) to produce combinations in excess of 10^{110} -- a system with merely 80 or so distinct components will suffice. In probabilistic terms, any event randomly comprised of more than 80 distinct elements is virtually certain never have occurred earlier in the history of the universe. Such a constellation is unique over all time past. It follows, then, that in ecosystems with hundreds or thousands of distinguishable organisms, one must reckon not just with occasional unique events, but rather with a legion of them. Unique, singular events are occurring *all the time, everywhere*! In the face of this reality, one must abandon any hope of determinism as a universal characteristic of natural systems, and it becomes difficult as well to conceive of living systems as reversible.

Despite the challenge that rampant singularities pose for the Baconian pursuit of science, a degree of regularity can still be observed in such ecological phenomena as succession. The question then arises as to the origins and maintenance of such order? Unfortunately, the conventional evolutionary narrative is constantly switching back and forth between the realms of strict determinism and pure stochasticity, as if no middle ground might exist. In referring to this regrettable situation, Karl Popper[22] remarked that it still remains for science to achieve a truly "evolutionary theory of knowledge", and one will not be forthcoming until fundamental attitudes toward the nature of causality have been reconsidered. True reconciliation, Popper suggested, lies in envisioning an intermediate to stochasticity and determinism. To meet this challenge, he proposed a generalization of the Newtonian conception 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_2, b_3, b_4, b_5, according to four possible eliciting causes, a_1, a_2, a_3, and 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

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represent predation by predator j, while the a's could represent donations of material or energy by host i.

One notices 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".
One now considers how the table of events might appear, were it possible to completely isolate phenomena, 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 the above discussion, one could view Popper's propensity as a constraint that is unable to perform unerringly in the face of confounding contingencies. Propensity encompasses under a single rubric the entire range of phenomena from singular events, through common chance, all the way to law-like behavior. One notices further that the transition depicted from Table 1 to Table 2 was accompanied by the addition of constraints, and it is the appearance of such progressive constraints that one implies when one invokes the term "development". Returning then to second question at the end of Section 2, one now asks how the incorporation of the aleatoric moves the ensuing dynamics out of the realm of the purely mechanical?

7.4. Autocatalysis and Non-mechanical Behavior

It was mentioned above how constraints can be concatenated and in some cases join 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, in connection with aleatoric events, qualify its action as a non-mechanical causal agency. Investigators such as Manfred Eigen,[23] Hermann Haken,[24] Maturana and Varela,[25] Stuart Kauffman[26] and Donald DeAngelis[27] all have contributed to the growing consensus that some form of positive feedback is responsible for most of the order one perceives in organic systems. It is useful now to focus attention upon a particular form of positive feedback, namely, 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, the reader's attention is drawn to the three- component interaction depicted in Figure 1. It is assumed that the action of process A has a propensity to augment a second process B. It must be emphasized that the use of the word "propensity" implies 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.

An ecological example of autocatalysis is the community that centers around the aquatic macrophyte, *Utricularia,* or bladderworts[28] All members of the genus *Utricularia* are carnivorous plants. Scattered along its feather-like stems and leaves are small bladders, called utricles (Figure 2a). Each utricle has a few hair- like triggers at its 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 (Figure 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.

Autocatalysis among propensities gives rise to at least eight system attributes, which, taken as a whole, comprise a distinctly non-mechanical dynamic. One first notes that by the definition adopted here, 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, one assumes 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. It is seen that 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, one perceives a tendency to reward and support those 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 (Figure 3.)

It follows that, whenever two or more autocatalyic loops draw from the same pool of resources, autocatalysis will *induce competition*. In particular, one notices that whenever two loops partially overlap, the outcome could be the exclusion of one of the loops. In Figure 4, 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 neurons, virtually none of the cells that compose the human body persist longer than seven years. Very few of the atoms in it at a given time were present eighteen months earlier. Yet if a mother were to see her offspring for the first time in ten years, chances are she would recognize him/her immediately.

