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II.7.1 Ascendancy: A Measure of Ecosystem Performance

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1. Introduction

One phenomenon central to ecology is that of ecosystem succession – the more or less repeatable temporal series of configurations that an ecosystem will take on after a major disturbance or upon the appearance of new areas of the given habitat. Initially, succession was described in terms of natural history (e.g., Clements 1916), but more recently ecosystem scientists have attempted to describe succession, or ecosystem development, in more formal terms (Odum 1969). The goal in quantitative ecology eventually is to describe the process of succession in purely numerical terms.

The quantification of succession is unlikely to prove easy, for, despite prevailing temporal regularities, the process is not as deterministic as many first portrayed it. Clements' almost mechanical description of succession was challenged almost immediately by Gleason (1917), who saw community assembly to be more stochastic by nature (Simberloff 1980). Contingencies, or novel perturbations, are very much a part of any ecosystem's history, and a quantitative theory of ecosystem succession cannot assume *a priori* that such chance events will always average out. What follows is a description of one particular attempt to quantifying the process of ecosystem development. The approach falls under the rubric of ecosystem *ascendancy*, so named after the key index spawned by the theory. Ascendancy was derived to gauge the activity and organisation inherent in an ecosystem. The approach is neither purely mechanical, nor unconditionally stochastic – extremes which to date have characterised most quantitative endeavours in ecosystems science. Rather, the formulation of ascendancy resembles Popper's (1990) call to develop a 'calculus of conditional probabilities.'

Popper regarded the processes of life as almost 'lawful' in the sense that they are guided by sets of 'propensities' – generalisations of Newtonian like forces that are constantly being disrupted by contingent events. Chance does not act on individual component processes in isolation, however, as is assumed in genetic theory (Fisher 1930). Ecosystem processes, almost by definition, are coupled to one another – a situation which allows for the effects of chance events to be incorporated into the ongoing history of the system. How a chance event affects a process will depend in part on conditions elsewhere in the system. Whence the need to describe chance, not in terms of the ordinary statistics common to most of contemporary biology and physics, but in terms of Bayesian, or *conditional* probabilities.

The trick, then, in constructing a broad, quantitative description of ecosystem development is to focus first upon the agency behind the 'law-like' progression towards a developed configuration, and thereafter to quantify the actions of this agency, not in conventional, deterministic fashion, but in contingent, probabilistic terms that can incorporate historical and non-local events.

2. A Vehicle for development

There is a growing consensus that life processes are so difficult to explain because they involve highly reflexive, self- referencing and, ultimately, self-entailing behaviours (Rosen 1991). While negative feedback is the crux of most internal system regulation, theorists now acknowledge that the pressures behind the proliferation and evolution of living forms have more to do with positive feedbacks, and with autocatalytic activities in particular (e.g., Eigen, 1971, Haken 1988, Kauffman 1995). Before going further, it is necessary to specify more precisely how the term, 'autocatalysis' will be used here.

Autocatalysis is a special case of positive feedback (DeAngelis et al. 1986). Positive feedback can arise according to any number of scenarios, some of which involve negative interactions. (Two negative interactions taken serially can yield a positive overall effect). By 'autocatalysis' we mean 'positive feedback comprised wholly of positive component interactions.' A schematic of autocatalysis among three processes or members is presented in Figure 1. In keeping with the idea of an open or contingent universe, we do not require that A, B and C be linked together in obligatory fashion. To achieve autocatalysis, we require only that the propensities for positive influence be stronger than cumulative decremental interferences. The plus sign near the end of the arrow from A to B indicates that an increase in the rate of process A has a strong propensity to increase the rate of B. Likewise, growth in process B tends to augment that of C, which in its turn reflects positively back upon process A.

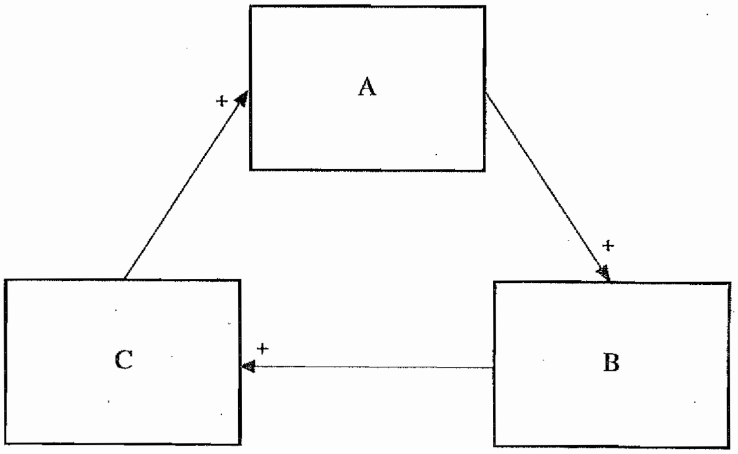


Figure 1: Schematic of a hypothetical three-component autocatalytic cycle.

