2.10 Network Orientors: Theoretical and Philosophical Considerations why Ecosystems may Exhibit a Propensity to Increase in Ascendency

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Abstract

Three disparate metaphors have dominated the discourse on ecosystem dynamics: The ecosystem as (1) machine, (2) organism, or (3) stochastic assemblage. Motivated, in part, by ambiguities of this nature, Karl Popper suggested the notion of "propensity" to generalize the Newtonian concept of force. Using propensities one can articulate a theory of ecosystem development that encompasses all three analogies. Probabilistic indices borrowed from information theory can be used to quantify the degree of trophic constraint operating in an ecosystem, the amount of flexibility available for it to adapt to new circumstances, and, ultimately, the propensity for each transfer to occur. Consequently, the ascendency of an ecosystem may be defined as the flow-averaged system level propensity for activity. Under this rubric, the observed propensity for ascendency to increase over time becomes the probabilistic counterpart for living systems to Newton's second law in mechanics.

2.10.1 Introduction

In his recent book, "An Entangled Bank", Joel Hagen (1992) traces the development of the concept of ecosystem. Throughout his narrative he lays great emphasis on the role that metaphors have played to express various concepts. From among the various metaphors for ecosystems, it is possible to identify three enduring themes: The ecosystem as (1) machine, (2) organism, or (3) chance assembly.

Of the three analogies, only that of the machine has deep roots in the modern synthesis. Thus do Depew and Weber (1994) argue that Darwin himself inherited his strictly mechanical vision of evolution from Newton via Malthus and Smith. George Clarke (1954), in his textbook on ecology, went so far as to depict ecosystem populations and processes as the gears and wheels of a machine. Elsewhere, the mechanical aspects of ecosystem behavior have been emphasized in

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recent years by Connell and Slatyer (1977) and most notably in the technocratic visions of Howard Odum (1960).

The machine notwithstanding, the analogy that motivated most of American ecology early this century was the simile of ecosystem as organism. It should be noted that it was precisely the Aristotelian notions of organicism that had been so vehemently eschewed by the early leaders of the modern movement, such as Francis Bacon and Thomas Hobbes (see below). Hagen traces the prominence of organismal thought in ecology to Frederic Clements (and Shelford 1939), who identified the romanticism of Jan Smuts (1926) as a leading influence in his thinking. Clements' notions have been defended in the face of withering criticism by such eminent personalities as G. Evelyn Hutchinson and Eugene Odum (1977).

Ironically, the strongest opposition to organicism in ecology has come not from the defenders of newtonianism, but rather from latter-day nominalists. In the eyes of these critics the structure and function of ecosystems have been greatly exaggerated (at best). What Clements regarded as intricate coordination among the biotic elements of a forest, Gleason (1917) viewed as only a random assembly of plant species. During the 1950's there was a significant defection of American ecologists from the Clementsian viewpoint towards the nominalist persuasion. Some see changing social fashions behind the shifts in metaphors for ecosystems (Barbour 1996; Schwarz, this volume).

Metaphors are intended to be loose analogies. That is, there must be some correspondence between the entities being compared, but it is also understood that significant differences remain. A fortiori, commonalties and discrepancies will also exist among the three metaphors. To discuss better the relationships among the three metaphors applied to ecosystems, it helps to focus upon one of them as a point of reference, describe briefly its fundamental tenets, and then discuss how the remaining two differ or agree as regards those items. (Table 2.10.1)

Ulanowicz (1997), following the lead of Depew and Weber (1994), has characterized the mechanical, or Newtonian perspective as based upon five fundamental postulates about the universe. Most importantly, the Newtonian world is assumed to be closed to all causes, save for those that are either material or mechanical (efficient). All other types are strictly enjoined. While the nominalists recognize material and mechanical causes as legitimate, they regard the world as being less lawful than Newtonians would maintain (see "determinism" below). The organicists have been heavily influenced by Aristotle's ideas on causality and allow, in addition to the material and mechanical, the workings of formal and final causes in nature.

Perhaps the four categories of causation are best illustrated in the (unfortunately, unsavory) example of a military battle. The material causes are taken to be the swords, guns, tanks or other ordnance used in the fray. The efficient agents are the individual soldiers who wield the swords, pull the triggers or drive the tanks in their efforts to inflict terrible harm upon their adversaries.

