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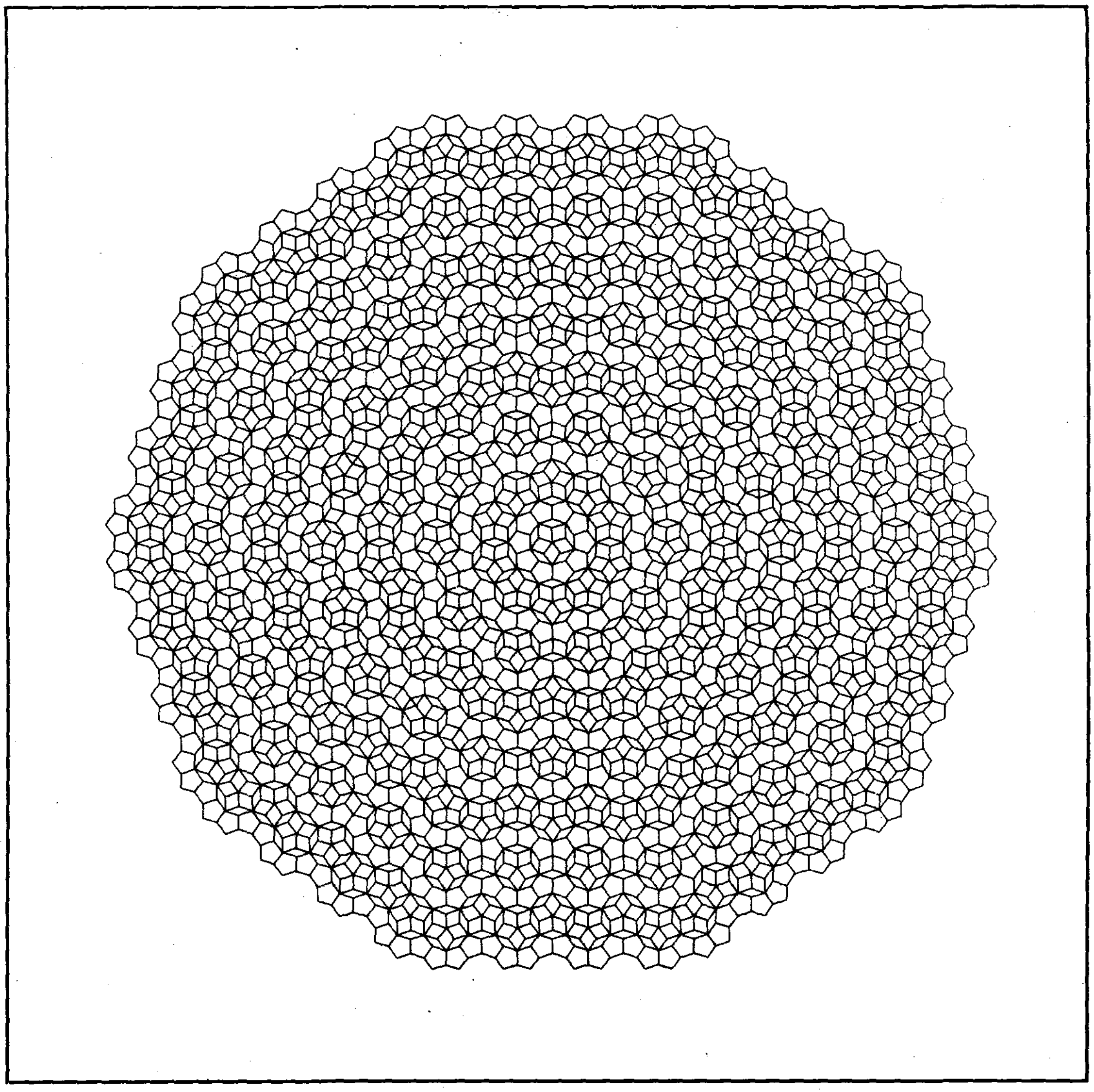

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ECOSYSTEM DEVELOPMENT: SYMMETRY ARISING?