Autocatalysis traditionally has been viewed in rather mechanical terms, but in the face of environmental contingenices, autocatalytic activities behave in ways that transcend mechanism (Ulanowicz 1997). For example, there is a *selection pressure* which the overall autocatalytic form exerts upon its components. If a random change should occur in the behaviour of one member that either makes it more sensitive to catalysis by the preceding element or accelerates its catalytic influence upon the next compartment, then the effects of such alteration will return to the starting compartment as a reinforcement of the new behaviour. The opposite is also true. Should a change in the behaviour of an element either make it less sensitive to catalysis by its instigator or diminish the effect it has upon the next in line, then even less stimulus will be returned via the loop.

Unlike Newtonian forces, which always act in equal and opposite directions, the selection pressure associated with autocatalysis is inherently *asymmetric*. Autocatalytic configurations impart a definite sense (direction) to the behaviours of systems in which they appear. They tend to ratchet all participants toward ever greater levels of performance.

Perhaps the most intriguing of all attributes of autocatalytic systems is the way they affect transfers of material and energy between their components and the rest of the world. Figure 1 does not portray such exchanges, which generally include the import of substances with higher exergy (available energy) and the export of degraded compounds and heat. The degradation of exergy is a spontaneous process mandated by the second law of thermodynamics. But it would be a mistake to assume that the autocatalytic loop is itself passive and merely driven by the gradient in exergy. Suppose, for example, that some arbitrary change happens to increase the rate at which materials and exergy are brought into a particular compartment. This event would enhance the ability of that compartment to catalyse the downstream component, and the change eventually would be rewarded. Conversely, any change decreasing the intake of exergy by a participant would ratchet down activity throughout the loop.

The same argument applies to every member of the loop, so that the overall effect is one of *centripetality*, to use a term coined by Sir Isaac Newton (Figure 2). The autocatalytic assemblage behaves as a focus upon which converge increasing amounts of exergy and material that the system draws unto itself (cf Jorgensen 1992). Taken as a unit, the autocatalytic cycle is not acting simply at the behest of its environment. It actively creates its own domain of influence. Such creative behaviour imparts a separate identity and ontological status to the configuration above and beyond the passive elements that surround it.

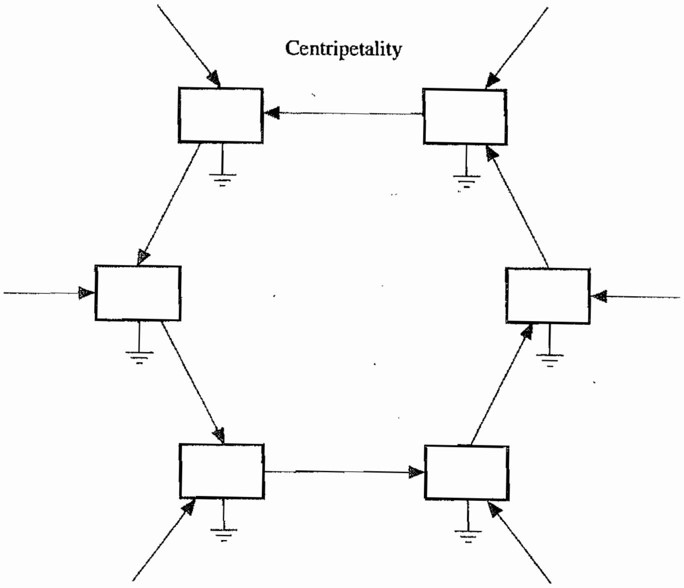


Figure 2: Autocatalytic cycle exhibiting centripetality.