Formal agencies can be either static or dynamical. The former is revealed in the influence that the landscape and topography has upon the conflict, whereas the latter exists in the ever-changing spatial juxtaposition of the armies with respect to each other. The final cause of the battle usually extends beyond the battlefield and is seen in the social, economic and political factors that brought the armies against each other.

Table 2.10.1. Comparisons of Outlooks

Mechanism (Newtonianism)	Organicism (Holism)	Stochasticism (Nominalism)
Material, Mechanical	Material, Mechanical, Formal, Final	Material, Mechanical
Atomistic	Integral	Atomistic
Reversible	Irreversible	Irreversible
Deterministic	Plastic	Indeterminate
Universal	Hierarchical	Local

The Newtonian world is considered to be atomistic. Newtonian systems can be divided for the sake of study, and the working of the ensemble is regarded to be naught but that of the individual parts in concert. Of course, atomism is the keystone of nominalism. At the other end of the spectrum is the organicist outlook, whereby living systems are considered to be integral and indivisible. Organicists always regard information about system parts acting in isolation to be insufficient for a full explanation of the dynamics of the whole.

Newtonianism alone assumes that the world is reversible. Newton's laws are all reversible with respect to time. A motion picture taken of a Newtonian event, such as the collision of two billiard balls, looks qualitatively the same, whether it is run forward or in reverse. Neither organicism nor stochasticism assumes reversibility.

To a newtonian the world is deterministic. Given the specifications of a system and its environment at any one time, the newtonian holds that it is possible in principle to predict the state of the system at any later time, insofar as the behavior of the environment during the interim is known. Any discrepancies between newtonian predictions and subsequent observations are ascribed to ignorance. At the other extreme is the stochastic, who regards order as passing illusion. Organicists fall somewhere between these two poles and usually regard systems as being what might best be termed "plastic". Organicists' opinions range the gamut from Clements with his rigid, almost mechanical version of holism, to Lovelock (1979) and his more liberal vision of the biotic control of the physical environment, where little in the way of a fixed endpoint is evident (other than life itself).

Finally, newtonian laws are considered to be universal across all scales of time and space. Nominalists patently eschew universals in favor of concentrating solely upon the individual, local event. Again, organicism falls between these extremes, taking what has been described as a "hierarchical" view of the world. The hierarchical worldview involves more than simply the (epistemic) nesting of biological order into sequences, such as biome, ecosystem, population, organism, etc. More importantly, hierarchicalists assume that there exist laws and regularities that pertain to each scale, but that the influence of any particular law diminishes in proportion to how remote is the scale at which the particular law was formulated from that of the event to which it is to be applied (Allen and Starr 1982). For example, to most biologists (but not to all, e.g. Wilson 1975) it would appear ill-advised to try to relate higher-level social behavior to some genetic antecedents. Physicists, on the other hand, mix gravitational and quantum-level phenomena with apparent abandon.

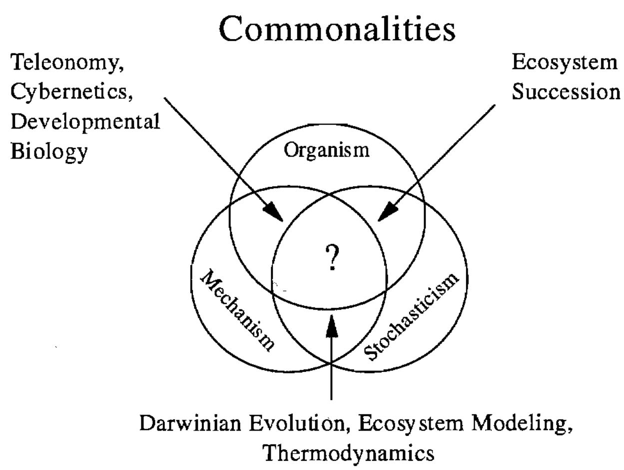

Fig. 2.10.1. Venn Diagram showing the relationships among the three perspectives prevalent in ecosystems science

By now it should be apparent that the three perspectives on ecosystems have certain features and assumptions in common (Fig. 2.10.1). Both the newtonian and stochastic outlooks, for example, are causally closed and regard systems as atomistic; the organismal and stochastic viewpoints both assume events are irreversible, etc. It should not be too surprising, therefore, to encounter narratives that are built upon these overlaps. For example, classical cybernetics and developmental biology combine some aspects of organisms with simple mechanisms. Darwinian evolution, conventional ecosystem modeling and even thermodynamics all include elements both of mechanism and chance. Ecosystem succession seems to involve both organic and stochastic dynamics.