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Abstract: *Ecology is unconventional in its treatments of symmetry and causality. Newtonian, or normal science deals only with the symmetry in events, at the expense of the irreversibility and asymmetry that perfuses most natural phenomena. The reason for such neglect lies with the newtonian proscription against any causalities other than those that are material and mechanical in origin. Ecology is grounded in a highly irreversible world that defies adequate description by such newtonian norms (statistical mechanics notwithstanding.) In addition, the phenomenon of indirect mutualism, or autocatalysis, in ecosystems behaves with marked resemblance to Aristotle's formal and final causes. Information theory is naturally tailored to the dual tasks (a) of quantifying the effects of formal and final causality and (b) of separating the amount of constraint within a system from the accompanying degrees of freedom. These latter two features (of b) are symmetric and asymmetric, respectively. Because "development" is taken to mean any increase in structural constraint, ecosystem development is seen to involve an increase in the symmetry among system processes. Symmetric processes, however, cannot reveal the direction of passing time. The cues for establishing the direction of time must be taken from the asymmetrical components of ecosystem complexity.*

1. INTRODUCTION

Ecology is unlike most other sciences. This fact seems to be widely-recognized, but exactly what makes ecology distinct usually is poorly articulated. Acknowledgement of ecology's distinguishing character usually is made implicitly in the way that labels are attached to expositions in other fields of inquiry, e.g., "computational ecosystems" (Kephart et al. 1989), or "the eco-psychology of..." That is, investigators who are having trouble relating their work to mainstream science often point to ecology as the exemplar for "post-normal" science (Funtowicz and Ravetz 1993).

But what, exactly, makes ecology post-normal? Before one can understand how different ecology is from other scientific endeavors, it helps first to consider the evolution of the more "conventional" disciplines. Crucial to the distribution is the concept of symmetry. For, according to the author of Genesis, God began his creation by saying "Let there be light!". To paraphrase Isaac Newton, mechanics began with "Let there be symmetry!" Not exactly in those words, of course, but his Third Law of Mechanics says as much — for every action there exists an equal and opposite reaction. This primary assumption perfuses all of classical mechanics and in turn all of the disciplines that patterned themselves upon the newtonian mold.

As a consequence of Newton's defining assumption, time itself takes on a peculiar cast in mechanics. In all newtonian descriptions of phenomena, the future can be exchanged with the past and the description remains perfectly lawful. Lawful, perhaps, but hardly in accord with experience, which never allows full access to the past. So successful was the newtonian juggernaut, however, that fully 130 years elapsed before someone made an observation that caused at least transient concern about the capability of mechanics to portray physical reality sufficiently.

The French military engineer, Sadi Carnot (1824) was interested in improving the design and operating characteristics of early steam engines, used then principally to pump water from mines. He set out to learn how much water could be pumped by machines that operated over different cycles of compression, heating, expansion and cooling. After numerous preliminary trials, he came to the most interesting conclusion that, "It is impossible to construct a device that does nothing except cool one body at a low temperature and heat another at a high temperature" (Tribus 1961).

In the years that followed, Carnot's principle appeared in any number of equivalent forms. Clausius, for example, restated Carnot's observation as, "Heat cannot of itself flow from a colder body to a warmer one." Of course, it is easy to imagine heat flowing of itself from a warmer body to a colder body. This happens all the time. It is the natural way for heat to behave in the absence of external influences, to put it in terms similar to Newton's First Law. So we are struck immediately by how Carnot's observations appear to violate newtonian assumption of symmetry. If we see heat flow from a hotter to a colder body, why, if we wait long enough, don't we see it flow the other way? Put another way, suppose we agree with Laplace (1814), who said that if we knew the positions and momenta of all the particles that comprise a system, we could predict all future states of that system. Combining the atomic hypothesis, which had been formulated by chemists like Dalton, with the decomposability inherent in all newtonian descriptions, one should, in principle, be able to describe this phenomenon at the atomic level. That is, at this scale one would see particles interacting with one another, and presumably be able to compute their trajectories using newtonian mechanics. If, however, time were reversed in the description of each individual interaction between particles, the reverse trajectories all would look wholly plausible. Combining all of these law-derived trajectories should yield a feasible prediction of system behavior. But that is not what results. Rather, one would see heat flowing of it's own from a colder to a hotter body, which, according to Clausius, never happens. It seemed apparent that newtonian reversibility does not accord with all events as they transpire in the real world.