To be sure, autocatalytic systems are contingent upon their material constituents and usually also depend at any given instant upon a complement of embodied mechanisms. But such contingency is not, as strict reductionists would have us believe, entirely a one-way street. By its very nature autocatalysis is prone to *induce competition*, not merely among different properties of components (as discussed above under selection pressure), but its very material and (where applicable) mechanical constituents are themselves prone to replacement by the active agency of the larger system. For example, suppose A, B, and C are three sequential elements comprising an autocatalytic loop as in Figure 3a, and that some new element D: (1) appears by happenstance, (2) is more sensitive to catalysis by A and (3) provides greater enhancement to the activity of C than does B (Figure 3b). Then D either will grow to overshadow B's role in the loop, or will displace it altogether (Figure 3c).

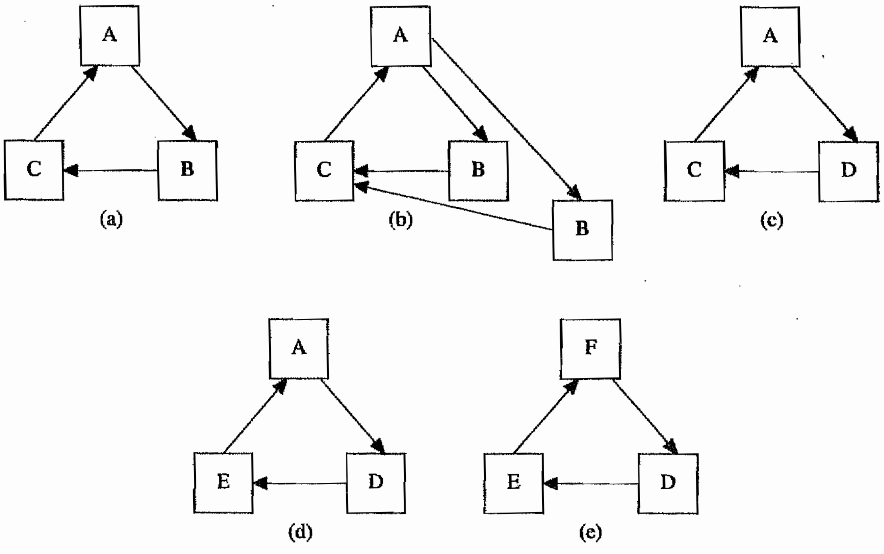


Figure 3: Successive replacement of the components in an autocatalytic loop

In like manner one can argue that C could be replaced by some other component E (Figure 3d), and A by F, so that the final configuration D-E-F contains none of the original elements (Figure 3e) (Simple induction will extend this argument to an autocatalytic loop of n members). It is important to notice in this case that the characteristic time (duration) of the larger autocatalytic form is longer than that of its constituents. Persistence of active form beyond present makeup is not an unusual phenomenon. One sees it in the survival of corporate bodies beyond the tenure of individual executives or workers; of plays, like those of Shakespeare, that endure beyond the lifetimes of individual actors. But it also is at work in organisms as well. One's own body is composed of cells that (with the exception of neurons) did not exist seven years ago.

Overall kinetic form is, as Aristotle believed, a causal factor. Its influence is exerted not only during evolutionary change, but also during the normal replacement of parts. For example, if one element of the loop should happen to disappear, for whatever reason, it is (to use Popper's own words) 'always the existing structure of the pathways that determines what new variations or accretions are possible' to replace the missing member (Popper 1990).

The appearance of centripetality and the persistence of form beyond constituents are decidedly non-Newtonian behaviours. Although a living system requires material and mechanical elements, it is evident that some behaviours, especially those on a longer time scale, are, to a degree, *autonomous* of lower level events (Allen and Starr 1982). Attempts to predict the course of an autocatalytic configuration by ontological reduction to material constituents and mechanical operation are, accordingly, doomed over the long run to failure.

It is important to note that the autonomy of a system may not be apparent at all scales. If one's field of view does not include all the members of an autocatalytic loop, the system will appear linear in nature. Under such linear circumstances, an initial cause and a final result will always seem apparent (see Figure 4). The subsystem can appear wholly mechanical in its behaviour. Once the observer expands the scale of observation enough to encompass all members of the loop, however, then autocatalytic behaviour with its attendant centripetality, persistence and autonomy *emerges* as a consequence of this wider vision.