The question remains whether any discipline can build upon the tripod of all three perspectives. Judging from how fragments particular to each of the three viewpoints are found throughout ecology, it would seem that only an amalgam of all three perspectives will suffice as a foundation for ecology. It will be argued here that such a trilateral common ground does exist. Furthermore, it will be suggested that the best approach to deriving an amalgamated ecosystem theory might be to concentrate first on the marriage of mechanism and chance at the macroscopic level into what Karl Popper (1990) has called "propensities". To this very general and abiotic concept can be subsequently appended the organic notions of cybernetics and autocatalysis. Finally, to implement these ideas it will be necessary to derive an explicit mathematical form by which propensities may be quantified and estimated.

2.10.2 A World of Propensities

Perhaps the central tenet in the modern synthesis is that all events are the results of material particles acting according to newtonian-like laws. Nothing happens that is not lawfully ordained. It is the portrait of a closed universe. As LaPlace (1814) speculated, if some superior intelligence could have complete knowledge of the positions and momenta of all particles in the universe, it would be able to hindcast all of history and forecast all of the future. We now realize that LaPlace was far too optimistic. Both the formulation of the second law of thermodynamics by Carnot (1824) and the more recent development of quantum physics have raised doubts about the plausibility of a closed universe. But the newtonian vision of a closed world has been altered only marginally as a result of these challenges. Conventional wisdom now allows as how causality may deteriorate at the edges of reality (i.e., at very small and very large scales), but the universe at the scale of direct human observation is still assumed to operate in newtonian fashion. For example, biology's "Grand Synthesis" permits chance to operate at the molecular scale of the genome, but restricts the remainder of the living world to lawful behavior (Ulanowicz 1997) .

In the neo-Darwinian scenario for evolution the observer is always being forced to switch back and forth abruptly from the stochastic netherworld of Boltzman (the genome) to the deterministic theater of Newton (the phonome and its environment). It is a rather schizoid depiction of reality, prompting some to seek a vision that is more inclusive of both true accident and limiting constraint. For example, Charles Sanders Pierce (1877) has suggested that the world is causally open, and Karl R. Popper (1990) has concluded that a full grasp of the nature of evolution is impossible under the assumption of a closed universe. To

Popper the key to his wider vision of nature lies in expanding the narrow newtonian concept of force. Forces are but special, limiting cases of a broader notion that he has called "propensities".

A propensity is the tendency for a certain event to occur under given circumstances. There are two noteworthy features of this definition. First is the notion of chance or probability; second is the requirement that surroundings always be taken into account. In the absence of both of these conditions, propensity degenerates into the conventional notion of a force. I.e., a force is a propensity that acts in isolation.

As an example, if situation B *always* follows upon condition A, then one may conclude that B is lawfully related to A in a way that allows one to search (or define) a causal "force" behind the transition. In terms of probabilities, this situation is trivial: Given A, B always follows-without exception. The conditional probability of B happening, given that A has been observed becomes unity [$p(B|A)=1$].

When phenomena are truly in isolation, as is nearly the case with gravitational attraction between heavenly bodies, or when ensembles of events are virtually independent of each other (so that the atomistic postulate holds), then it suffices to describe events in terms of newtonian forces. Ecologists are keenly aware that such conditions rarely occur in the field, and true isolation is usually difficult, if not impossible, to achieve in the laboratory. A more realistic scenario is that when A happens, then B occurs *most of the time*. But not always! On occasion, A is followed by C, or by D, or by E, etc. As a consequence, $p(B|A)<1$, and $p(C|A)$, $p(D|A)$, etc., are all >0. Popper attributes these latter, non-zero conditional probabilities to unavoidable "interferences" among processes.

Popper is always relating propensities to conditional probabilities, but he never claims that conditional probabilities by themselves quantify propensity. He regards the quantification of propensities as an unsolved problem and counsels only that "We need to develop a calculus of conditional probabilities." Hence, the task remains to derive a formula involving conditional probabilities that fully characterizes the notion of propensity and merges smoothly with existing phenomenology.