But today one seldom hears about the conflict between the thermodynamic second law and newtonian symmetry. This is because a reconciliation was assumed to have been accomplished between newtonian mechanics and phenomenology in the guise of what is known as "statistical mechanics". In statistical mechanics one begins with the assumption that gases are comprised of atomistic particles that move about according to the symmetrical laws of classical mechanics. Since there is no way that anyone could treat analytically the immense numbers of particles in any visible volume of gas, one sidesteps the details by assuming that the positions and momenta of the point-like particles follow some statistical distributions. Through the application of the methods of statistics one is able to show how the perfect gas laws arise.

Of more interest to the discussion here, Boltzmann asked how any initial statistical distribution of particles would most likely evolve, if left free of outside influences. He discovered a particular function of the particle probability distribution that always increased monotonically in time. He identified this function with the entropy of the gas (broadly speaking, a measure of its disorganization), and it became conceivable that a collection of particles could act in newtonian, symmetrical fashion at the microscopic scale, but nevertheless exhibit irreversibility in the large. The observations of Carnot and Clausius it seemed, had been reclaimed into the orbit of Newton.

If one subscribes to the positivist's view of science, this rush to the consensus that newtonian symmetry had been redeemed *should* seem a bit premature. After all, the positivist doctrine bids one consider only hypotheses that are capable of being proved wrong, i.e., falsified. A hypothesis, once abroad, should be subjected to repeated attempts to falsify it under a myriad of different conditions. A failure of the hypothesis anywhere is grounds at the very least for amending it, and possibly, for rejecting it entirely. The scientific community, however, has acted in quite the reverse way as regards the reconciliation provided by statistical mechanics. The body of scientists wants to cling tenaciously to the newtonian perspective in spite of the thermodynamic challenge. Despite the fact that the gas laws and newtonian mechanics were found to agree over only a very narrow set of conditions (rare gases, close to thermodynamic equilibrium), the case was immediately closed. Symmetrical newtonian mechanics and thermodynamics are now implicitly considered compatible over all conceivable circumstances. Such is the power and attraction of the notion of symmetry over the collective psyche.

If indeed irreversibility and asymmetry do exist in the world, what are their origins? Obviously, there is no agreement on an answer to this basic question. Benjamin Gal-Or (1993), for example, perceives irreversibility and asymmetry as necessary consequences of the fact that the universe is expanding. If, for example, the expanding universe is populated with emitters of photons, one can show that there is asymmetry between the probability that a photon is emitted from any small neighborhood of space and the probability that photons enter the same segment. The conclusion is that in a contracting universe the laws of thermodynamics might look quite different, and the second law, in particular, might not hold at all. Richard McGarvey (personal communication) has speculated that irreversibility stems from the basic tension between the anti-symmetric electromagnetic forces vis-a-vis the other three symmetrical forces (gravitation and weak and strong nuclear forces.)