In our consideration of autocatalytic systems, however, we have seen that agency can arise quite naturally at the very level of observation. This occurs via the relational form that processes bear to one another. That is, autocatalysis takes on the guise of a *formal cause*, sensu Aristotle. Nor should we ignore the directionality inherent in autocatalytic systems by virtue of their asymmetric nature. Such rudimentary *telos* is a very local manifestation of final cause that potentially can interact with similar agencies arising in other parts of the system.

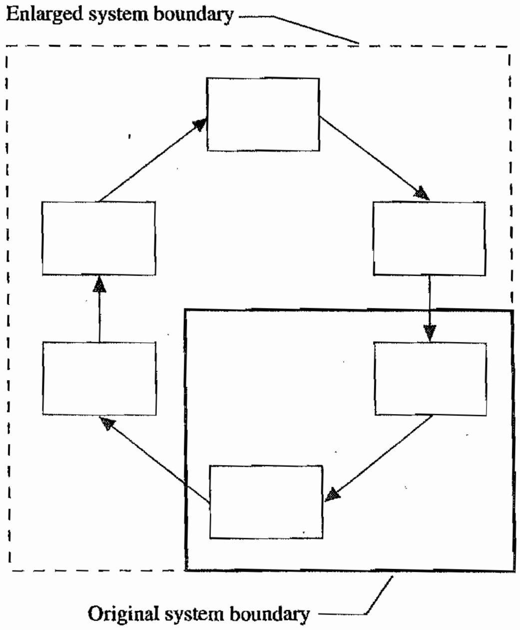


Figure 4: The emergence of non-mechanical behaviour as scope of observation is enlarged.

Finally, autocatalytic configurations, by definition, are *growth enhancing.* An increment in the activity of any member engenders greater activities in all other elements. The feedback configuration results in an increase (growth) in the aggregate activity of all members engaged in autocatalysis over what it would be if the compartments were decoupled.

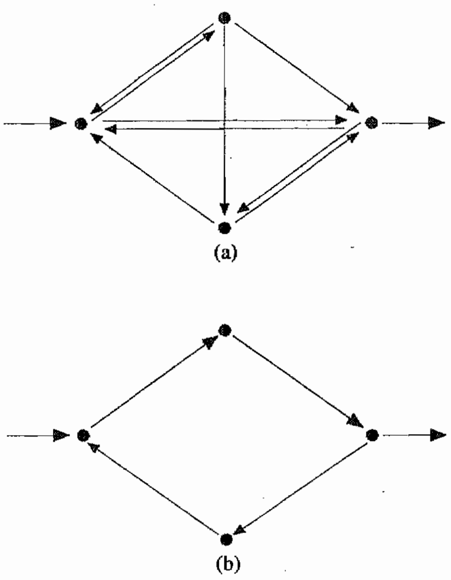


Figure 5: Schematic representation of the major effects that autocatalysis exerts upon a system.

To recapitulate, autocatalytic systems can exhibit at least eight behaviours, which, taken together, mitigate against viewing them as mechanical systems that will yield to reductionistic analysis. Autocatalysis induces (1) growth and (2) selection. It exhibits an (3) asymmetry that can give rise to the (4) centripetal amassing of material and available energy. The presence of more than a single autocatalytic pathway in a system presents the potential for (5) competition. Autocatalytic behaviour is (6) autonomous, to a degree, of its microscopic constitution. Its attributes (7) emerge whenever the scale of observation becomes large enough, usually in the guise of an Aristotelian (8) formal cause.

The overall effects of autocatalytic behaviour are exhibited both extensively (as a function of system size) and intensively (independent of size). The former is expressed as an increase in total system activity, while the latter resembles the topological 'pruning' of those processes that participate less effectively in autocatalytic activities. The combined result is depicted schematically in Figure 5. The task now at hand is to quantify both aspects of growth and development.

3. Quantifying growth and development

The extensive nature of growth is rather easy to quantify. To do so, we denote the magnitude of any transfer of material or energy from any donor (prey) i to its receptor (predator) j by T_{ij}. Then one measure of total system activity is the sum of all such exchanges, a quantity referred to in economic theory as the 'total system throughput', T.

$$T = \sum_{i,j} T_{ij} \tag{1}$$

If reckoning the 'size' of a system by its level of activity seems at first a bit strange, one should recall that such is common practice in economic theory, where the size of a country's economy is gauged by its 'gross domestic product'.