At this point it should be noted that Popper has advocated a subtle, but very significant shift regarding the interpretation of probabilities. Since their inception, probabilities have been invoked to treat an observer's ignorance about the details of a situation. For example, one says that the probability that any given number will turn up after the throw of a die is 1/6. Presumably, if one knew the exact translational and rotational momenta, as well as the exact position and attitude of the die at any given instant during its trajectory, then that information, along with the values of certain parameters such as the elasticity of the die and the surface, the precise shape of the die, etc., one would be able to predict which face would show.

Popper, however, is advocating the use of conditional probabilities, not simply to cover the ignorance of the observer, but also to pertain to a degree of indeterminacy *inherent in the situation itself.* This shift is from the epistemic toward the ontological. Some readers probably will be reluctant to accept such interpretation and cling instead to the faith expressed by LaPlace. It is worthwhile noting, however, that the argument from knowledge of detail is predicated upon the assumption of atomism, which is not an element of the organic perspective.

Finally, Popper emphasizes that propensities, unlike forces, cannot exist divorced from their surroundings. An essential element of propensities is their context, which invariably includes other propensities. Thus, one sees how circularity is actually built into the definition of propensities, and one may exploit that circularity to help articulate Popper's "calculus of conditional probabilities".

2.10.3 Propensities in Propinquity

What, indeed, does happen when many propensities interact with each other? One may begin by focusing upon bilateral interactions. If unilateral effects can be characterized as being either positive (+), negative (-), or neutral (0), then the nature of bilateral interactions can be denoted by couples of unilateral interactions, i.e., predation (+,-), competition (-,-), neutralism (0,0), etc. Of the nine possible couples, mutualism (+,+) exhibits singular characteristics that impart to its participants the advantage to persist, on the average, beyond the duration of components engaged in other types of interactions. Furthermore, it may be argued that ensembles of mutualistic interactions, or what in chemistry is called "autocatalytic configurations", exhibit behaviors that are decidedly non-mechanical (i.e., organic) in nature (Ulanowicz 1989, 1997).

To illustrate and study the nature of autocatalysis it helps to consider a triad of processes, A, B, and C. It is assumed that the activity of A has a *propensity* to increase the activity of B. B, in turn, exerts a similar propensity upon C, which has the same effect upon A. Thus, the indirect effect of A upon itself is positive, giving rise to autocatalysis. It should be noted, however, that, unlike in chemistry, A, B, and C do not have to be mechanically linked. That is, the activity of A does not have to abet that of B in every instance–just in most.

To elaborate upon the special attributes of autocatalysis, one may cite at least eight significant properties (Ulanowicz 1989, 1997):

1. That autocatalysis is *growth enhancing* is virtually tautological in that activity anywhere in the loop tends to increase activity in all the other members.
2. It is *selective,* because perturbations that enhance catalysis are rewarded, whereas those that impair activity are decremented. For example, suppose a chance perturbation occurs to element B that happens to increase either its sensitivity to A or the catalytic effect it has upon C. Then the effects of that change will be propagated around the loop in such a way that the activity levels of all elements will be augmented. In particular, the perturbation in B will be rewarded. The opposite occurs when a random change to B either de-

creases the catalytic effect of A or diminishes B's effect upon C. The same feedback results in B's receiving less catalysis from A.

3. Autocatalysis is *symmetry-breaking* in that the selection it engenders defines a preferred direction for change. The direction of catalysis (A --> B --> C) prevails strongly over anything occurring in the counter sense.
4. Selection favors those changes that bring more material and energy into the autocatalytic cycle, thereby inducing what may be called *centripetality*. As a particular example of the selectivity, suppose that the change to B is such that it brings in more of the material and energy necessary to support B's activity. This change will be rewarded. By induction one may conclude that the reward structure for *each* component works to increase the input of elements necessary for the functioning of that compartment. The net result is that the autocatalytic loop resembles the focus of a radial pattern of centripetal flows.
5. Selection and centripetality thus work to *induce competition* between autocatalytic cycles and favor the replacement of components by taxa that are more efficient at sustaining autocatalytic activity. Particular compartments may come and go like actors in a play, whilst the overall feedback structure (the play itself) persists. In other words, the overall cycle is likely to have a characteristic lifetime that exceeds that of any particular constituent.
6. The combined attributes of selection, centripetality and longer lifetime all point toward of a degree of *autonomy* that the autocatalytic configuration as a whole possesses from the properties and histories of its parts. (No one is suggesting the complete autonomy of higher level processes - they remain dependent upon events at the lower levels. The former, however, can no longer be reduced entirely to the latter. I.e., the autocatalytic system is not atomistic.)
7. The foregoing considerations should make it clear that autocatalysis can be characterized as *emergent,* in the sense that some or all of the foregoing properties might be missed if one were to observe only a part of the cycle. By considering only a fragment of an autocatalytic cycle one might mistakenly be led to identify an input as an autonomous initial cause and an output as a determined terminal effect. As soon as one increases the scope of observation so as to encompass all members of the loop, however, the interdependence of such causes and effects becomes apparent, and the foregoing attributes begin to emerge.
8. Finally, autocatalysis is *formal* in the sense that the cycle is a relational form of individual processes.