Against this background of an all-prevailing symmetry in the natural world, ecology comes quickly to seem out-of-place. For the ecosystem scientist, for example, natural communities are viewed almost exclusively in terms of the irreversible processes of material and energy transfers among ecosystem components. It is only in fairy tales like Tchaikovsky's "Peter and the Wolf" that ducks pop out of wolves'stomachs alive and functioning. In reality, predation is a one way street — or so it seems at first sight. The foodweb takes the form of a tree of one-way transfers of ever-diminishing energetic content. There seems no way to reconcile newtonian symmetry with such an unrelenting chain of degradations — Boltzmann and Gibbs et al., notwithstanding. Nonetheless, symmetry does play a major role in ecosystem development. To appreciate this role, however, it is necessary first to delve into another issue on which ecology parts company with more conventional disciplines — namely, the nature of the causal agencies behind ecosystem transactions.

2. OTHER CAUSALITIES

Newton's *Principia* rightfully is regarded as a revolutionary work that changed forever how we view the world. What is not as widely known or acknowledged is that the most radical change in perspective wrought by this work — a new view on natural causality — happened quite by accident (Ulanowicz 1995a). Before *Principia*, Newton's published works took the form of very ornate and embellished discourses, with copious references to theology and alchemy. For reasons that are omitted here for the sake of brevity, Newton felt enormously pressed to finished Principia as quickly as possible. (The entire three volumes took only 9 months to complete.) There simply was insufficient time to make peripheral references to phenomena other than the minimal mechanical and material details necessary to complete his essential demonstrations.

Such a minimalist rendition of the causes behind the movements of the heavenly spheres was utter serendipity to materialists like Edmund Halley, who urged Newton to publish and immediately distribute the volumes of *Prinicpia* in their initial form. For *Principia* constituted the first explanation of the movement of planetary bodies without recourse to supernatural entities. Newton invoked only material and mechanical agencies to predict the trajectories of the orbs. Initiated by the treatises of Descartes and Hobbes, the growth of materialism had been stunted for want of any convincing demonstration of the sufficiency of such a simplified view of nature. Newton inadvertently provided, not just an example, but a whole new paradigm cast in the material/mechanical mold. Almost immediately, Newton's approach was copied by investigators of virtually every natural realm, and Newtonianism spread like wildfire across the Western world of the Eighteenth Century.

It is imperative to note exactly what had disappeared in the wake of the newtonian revolution. Prior to Newton's work, the prevailing view on causality had been authored by Aristotle during the Fourth Century B.C. Aristotle's image of causality was more complicated than what took form post-Newton (Rosen 1985). Aristotle had taught that a cause could take any of four essential forms: (1) material, (2) efficient, or mechanical, (3) formal, and (4) final. Examples were usually drawn from some field of human endeavor, such as the building of a house. Perhaps a more appropriate exemplar is that of a military battle, which, despite its unsavory image, nonetheless provides clearer distinctions among the four categories: The material causes of a battle are the weapons and ordnance that individual soldiers use against their enemies. Those soldiers, in turn, serve as the efficient agents, as it is they who actually swing the sword, or pull the trigger to inflict unspeakable harm upon each other. The officers who direct the battle concern themselves with the formal elements, such as the juxtaposition of their armies via-a-vis the enemy in the context of the physical landscape. It is these latter forms that impart shape to the battle. In the end, the armies were set against each other for reasons that were economic, social and/or political in nature. Together they provide the final cause or ultimate context in which the battle is waged.

Subsequent to Newton, all references to formal and final agents disappeared from narratives on natural phenomena. In fact, the newtonian perspective has come to define exactly what is natural as distinct from what is metaphysical. The world was considered to exist purely of material and mechanical (symmetrical) elements. The alacrity with which the Aristotelean perspective was abandoned was fueled no doubt by an anticlerical sentiment that spread wide through Europe about that time. The Aristotelean description readily lent itself to a hierarchical interpretation (David Depew, personal communication.) For example, all considerations of political or military rank aside, soldiers, officers and heads of state all participate in a battle at different scales. It is the officer whose scale of involvement is most commensurate with those of the battle itself. In comparison, the individual soldier usually affects only a subfield of the overall action, whereas the head of state influences events that extend well beyond the time and place of battle.