Autocatalytic selection pressure and the competition it engenders define a preferred direction for the system – that of ever- more effective autocatalysis. In the terminology of physics, autocatalysis, predicated as it is upon eliciting internal constraints, each of which can be asymmetric, is therefore itself *symmetry- breaking*. One should not confuse this rudimentary directionality with full- blown teleology, however. It is not necessary, for example, that there exists 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. Perhaps the simple Greek term "*telos*" connotes better this weaker form of directionality and distinguishes 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, it must be stressed that 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 just described can be considered *emergent*. In Figure 5, 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 just described appear to emerge spontaneously.

7.5. 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, 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. The swords, guns, rockets and other weapons comprise the material causes of the battle.[29] 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. Contemporary thinkers, such as the late Robert Rosen[30] are urging a reconsideration of whether these discarded categories might not serve the interpretation of complex phenomena. Indeed, there appear to be especial reasons why Aristotle's scheme 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 one notices that the domains of influence by soldier, officer and prime minister extend over progressively larger and longer scales. It becomes apparent that autocatalytic loops of constraints 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, [31] Salthe[32]). 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.

7.6. Quantifying Constraint in Ecosystems

With these considerations on contingency, autocatalysis and causality in mind, one may now embark upon quantifying the overall degree of constraint in an ecosystem as manifested by its network of material/energy flows. Two major facets pertaining to the action of autocatalysis are relevant here: (a) Autocatalysis 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 Figure 6. The upper figure represents a hypothetical, inchoate 4- 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. To the right appear the matrices that correspond to the pattern of flows. One recognizes that the transition between matrices resembles that between Tables 1 and 2 that was presented earlier in connection with Popper's propensities.

One begins the analysis 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". (Henceforth a dot in the place of any subscript will denote summation over that index.) The first aspect of autocatalysis can thus be represented 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. The quantification of constraint begins by estimating the joint probability that a quantum of medium is *constrained* both to leave i and enter j as the quotient $T_{ij}/T_{..}$. It should be noted 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 $T_{i.}/T_{..}$ Similarly, the unconstrained probability that a quantum enters j becomes $T_{.j}/T_{..}$ Finally, one notes how the probability that the quantum could make its way by pure chance from i to j, *without* the action of any *constraint*, would be equal to the product of the latter two frequencies, or $T_{i.}T_{.j}/T_{..}^2$.

This last probability obviously is not equal to the constrained joint probability, $T_{ij}/T_{..}$. Recalling that Tribus and McIrvine[33] defined information as "anything that causes a change in probability assignment", one may conclude that Tribus essentially equated information to constraint. Information theory, therefore, must contain clues as to how to quantify constraint. It does not, however, address information (constraint) directly. Rather it uses as its starting point a measure of the rareness of an event, first defined by Boltzmann[34] 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 Boltzmann[34] formula to the probability just defined, i.e., $-k \log(T_{.j}T_{i.}/T_{..}^2)$, 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 $k \log(T_{ij}T_{..}/T_{.j}T_{i.})$. (It is noted in passing that this quantity also measures the *propensity* for flow from i to j (Ulanowicz[35])).

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,

$$AMC = k \sum_{i,j} \left(\frac{T_{ij}}{T_{..}} \right) \log \left(\frac{T_{ij}T_{..}}{T_{.j}T_{i.}} \right) \qquad (1)$$

where AMC is the "average mutual constraint" (known in information theory as the average mutual information.)

To illustrate how an increase in AMC actually tracks the "pruning" process, the reader is referred to the three hypothetical configurations in Figure 7. 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, and the AMC assumes its maximal value for a network of dimension 4. Zorach and Ulanowicz[36] have shown how the geometric mean number of roles (trophic levels) in a flow network can be estimated as b^{AMC}, where b is the base used to calculate the logarithms in the formula for AMC.