As to the overall effects these combined properties have upon the development of a flow network, it may be said that they change both its extensive and intensive natures. Extensive properties are those that depend upon the size of the system, and the growth enhancing nature of autocatalysis acts like a ratchet to push the activity level of the cycle ever higher. Meanwhile, selection and associated properties change the qualitative (intensive) character of the network by "pruning" away (or at least diminishing) those elements of the network that are less engaged in autocatalytic activities. The net effect of indirect mutualism is depicted schematically in Fig. 2.10.2. Fig. 2.10.2a represents an inchoate network with ill-defined transfers among the components. After autocatalysis has increased the activity level of the system (indicated by the thicker arrows) and pruned away the autocatalytically less efficient links, the network comes to resemble more the configuration in Fig. 2.10.2b.

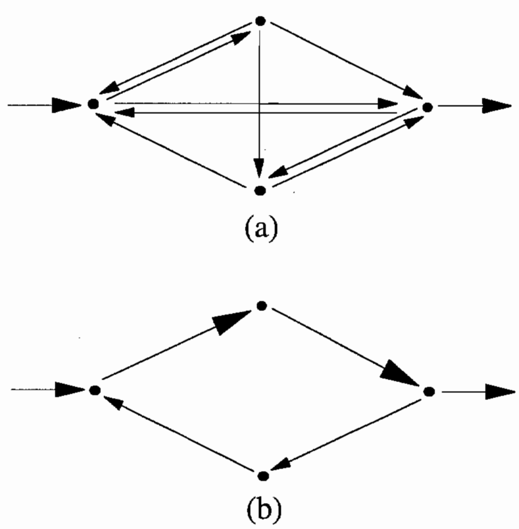

Fig. 2.10.2. Schematic representation of the effects of autocatalysis upon flow networks: (a) A typical inchoate starting network. (b) Same system after autocatalysis has reinforced certain pathways and winnowed others.

2.10.4 Quantifying Constraint and Freedom

Regarding the transition from configuration 2.10.2a to 2.10.2b, it is obvious that flow is more constrained in the latter. That is, for any compartment in 2.10.2a there are more possibilities for transfer (or, more generally, influence) than are evident in 2.10.2b. All other things being constant (an important assumption that will be discussed below), the effects of autocatalysis and competition are progressively to constrain influence to operate along those pathways that are most efficient at autocatalysis. Hence, to quantify the transition from 2.10.2a to 2.10.2b, one must derive expressions for the relative amounts of constraint and freedom in each case.

Quantifying constraint is a task accomplished most effectively by using information theory. Most unfortunately, there is a widespread opinion that information theory, because it was first formulated in communication theory, has only metaphorical application outside of that narrow domain. This is a very mistaken and counterproductive mind set. Fundamentally, information theory is about quantifying changes in probability assignments, and is legitimately applicable anywhere one can define a proper probability (Tribus and McIrvine 1971; Ulanowicz 1986). To help emphasize this generality, the following derivation will be accomplished using a lexicon of constraint and freedom, rather than the conventional terms, information and uncertainty. This alternative nomenclature also has the advantage of emphasizing that freedom may stem, in part, from the inherent nature (ontology) of a situation, and not entirely from inadequacies on the part of the observer (epistemology).

Following the lead of Boltzman, the *indeterminacy* of any particular outcome is defined to be proportional to the negative logarithm of the probability of that outcome, i.e.,

$$f_i = -k \log p(A_i) \tag{2.10.1}$$

where $p(A_i)$ is the probability that event A_i will occur, f_i is the indeterminacy of A_i and k is a scalar constant (which will be discussed presently). Now $p(A_i)$ is the unconditional probability that A_i will occur under all possible conditions. If, in some instances, B_j were to occur just prior to A_i, then one could speak of the *conditional* probability, $p(A_i|B_j)$, which , in general, would be different from $p(A_i)$. As in Equation 2.10.1, the indeterminacy of A_i consequent to B_j (call it f_{ij}) would be

$$f_{ij} = -k \log p(A_i|B_j) \tag{2.10.2}$$

If B_j somehow constrains A_i, the situation becomes less indeterminate, and one would expect f_{ij} to be smaller than f_i.