In fact, it was rather difficult to pose an example of a process with all four classes of causality at work that didn't involve some human agents, who necessarily interject their goals and intentions. To avoid all references to hierarchical matters, these latter phenomena were proscribed outright from descriptions of nature and relegated to the limbo-like status of "epiphenomena", by which was meant the appearance of agency where none truly exists. (A common example is that of a motion picture, where celluloid, lights, motors and gears give rise to the apparent motion of living figures in a recipient's visual field.) The overall strategy of science became to elucidate all natural phenomena in terms of the motions of their simplest atomistic elements — precisely the job of LaPlace's (1814) "divining angel".

Much has changed since the beginning of the Eighteenth Century. Clericalism, with the exception of some non-Western redoubts, no longer appears a threat to anyone. Yet old habits die hard An hierarchical view of natural phenomena is still regarded as anathema in most scientific circles. Any attempt to reconsider formal or final causes is immediately painted with an extremist brush as "teleology" and categorically dismissed. But in spite of such obstacles, ecology suggests itself as a plausible domain in which formal and final agencies can arise in perfectly natural ways.

3. NON-NEWTONIAN ECOSYSTEMS

Ecology affords the ideal domain in which to consider the possible existence of non-newtonian organizational agencies. In the field of ontogeny, for example, organizational influences per se are overshadowed by the mechanisms of transcription from genome to phoneme. At the other end of the living spectrum, human sciences, such as economics, sociology, anthropology, etc. all involve the explicit exercise of volition. It clouds the issue to search for the most rudimentary of nonmechanical organizing agencies amidst such higher-level complications that render one's arguments vulnerable to charges of blatant anthropomorphism. Ecology occupies the propitious middle ground. Here it should still be possible to study ecological organization as it has emerged in systems relatively unimpacted (until recently) by human activity and unfettered by overbearing mechanisms.

One of the key characteristics of ecosystems with which most readers are familiar is their tendency to cycle materials (and to a lesser degree, bound energy.) That recycle of materials is necessary follows from the observation that most of the essential constitutive elements of life (e.g., carbon, nitrogen, phosphorus, hydrogen, oxygen) are at any instant incorporated into living protoplasm. For life to have continued over hundreds of millions of years, it must have been necessary to reuse those same materials countless times. (Actually, the vast majority of elements cycle over periods of one to ten years or less.)

The existence within ecosystems of cyclical pathways presents an opportunity to living populations of organisms to organize themselves in ways that facilitate the appearance of necessary resources when and where they are needed. The key process behind such cooperative behavior is what is known as indirect mutualism, or "autocatalysis". Autocatalysis has long been studied in the field of chemistry, where it is often referred to as a "mechanism". Under the conditions which chemists study the phenomenon, i.e., reactions among relatively simple, fixed structures, this designation seems justified. But in the realm of ecosystems, where organisms are complicated and their behaviors are quite plastic, autocatalysis acquires characteristics that are decidedly non-mechanistic. One is thus led to question the appropriateness of the newtonian mandate to view ecosystems as complicated machines.

"Autocatalysis" can be defined as "positive feedback comprised entirely of positive component interactions." While mutualism is commonly considered to occur between two populations of organisms, there is no reason to restrict the action of autocatalysis to pairwise interactions. As an example, the reader is urged to consider positive feedback among three populations, A, B and C. In accordance with the definition just stated, any increase in the rate of process A will have a strong propensity to increase the rate of B (but the two need not be linked in rigid, mechanical fashion [Ulanowicz, in press].) Likewise, growth in process B tends to augment that of C, which in its turn reflects positively back upon process A.