Quantifying the intensive process of development is somewhat more complicated. The object here is to quantify the transition from a very loosely coupled, highly indeterminate collection of exchangesto one in which exchanges are more constrained by autocatalysis to flow along the most efficient pathways. One begins, therefore, by invoking information theory to quantify the indeterminacy, h_j, of category j,

$$h_j = -k \log p(B_j) \tag{2}$$

where $p(B_j)$ is the marginal probability that event B_j will happen, and k is a scalar constant. Roughly speaking, h_j is correlated with how surprised the observer will be when B_j occurs. If B_j is almost certain to happen, $p(B_j)$ will be a fraction near 1, making h_j quite small. Conversely, if B_j happens only rarely, $p(B_j)$ will be a fraction very near zero, and h_j will become a large positive number. In the latter instance the observer is very surprised to encounter B_j.

Constraint abrogates indeterminacy. That is, the indeterminacy of a system with constraints should be less than what it was in unconstrained circumstances. Suppose, for example, that an *a priori* event A_i exerts some constraint upon whether or not B_j subsequently occurs. The probability that B_j will happen in the wake of A_i is defined as the conditional probability, $p(B_j|A_i)$. Hence, the (presumably smaller) indeterminacy of B_j under the influence of A_i (call it h_j^*), will be measured by the Boltzmann formula as

$$h_j^* = -k \log p(B_j|A_i). \tag{3}$$

It follows that one may use the decrease in indeterminacy, $(h_j - h_j^*)$, as one measure of the intensity of the constraint that A_i exerts upon B_j. Call this constraint h_{ij} , where

$$h_{ji} = h_j - h_j^* = [-k \log p(B_j)] - [-k \log p(B_j|A_i)] = k \log [p(B_j|A_i)/p(B_j)] \tag{4}$$

One may use this measure of constraint between any arbitrary pair of events A_i and B_j to calculate the amount of constraint inherent in the system as a whole: one simply weights the mutual constraint of each pair of events by the associated joint probability, $p(A_i,B_j)$, that the two will co-occur, and then sums over all possible pairs. This yields the expression for the average mutual constraint, A, as

$$A = k\sum_{i,j} p(A_i, B_j)\log\left[\frac{p(A_i, B_j)}{p(A_i)p(B_j)}\right] \tag{5}$$

In order to apply A to quantify constraint in ecosystems, it remains to estimate $p(A_i,B_j)$ in terms of measurable quantities. To keep matters strictly operational, we shall henceforth focus upon trophic exchanges. Then, a convenient interpretation of A_i becomes ‘a quantum of medium leaves compartment i’, and of B_j ,’a quantum enters compartment j’. The T_{ij} may be regarded as entries in a square events matrix, similar to Tables 1 and 2. The joint probabilities can be estimated by the quotients T_{ij} /T, and the marginal probabilities become the normalised sums of the rows and columns,

$$p(A_i) \sim \sum_j T_{ij} / T, \tag{6}$$

and

$$p(B_j) \sim \sum_i T_{ij} / T \tag{7}$$

In terms of these measurable exchanges, the estimated average mutual constraint takes the form

$$A = k\sum_{i,j}\left(T_{ij} / T\right)\log\left[\frac{T_{ij}T}{\sum_{k} T_{ik}\sum_{l} T_{lj}}\right] \tag{8}$$

That A indeed captures the extent of organisation created by autocatalysis can be seen from the example in Figure 6. In Figure 6a there is equiprobability that a quantum will find itself in the next time step in any of the four compartments. Little is constraining where medium may flow. The average mutual constraint in this kinetic configuration is appropriately zero. One infers that some constraints are operating in Figure 6b, because medium that leaves any compartment can flow to only two other locations. These constraints register as k units of A. Finally, Figure 6c is maximally constrained. Medium leaving a compartment can flow to one, and only one, other node.