Hence, one may speak of the constraint, C_{ij}, that B_j exerts upon A_i as

$$C_{ij} = f_i - f_{ij} \tag{2.10.3a}$$

$$= -k \log p(A_i) - [-k \log p(A_i|B_j)] \tag{2.10.3b}$$

$$= k \log[p(A_i|B_j) / p(A_i)]. \tag{2.10.3c}$$

It is worthwhile noting that $C_{ij} = C_{ji}$. This is a result of Bayes' Theorem, which may be invoked to show that

$$\frac{p(A_i|B_j)}{p(A_i)} = \frac{p(A_i|B_j)}{p(B_j)} = \frac{p(A_i, B_j)}{p(A_i)p(B_j)}, \tag{2.10.4}$$

where $p(A_i, B_j)$ is the (symmetrical) joint probability that A_i and B_j occur together. In words, the constraint that B_j the exerts upon A_i is equal to the constraint that A_i exerts upon B_j. One may regard this symmetry as the probabilistic analog to Newton's Third Law, which states that for every action there is an equal and opposite reaction.

To estimate the aggregate constraint that all A_i and B_j are exerting upon each other, one weights each C_{ij} by the probability $p(A_i, B_j)$ that A_i and B_j co-occur, and then sums these products over all combinations of i and j:

$$C = k \sum_i \sum_j p(A_i, B_j) \log[p(A_i, B_j)/p(A_i)p(B_j)], \tag{2.10.5}$$

where C represents the average mutual constraint at work in the system as a whole.

To estimate C for a given system, one first must attach specific physical events to A_i and B_j. One convenient identification is with the transfers of some particular form of material or energy. Thus, A_i might represent a quantum of medium entering compartment i. B_j is associated with a quantum of medium leaving compartment j. In order to account for all medium passing through an n-compartment system, one must include exchanges with the external world. This can be done by letting j=0 be the origin of all external inputs to the system, and i=n+1 be the sink for all exports (Hirata and Ulanowicz 1984). If the amount transferred from i to j is denoted by T_{ij}, then one possibility for estimators for the probabilities in Equation 2.10.5 might be

$$p(A_i, B_j) \sim T_{ij}/T \tag{2.10.6}$$

$$p(A_i) \sim (\sum_{q=1}^{n+1} T_{iq})/T \tag{2.10.7}$$

$$p(B_j) \sim (\sum_{p=0}^{n} T_{pj})/T, \tag{2.10.8}$$

where

$$T = \sum_{p=0}^{n} \sum_{q=1}^{n+1} T_{pq} \tag{2.10.9}$$

is a measure of aggregate activity, called the "total system throughput". (These probabilities could have been defined in a number of ways. Ulanowicz and Abarca-Arenas [1997], for example, use compartmental stocks to estimate apriori rates of exchange, but the original definitions, cast wholly in terms of flows, are retained here for the sake of simplicity.)

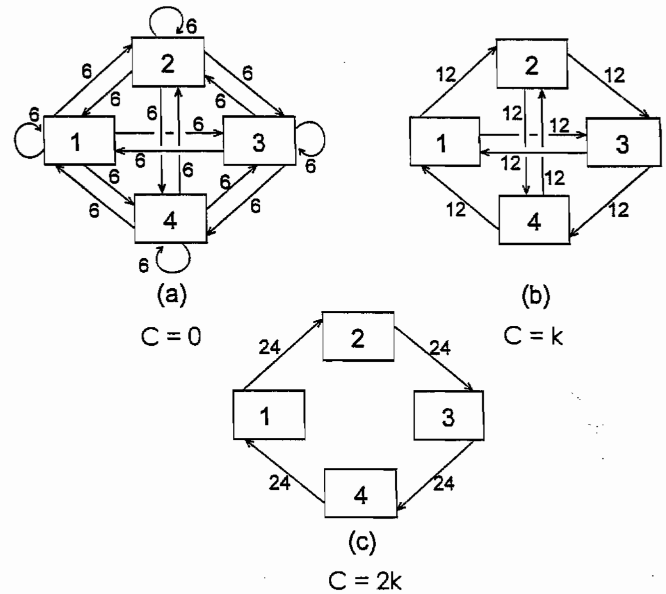

Fig. 2.10.3. Three progressively constrained configurations of flow among four compartments: (a) The wholly equivocal scenario. Medium is equally likely to flow to any component in the system. (b) Flow exiting any compartment is constrained to flow to only two other compartments. (c) Fully constrained configuration. Each compartment can contribute to only one other component. The value of "C" or "constraint" is calculated from formula (2.10.10)