Many examples of indirect mutualism in ecology are subtle and require much elaboration, but one example is unusually explicit and straightforward (Ulanowicz 1995b). Inhabiting freshwater lakes over much of the world, and especially in subtropical, nutrient-poor lakes and wetlands are various species of aquatic vascular plants belonging to the genus *Utricularia*, or the bladderwort family. Although these plants are sometimes anchored to lake bottoms, they do not possess feeder roots that draw nutrients from the sediments. Rather, they absorb their sustenance directly from the surrounding water. One may identify the growth of the filamentous stems and leaves of *Utricularia* into the water column with process A mentioned above.

Upon the leaves of the bladderworts invariably grows a film of bacteria, diatoms and blue-green algae that collectively is known as periphyton (Bosserman 1979). Bladderworts are never found in the wild without their accoutrement of periphyton. Process B may be identified with the growth of the periphyton community. It is clear, then, that bladderworts provide an areal substrate which the periphyton species (not being adapted to grow in the pelagic, or free floating mode) need to grow.

Now enters component C in the form of a community of small, almost microscopic (ca. 0.1mm) motile animals, collectively known as zoophytes, which feed on the periphyton film. These zoophytes can be from any number of genera of cladocerae (water fleas), copepods (other microcrustacea), rotifers and ciliates (multi-celled animals with hairlike cilia used in feeding). In the process of feeding on the periphyton film, these small animals occasionally bump into hairs attached to one end of small bladders, or utricles, that comprise part of the *Utricularia* structure. When moved, these trigger hairs open a hole in the end of the bladder, the inside of which is maintained by the plant at negative osmotic pressure with respect to the surrounding water. The result is that the animal is sucked into the bladder, and the opening quickly closes behind it. Although the animal is not digested inside the bladder, it does decompose, releasing nutrients that can be absorbed by the surrounding bladder walls.

Apropos the subject of symmetry in nature, it is well to note that the interactions between any two components in the *Utricularia* example are not entirely "anti- symmetric", as most predator-prey interactions in ecology are accounted. It is true that the zoophytes are nourished by the periphyton (+ interaction) and their predation upon the latter directly decreases periphyton biomass (– effect.) But the zoophytes also subsidize the growth of *Utricularia*, upon which the periphyton must anchor itself. Hence, it would be incomplete to characterize the interaction of zoophytes and periphyton as purely anti-symmetric when a palpable symmetric mutualism also exists between the two (Ulanowicz and Puccia 1990, Patten and Higashi 1991). One sees that by it's very nature, the process of autocatalysis is a vehicle upon which symmetry can enter into an otherwise amorphous situation.

Returning to the theme of non-mechanical behavior in ecosystems, autocatalytic systems possess a number of attributes that distinguish them from machine-like action (Ulanowicz 1996). For example, 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 in the aggregate activity of all members engaged in autocatalysis over what it would be if the compartments were decoupled.

As mentioned, classical chemistry also acknowledges the growth enhancing characteristic of autocatalysis. Less attention is paid there, however, to the selection pressure which the overall autocatalytic form can exert upon its components. For example, if a random change should occur in the behavior 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 behavior. The opposite is also true. Should a change in the behavior 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.

Having already mentioned how autocatalysis can introduce symmetry into a system, it should also be noted that the same configuration of processes, as an outgrowth of its selection pressure, also imparts a preferred temporal direction to system development. (This is symmetry-breaking, in the jargon of the physicist.) Autocatalytic configurations impart a definite sense (direction) to the behaviors of systems in which they appear. They tend to ratchet all participants toward ever greater levels of autocatalytic 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. Such exchanges generally include the import of substances with much available energy and the export of degraded compounds and heat. The degradation of energy 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 driven merely by gradients in the quality of energy. Suppose, for example, that some arbitrary change happens to increase the rate at which materials and energy are brought into a particular compartment. This event would enhance the ability of that compartment to catalyze the downstream component, and the change eventually would be rewarded. Conversely, any change decreasing the intake of resources 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. The autocatalytic assemblage behaves as a focus upon which converge increasing amounts of energy and material that the system draws unto itself. It is just such centripetality that the *Utricularia* complex exhibits to maintain itself in nutrient-poor waters.