One notes in the formula for AMC that the scalar constant, k, has been retained. Although autocatalysis is a unitary process, separate measures have been defined for its two attributes. One 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 k is set equal to T.., and the resulting product is called the system *ascendency*, A, where

$$ A = \sum_{i,j} T_{ij} \log\left(\frac{T_{ij} T_{..}}{T_{.j} T_{i.}} \right). \tag{2} $$

In his seminal paper, "The strategy of ecosystem development", Eugene Odum[37] 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[35]). It follows as a phenomenological principle that *"in the absence of major perturbations, ecosystems have a propensity to increase in ascendency."*

It should be emphasized 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, which is complementary to the ascendency (Ulanowicz and Norden[38]):

$$ \Phi = -\sum_{i,j} T_{ij} \log\left(\frac{T_{ij}^2}{T_{.j} T_{i.}} \right). \tag{3} $$

Overhead quantifies the inefficiencies and incoherencies present in the system. As with the ascendency, Zorach and Ulanowicz[36] have demonstrated how the logarithm of the geometric mean of the network link-density, LD, is equal to one-half of the overhead. That is, $LD = b^{\left(\frac{\Phi}{2}\right)}$. (Link- density is the effective number of arcs entering or leaving a typical node. It is one measure of the connectivity of the network.) Although the inefficiencies contributing to overhead may encumber the system's overall 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 arbitrary rigors of its

environment. The configurations observed in nature, therefore, appear to be the results of a dynamical tension between two antagonistic tendencies (ascendency vs. overhead.)

Experience has revealed that the effective numbers of roles and the connectivities of real ecosystems are not arbitrary.[39] (Ulanowicz, in press.) It has long been known, for example, that the number of trophic roles (levels) in ecosystems is generally fewer than 5 (Pimm and Lawton[40]). Similarly, the effective link- density of ecosystems (and a host of other natural systems) almost never exceeds 3 (Pimm[41], Wagensberg *et al.*[42] 1990.) Regarding this last stricture, Ulanowicz[43] (2002) suggested how the May-Wigner stability criterion[44] could be re-interpreted in information- theoretic terms to identify a threshold of stability at $e^{\left(\frac{e}{3}\right)}$, or ca 3.015 links per node.

Both limits appear quite visibly when one plots the number of roles versus the effective connectivity of a collection of 44 estimated ecosystem flow networks (Figure 8.) Whereas the pairs of numbers generated by randomly- constructed networks are scattered broadly over the positive quadrant, those associated with actual ecosystem networks are confined to a small rectangle near the origin. Ulanowicz[45] has labeled this rectangle the "window of vitality", because it appears that the entire drama of ecosystem dynamics plays out within this small theatre: As mentioned above, the *endogenous* tendency of ecosystems is to drift towards the right within this window (i.e., toward ever-increasing ascendency, or higher system performance.) At any time, however, singular events can appear as exogenous perturbations that shift the network abruptly to the left. (Whether the link- density rises or falls during this transition depends upon the nature and severity of the disturbance.) In particular, whenever the system approaches one of the outer edges of the window, the probability increases that it will fall back towards the interior. Near the top, horizontal barrier (LD = ~ 3.015 links per node) the system lacks sufficient cohesiveness and disintegrates spontaneously. As the system approaches the right- hand frame (# roles = 4.5 to 5.0), it presumably undergoes something like a "self-organizing catastrophe" (Bak[46]) as described by Holling[47] (see also Ulanowicz[29]).

As one follows the historical trajectory of an ecosystem within the window of vitality, it is important to hold firmly in mind that any description of a history solely in terms of mechanisms and the actions of individual organisms will perforce remain inadequate. Rather, the prevailing agencies at work are the tendency of configurations of processes (sub graphs) to increase in ascendency acting in opposition to the entropic tendency generated by complex, singular events.