Substitution of (2.10.6) - (2.10.9) into (2.10.5) yields

$$C = k \sum_{i=0}^{n} \sum_{j=1}^{n+1} (T_{ij}/T) \log[T_{ij} T / (\sum_{p=0}^{n} T_{pj})(\sum_{q=1}^{n+1} T_{iq})] \tag{2.10.10}$$

as the estimate of constraint inherent in any network of quantified flows. Fig. 2.10.3 illustrates that C behaves in the desired manner. In Fig. 2.10.3a, there is maximal indeterminacy about where a quantum of medium will flow next. In Fig. 2.10.3b medium is more constrained in where it may flow. Finally, flow in Fig. 2.10.3c is maximally constrained: from any given compartment flow may proceed to only a single prescribed recipient.

Although C characterizes the intensive consequences of increasing autocatalysis, it does not address the extensive change, namely, the increase in system activity. Also, the scalar constant, k, remains undefined. Both of these deficiencies can be corrected by using the scalar constant to impart physical dimensions to the constraint index (Tribus and McIrvine 1971).

By setting k=T one scales the constraint index by the total system activity and simultaneously eliminates the denominator from the multiplier of the logarithm. This scaled measure of constraint is renamed the system "ascendency". It quantifies both the "size" of the system and the degree to which the system activity is organized by its internal constraints.

$$A = \sum_{i=0}^{n}\sum_{j=1}^{n+1} T_{ij} \log[T_{ij}T/(\sum_{p=0}^{n} T_{pj})(\sum_{q=1}^{n+1} T_{iq})] \tag{2.10.11}$$

Ascendency was formulated initially as a phenomenological index that encapsulates several of the criteria that Odum (1969) had identified as characteristics of systems in the later phases of ecosystem succession (Ulanowicz 1980). His list of 24 criteria can be summarized in terms of four tendencies: Natural ecosystems tend to increase in species richness, predator/prey specificity, internalization, and cycling. *Ceteris paribus*, increases in each of these attributes contribute to a higher ascendency. A larger number of species means that all summations in formula (2.10.11) will be extended. Narrower predator/prey specificity was seen in Fig. 2.10.3 to be an explicit contribution to C, the measure of constraint. Finally, both internalization and cycling contribute toward greater system activity (total system throughput.) Whence, observation suggests that "in the absence of major perturbations, ecosystems naturally tend towards configurations of ever-greater ascendency".

2.10.5 Caveat

Ascendency seems to provide an appropriate goal function with which to describe ecosystem development. While this is true to an extent, it is imperative to emphasize immediately two important disclaimers.

This first caveat is that ascendency tells only a part of the story of ecosystem development. If ecosystems were fully constrained, then the metaphor of the machine would have been sufficient. But organic behavior requires certain freedom from total constraint. Of course, without constraint there would be no system worth studying (the nominalist extreme). Without sufficient freedom, however, a system becomes brittle (Holling 1986) and unable to adapt to a changing environment. It dies or collapses to some inchoate configuration.

Fortunately, it is straightforward to quantify the freedom still possessed by A_i and B_j beyond their mutual constraint. In fact, the residual freedom that A_i possesses in the presence of B_j already has been defined as, f_{ij}, the indeterminacy of

A_i consequent to B_j. (See equation 2.10.2). Calculated in similar fashion, f_{ji} expresses the indeterminacy (freedom) of B_j in the presence of A_i. If one adds f_{ij} to f_{ji} , substitutes the probability estimators (2.10.6) - (2.10.8) into the sum, averages the outcome using the joint probabilities, and scales the result by the total system throughput, one arrives at an expression for the residual freedom (Φ) of the system,

$$\Phi = - \sum_{i=0}^{n} \sum_{j=0}^{n+1} T_{ij} \log[T_{ij}^2 / (\sum_{p=0}^{n} T_{pj})(\sum_{q=1}^{n+1} T_{iq})]. \qquad (2.10.12)$$