4. System Ascendancy

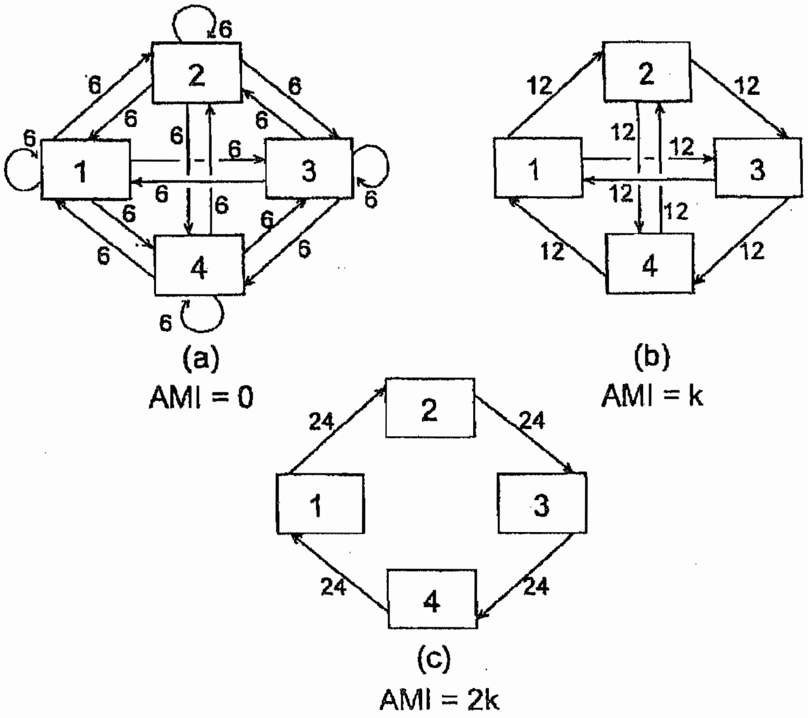
Having quantified separately the extensive and intensive effects of autocatalysis, it remains to combine them into a single index. This amalgamation follows in a very natural way, because we have elected to retain the scalar constant 'k' in all the information measures just cited. (The conventional practice in information theory is to designate the base to be used in calculating the logarithms [usually 2, e or 10] and set the value of k=1).

The units of A would then appear as 'bits', 'napiers' or 'hartleys', respectively. The problem with this convention is that the calculated value conveys no indication as to the physical size of the system. By retaining k in the formulae, one now has a convenient way to impart physical dimensions to the measure of organisation (Tribus and McIrvine 1971, Ulanowicz 1980). That is, we set k=T, and the dimensions of A will contain the units used to measure the exchanges. For example, if the transfers in Figure 6 had been measured as g/m^2/d, and the base of the logarithm was 2, then the values of A would be expressed in the units g-bits/m^2/d. The ascendancy expressed in terms of trophic exchanges becomes,

$$A = \sum_{i,j} T_{ij}\log\left[\frac{T_{ij}T}{\sum_{k} T_{ik}\sum_{l} T_{lj}}\right] \tag{9}$$

To signify that the scaled measure has changed its qualitative character, we choose to rename A as the system 'ascendancy' (Ulanowicz 1980). It measures both the size and the organisational status of the network of exchanges that occur in an ecosystem. In an attempt to characterise what it means for an ecosystem to develop, Eugene Odum (1969) catalogued ecosystem attributes that were observed to change during the course of ecological succession. His list of 24 properties can be sub-grouped according to whether they pertain to speciation, specialisation, internalisation or cycling – all of which tend to increase during system development. But increases in these same four features of network configurations lead, *ceteris paribus*, to increases in ascendancy. Whence, Odum's phenomenology can be quantified and condensed into the following principle:

In the absence of major perturbations, ecosystems exhibit a propensity towards configurations of ever-greater network ascendancy.



(a) AMI = 0

(b) AMI = k

(c) AMI = 2k

Figure 6: The increase in mutual information as flows become progressively constrained.

5. Ecological Persistence

The tendency towards increasing ascendancy, if allowed to progress unimpeded, would result in a very rigid, mechanical-like configuration. With ecosystems, matters never reach such a pass because of the contingent nature of the world in which they reside. That is, the accretion of system ascendancy is always being disrupted by chance perturbations. In time, depending upon how rigorous and stochastic the surrounding environment is, advances and setbacks will roughly balance. This is not to say the system will achieve equilibrium as regards to the list of species, which may continue to change.

The inability of the system to reach an arbitrarily high ascendancy looks at first like a glass half-empty. All does not appear quite so negative, however, once one realises that any rigid, mechanical ecosystem would be a catastrophe waiting to happen (Holling 1986). Such 'brittle' systems lack sufficient freedom to reconfigure themselves when beset by novel impacts. There is nothing left for them to do but collapse. A less-ordered configuration, by virtue of the ambiguities in its makeup can access these very inefficiencies to reconfigure itself in a way that mitigates, nullifies or incorporates the disturbance. The glass is really half-full.