7.7. New Constraints to Help Focus a New Perspective

It is worthwhile at this juncture to recapitulate what has been accomplished: First, the focus in ecosystem dynamics has been shifted away from the normal (symmetrical) field equations of physics and directed instead towards the origins of asymmetry in any system -- the boundary constraints. It was 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. Then a palpable and measurable entity (the network of material/energy exchanges) was identified upon which the myriad of (mostly hidden) constraints could write its signature. Finally, a calculus was developed that could quantify the effects of all the hidden constraints. As a result, by following changes in the ascendency and overhead of an ecosystem flow network, one is focussing squarely upon that which makes ecodynamics fundamentally different from classical dynamics.

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 one is to look at nature. It is only fair to ask how well does that metaphysic support the emerging ecodynamics that have just been described (Ulanowicz[48])? To provide a basis for comparison, one must first describe the Newtonian metaphysic as it appeared at its zenith.

Depew and Weber[49] 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.

> To Depew and Weber's list may be added a fifth article of faith (Prigogine and Stengers [50], Ulanowicz[29]), 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.

Given the ground that has been covered here, it becomes apparent that the Newtonian metaphysic accords rather poorly with ecodynamics. In fact, the new dynamics appear to be dissonant with *each* of the five Newtonian precepts. To wit:

> 1. Ecosystems are not causally closed in that 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[6]; Ulanowicz[29])

> 2. Ecosystems are not deterministic machines. They are *contingent* in nature, and such contingency is often singular. 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 (often singular) 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 this ecological worldview may at first blush seem wholly revolutionary, it actually follows Popper's *evolutionary* leads and thereby retains 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[48])
 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 mistakenly still referred to as "quantum mechanics", despite the fact that there is virtually nothing mechanical about the phenomena.) As Casti has admonished, it is past time to make a clean break with the vision of "*natura cum machina*" (Dennett[51]). If it doesn't look like a machine, if it doesn't act like a machine, if it doesn't smell like a machine, why then persist in calling it a machine? Such procrustean nostalgia only fosters a highly distorted vision of the natural world. Metaphors and methods are emerging that are far more effective and appropriate to charting the pathways that the living world has blazed for itself (Ulanowicz[52]) The era of climbing trees is passing; the time is well-nigh to move beyond rocket science.

Acknowledgements

7.8. References

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TABLES

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	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

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

FIGURE CAPTION

Figure 1. Schematic of a hypothetical 3-component autocatalytic cycle.

Figure 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*.

Figure 3. Centripetal action as engendered by autocatalysis.

Figure 4. (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

Figure 5. 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.

Figure 6. 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.

Figure 7. (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.