The quantity Φ is complementary to the ascendency and is termed the system overhead (Ulanowicz and Norden 1990). The ascendency and the overhead together quantify the structured complexity of the system, X, which includes both organized and inchoate attributes,

$$X = A + \Phi. \qquad (2.10.13)$$

The complementarity expressed in this definition of complexity (2.10.13) signifies that an increase in ascendency could adversely affect the system overhead. Thus, if more ascendency signifies a tighter degree of organization, one immediately realizes that there can be "too much of a good thing". It cannot be emphasized enough that too high a proportion of ascendency might impair system integrity by crowding out system overhead, which functions as a "strength in reserve" that is essential to a system for adaptation and survival.

The second warning is that ascendency, in spite of being a surrogate for constraint and efficiency, is itself a non-mechanical attribute. Ascendency, after all, is based upon a probabilistic rather than a mechanistic depiction of reality. Any directed change, such as the tendency for living systems to increase in ascendency, should not be likened to a mechanical goal function, such as the Hamiltonian operator. Probabilistic goal functions do not "drive" the system toward a fixed, pre-determined endpoint, as is the common, deterministic notion of a goal function. Rather, probability operators behave more like Bossel's (1987) "orientator" functions, which merely guide the system along a vague direction. It appears ascendency should be regarded as such an "orientator" function. As such, it is immune to most of the criticisms leveled against goal functions for introducing teleology into biology.

2.10.6 Quantifying Propensities

The reader should recall that the above definition of autocatalysis incorporated the notion of propensities in a cyclical juxtaposition. It should not be too surprising, therefore, to find that the quantification of propensity lies buried somewhere within the ascendency calculus.

To identify the explicit formula for propensity, it helps to recall some early definitions underlying irreversible thermodynamics that were laid down by Onsager (1931). Onsager generalized the work of earlier phenomenologists, such as Fourier, Fick and Ohm. Each of these investigators had attached a putative force to an observed flow. Thus did Fourier show how the rate of thermal conduction varies in proportion to the negative of the imposed gradient in temperature. Similarly, Fick traced the origins for mass diffusion to a gradient in species concentration, and Ohm connected electrical current to a concomitant gradient in voltage. Onsager was able to show how, by careful choice of dimensions, one could identify a thermodynamic "force" conjugate to each simple physical flow in such a way that the product of each force-flux pair has the dimensions of production of entropy $[ML^2T^{-3}\theta^{-1}]$.

Following Onsager's lead, the aggregate entropy production for any system of processes became the sum of all force-flux pairs that comprise the system. Any calculation with the form

$$\sum_i Flow_i \ x \ Force_i \qquad (2.10.14)$$

became known as a "power function". One immediately notes that the equation for ascendency (2.10.11) has this form. Each flow, T_{ij}, is multiplied by a corresponding logarithmic term, and the results are summed. Ascendency is what is known as a "quasi-power function" (James Kay, personal communication). In drawing this analogy, each logarithmic term becomes the homolog of a thermodynamic force, and the temptation is to equate the counterparts. But the probabilistic nature of the ascendency, as just mentioned, precludes calling any of its components a force in the mechanical sense of the word. Rather one should regard the term more as a tendency, or a *propensity* for the transfer T_{ij} to happen.

That is, one identifies

$$\log[T_{ij}T/(\sum_{p=0}^{n} T_{pj})(\sum_{q=1}^{n+1} T_{iq})] \qquad (2.10.15)$$

as the propensity for medium to flow from i to j.

Under this rubric, ascendency appears as the system-averaged propensity for activity to occur. Furthermore, the propensity for ascendency to increase over time becomes the propensity of a propensity-in loose analogy with Newton's second law, which defines force as something proportional to acceleration – the rate of change of a rate of change. Whence the statement, "In the absence of additional external influences, the ascendency of a living system has a propensity to increase" comes to bear loose analogy to both Newton's first and second laws. It resembles the first law (A body in motion will continue along a straight line, unless acted upon by an external force.) in that it describes what happens in the absence of new external influence. Like Newton's second law, it is a second-order statement, describing the propensity of a propensity. It differs markedly, however, from Newtonian dogma because it is highly non-conservative. Just as entropy may appear *ex nihilio*, ascendency may do likewise. It is the law of a new order-the living order-that ecosystems exhibit the propensity to increase in ascendency.

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