It is possible to quantify the residual freedom in a system using the same informational calculus we just employed to develop the system ascendancy. One begins with the theoretical result from information theory that the mutual information is always bounded by the functional indeterminacy. This functional indeterminacy is simply the diversity of the flows that occur in the system. That is, if T_{ij}/T is the joint probability that matter both leaves i and enters j, then the formula

$$H=-\sum_{i,j}\left(\frac{T_{ij}}{T}\right)\log\left(\frac{T_{ij}}{T}\right) \tag{10}$$

quantifies the system's functional diversity. After this measure has been scaled by T in exactly the same manner as was done with A, the result is called the system 'capacity',

$$C=-\sum_{i,j}T_{ij}\log\left(\frac{T_{ij}}{T}\right) \tag{11}$$

and it can be proved that

$$C \geq A \geq 0. \tag{12}$$

The amount by which the capacity, C, exceeds the measure of constraint, A, is called the system 'overhead',

$$\Phi=-\sum_{i,j}T_{ij}\log\left(\frac{T_{ij}^2}{\sum_k T_{kj}\sum_l T_{il}}\right) \tag{13}$$

and this quantity signifies the potential for the system to recover from novel perturbation. The overhead, F, may be decomposed into four components representing the indeterminacies in the inputs, exports, dissipations and internal connections, respectively (Ulanowicz and Norden 1990). The limits that each of these terms imposes upon any increase in ascendancy can be parsed along hierarchical lines. Indeterminacy in the internal connections, or *redundancy*, represents an encumbrance upon the system for maintaining secure the internal lines of transfer. The indeterminacy in the exports has been likened to *tribute* and quantifies the 'tax' the given system must contribute to the next higher level to maintain system integrity there. Conversely, the indeterminacy among the dissipations represents the cost of maintaining kinetic order in structures at the next lower level. Finally, the indeterminacy among the inputs to the system represents the extent to which inefficient sources must be tapped in order to insure adequate sustenance for the system.

6. Using ascendancy

Ascendancy is a rather abstract concept, and much has been packed into a small set of indices. But that same richness makes the measures useful in any number of practical circumstances. To begin with, ascendancy was created to assess the developmental status of an ecosystem. If the manager of an ecosystem suspects that a particular impact has negatively affected his/her area, that hypothesis could be put to a quantitative test whenever sufficient data were available to construct the network of exchanges before and after the impact. In like manner, the developmental stages of disparate ecosystems can be compared with one another (e.g., Ulanowicz and Wulff 1991). One is now able to say quantitatively whether a system has grown or receded, developed or disintegrated. Furthermore, particular patterns of changes in the information variables can be used to identify processes that hitherto had only verbally been described. The process of eutrophication, for example, is characterised by a rise in ascendancy that is due to an overt increase in the activity of the system (T) which more than compensates for a concomitant decrease in its developmental status (average mutual information). This particular combination of changes in variables allows one to draw quantitative distinction between instances of enrichment and cases of eutrophication (Ulanowicz 1986).

The concepts of ecosystem 'health' and 'integrity' have been written into legislation in the U.S. (Costanza 1992) and Canada (Westra 1994) apparently before anyone had investigated whether those attributes can somehow be defined, quantified and measured. Because the conventional notion of health is normally associated with system vigour, performance and resilience (Costanza 1992), ascendancy and its associated indices become natural variables with which to give these metaphors real quantitative significance (Mageau et al. 1995).

If indeed ecosystems do exhibit an intrinsic direction in their development, then quantifying that direction using ascendancy might also provide a way to attach an 'intrinsic value' to the contribution that a particular process or taxon makes in that direction. Ascendancy, for example, has the same mathematical form as a 'production function' in economic theory. A production function is the sum of products of each process activity multiplied by the value added by that process. In a way yet to be specified, the logarithmic terms in the ascendancy formula are homologous to the values-added by the processes, and hence to any putative values put on the taxa themselves.

Although the ascendancy and related variables were invoked to quantify systems that are subject to contingencies, there is no reason why the same set of measures cannot be used to evaluate the performance of mechanical models (Field et al. 1989) or even networks of computational machines. The latter, for example, could be cast as a network of individual computers that exchange data at quantifiable rates. The overhead of this network, calculated according to the formula given above, should be lowest for those configurations that perform most effectively (Ulanowicz 1997).