Figure 8. Combinations of link densities and numbers of roles pertaining to random networks (open circles) and actual ecosystems networks (solid squares.) The "window of vitality" is indicated by the dotted lines.
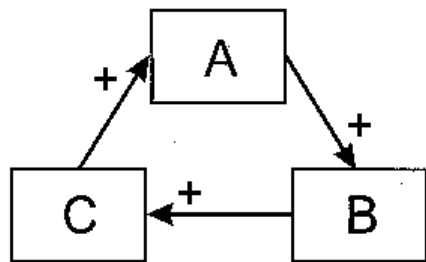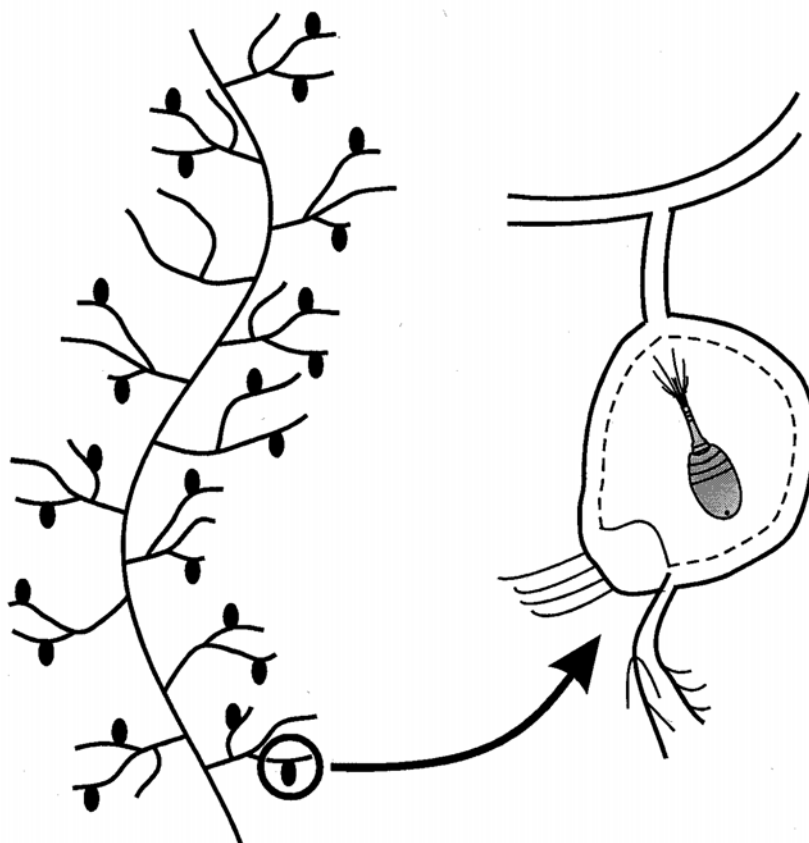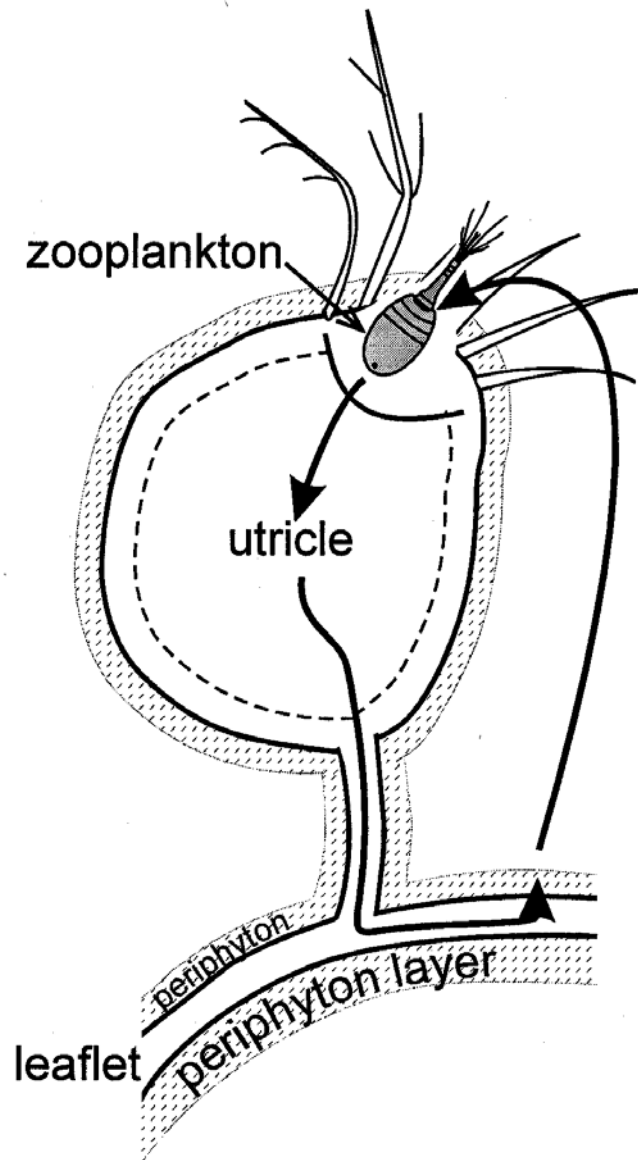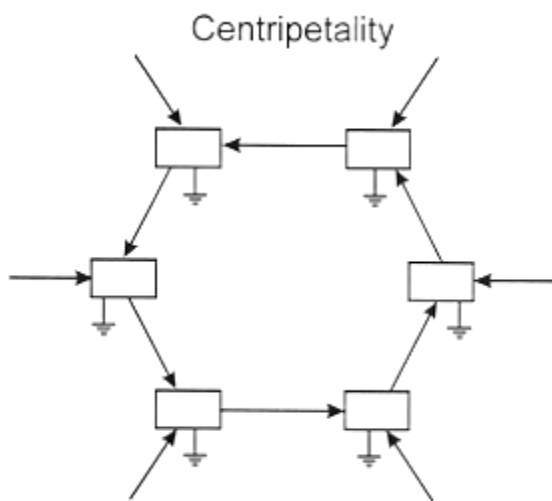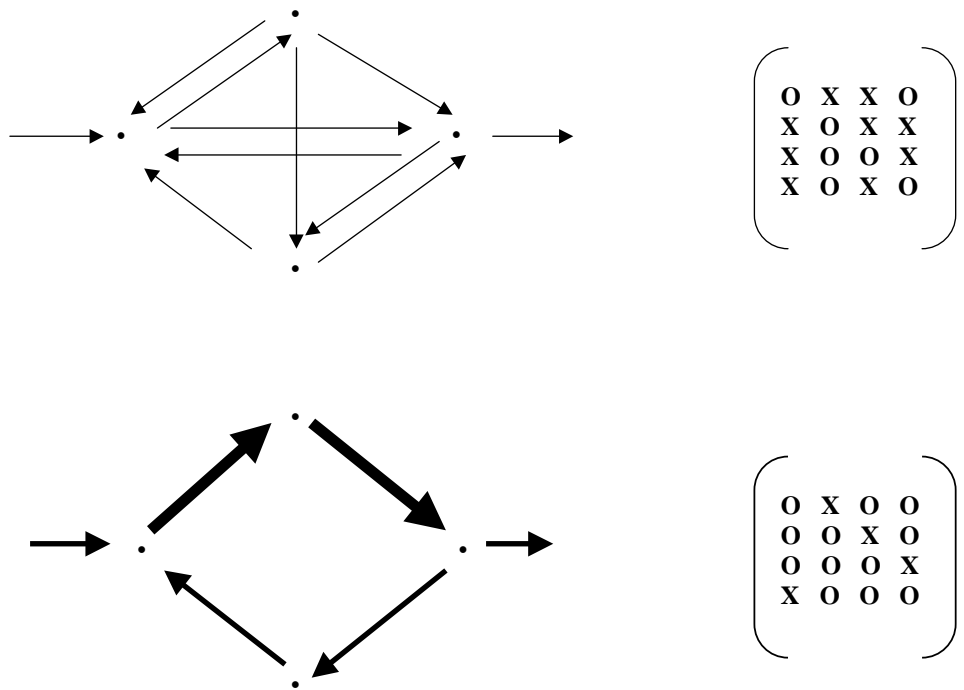
Figure 1

Figure 2a

Figure 2b)

Centripetality

Figure 3

(a)

(b)

(c)

Figure 4

enlarged system boundary

original system boundary

Figure 5

$$\begin{pmatrix} O & X & X & O \\ X & O & X & X \\ X & O & O & X \\ X & O & X & O \end{pmatrix}$$

$$\begin{pmatrix} O & X & O & O \\ O & O & X & O \\ O & O & O & X \\ X & O & O & O \end{pmatrix}$$

Figure 6

(a)
AMC = 0

(b)
AMC = K

(c)
AMC = 2K

Figure 7

Figure 8