7. Extending Ascendancy

Because ascendancy initially was formulated on the basis of steady-state snapshots of homogenous ecosystems, some might be inclined to regard the index as restricted to only equilibrium situations. Such an attitude, however, would do grave injustice to the robustness and broad relevance of contemporary information theory. The days when information theory was limited to the Shannon formula as applied to a communications channel are long gone. Information indices have been formulated to extend the basic notions to cover temporal and spatial inhomogenities as well (Pahl-Wostl 1992, Ulanowicz 1997). What mostly limits the extension of ascendancy theory into these realms is the extremely data-intensive nature of any such endeavour. One needs to know the full configurations of trophic exchanges at each time or spatial point (or both).

Failing sufficient data, one could still employ models to generate suites of data that could be used to test the capabilities of multi-dimensional information indices at identifying those times and places where system dynamics are most interesting and influential. Recently, a cellular automaton was programmed to represent the migration of animals across a landscape interspersed with barriers. The dynamic patterns were analysed using the components of the ascendancy to quantify the contribution that each spatial point makes to the overall ascendancy. The 'field' of components was plotted over the landscape, and the resulting profile indicated those points at which the critical actions were taking place (Ulanowicz, in press).

Ascendancy and its ancillary indices were originally defined (as above) entirely in terms of process rates. The full dynamics of systems, however, are known to depend also upon the biomass stocks in the taxa. Only recently has a way been found to incorporate biomass stocks into the calculation of ascendancy in a way fully consonant with the algebra of information theory (Ulanowicz and Abarca 1997): If B_i represents the amount of biomass in taxon i, and B, the total amount of biomass in the system, then B_i/B will estimate the a priori likelihood that a quantum of material is leaving taxon i. Similarly, B_j/B will estimate the a priori probability that a quantum will enter j. The a priori joint probability that material both leaves i and enters j thereby becomes B_iB_j/B^2. One may compare this estimate with the observed *a posteriori* joint probability, T_{ij}/T, in what is known as the Kullback- Leibler index,

$$I = k\sum_{i,j}\left(\frac{T_{ij}}{T}\right)\log\left(\frac{T_{ij}B^2}{B_iB_jT}\right) \tag{14}$$

As with the original ascendancy, one may scale I by T to obtain a biomass-inclusive ascendancy,

$$A_b = \sum_{i,j} T_{ij}\log\left(\frac{T_{ij}B^2}{B_iB_jT}\right) \tag{15}$$

It is possible to demonstrate that the original ascendancy is bounded from above by the biomass-inclusive ascendancy, i.e., $A_b \geq A$, and that the difference between the two is due to the departure of the biomass distribution from what it would be at chemical equilibrium. This difference, therefore, should be related to the exergy content of the system (S.E. Joergensen, personal communication).

Unfortunately, the Kullback-Leibler index possesses no upper bound, and therefore does not yield expressions homologous to either the capacity or the overhead. The advantage that the new index does afford, however, is that biomass dynamics become implicit in A_b (Ulanowicz and Baird, In press). For example, one may construct separate but parallel networks, each pertaining to one of several chemical elements (e.g., C, N, and P) circulating within the same ecosystem. With multiple elements, T_{ijk} can represent the amount of element k flowing from i to j, and B_{ik}, the amount of element k incorporated into i. One may then use the sensitivities of the resultant A_b with respect to each of the B_{ik} to determine which element is limiting the activity of each taxon. In other words, the principle of increasing ascendancy subsumes Liebig's Law of the Minimum. Such 'theory reduction' is one of the hallmarks of a robust theory, but the advantages of A_b don't end there. If one further calculates the sensitivities of A_b to the flows, T_{ijk}, one can then determine which input of the limiting element plays the pivotal role to that taxon. Liebig's principle offers no guidance on how to identify which flow might be limiting, so that this method yields a theoretical prediction to be compared with experiment.

8. Ascendancy, the New Perspective

As the concepts surrounding ascendancy evolve, it becomes ever clearer that ecosystems exhibit very non-traditional dynamics – or what Eber et al (1989) have called 'infodynamics.' As Popper discerned, new dynamics require a new calculus, and it now appears that the cluster of variables defined using information theory might be prime candidates with which to begin the development of a post-Newtonian ecology (Ulanowicz 1997).

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