Taken as a unit, then, an autocatalytic cycle within an ecosystem is not simply acting at the behest of its environment. It actively creates its own domain of influence. Such creative behavior imparts a separate identity and ontological status to the configuration above and beyond neighboring passive elements. We see in centripetality the most primitive hint of entification, selfhood and id. In the direction toward which the asymmetry of autocatalysis points we see a suggestion of a *telos*, an intimation of final cause (Rosen 1991). Popper (1990) put it all most delightfully, "Heraclitus was right: We are not things, but flames. Or a little more prosaically, we are, like all cells, processes of metabolism; nets of chemical pathways."

To be sure, autocatalytic systems are contingent upon their material constituents and also depend at any given instant upon a complement of embodied mechanisms. But such contingency is not, as material reductionists would lead one to 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 that by happenstance some new component D were brought into proximity to elements A, B, and C in the example above. Suppose further, as is often the case, that D is more sensitive to catalysis by A and also provides greater enhancement to the activity of C than does B. Then D either will grow to overshadow B's role in the loop, or will displace it altogether.

In like manner one can argue that C could be replaced by some other component E, and A by F, so that the final configuration D-E-F contains none of the original elements. It is important to notice in this case that the characteristic time (duration) of the larger autocatalytic form is longer than any of its constituents'. Persistence of active form beyond present constitution is hardly an unusual phenomenon. One sees it in the survival of corporate bodies beyond the tenure of individual executives or workers; of plays that endure beyond the lifetimes of individual actors. But it also is at work in organisms. The human body is composed of cells that (with the exception of neurons) did not exist seven years ago. The residence times of most chemical constituencies are of even shorter duration. Yet most people still would be recognized by friends they haven't met in the last ten years.

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 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 configuration beyond constituents make it difficult to maintain any hope for a strictly reductionist, mechanical approach to describing organic systems. Although the system requires material and mechanical elements, it is evident that some behaviors, especially those on a longer time scale, are, to a degree, autonomous of lower level events. It is important to note that this system autonomy 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. One can, in this abridged case, seem to identify an initial cause and a final result. The subsystem can appear wholly mechanical in its behavior. For example the phycologist who concentrates on identifying the genera of periphyton found on *Utricularia* leaves would be unlikely to discover the unusual feedback dynamics inherent in this community. Once the observer expands the scale of observation enough to encompass all members of the loop, however, then autocatalytic behavior with its attendant centripetality, persistence, symmetry and autonomy emerges as a consequence of this wider vision.

These many non-mechanical attributes, taken together, constitute the case for the rehabilitation of formal and final causes as legitimate actors behind the process of ecosystem development. Their principal manifestations come as the results of the actions of autocatalytic configurations of trophic exchanges. Autocatalysis brings with it alterations in the symmetry properties of ecosystem processes. Mutualisms by their very nature introduce symmetry into the kinetic structures of which they are a part. But they also can engender a temporal asymmetry that takes on the guise of a system-level *telos*. It remains to quantify the relative degrees of symmetry and disorder within ecosystems structures (and, by inference, within higher social structures.)

4. QUANTIFYING SYMMETRY IN ECOSYSTEM KINETICS

One may summarize the effects that autocatalysis can have on a network of ecosystem transfers as twofold: Firstly, mutualism works to increase the overall level of system activity. Secondly, it acts to subdue or excise those pathways that are less effective branches of autocatalytic configurations. These two phenomena can be quantified using (1) a notation common to economic input-output theory and (2) indices derived from information theory, respectively.

To begin, let T_{ij} represent the transfer of some form of material or energy from system component i to some other member, j, where indices i and j can represent any of the n members of the community or can designate a finite number of external sources and sinks. The total activity of the system is readily identified with the sum of all such exchanges, or $T_{..}$, where a dot in the place of a subscript indicates that its sum has been taken. That is,

$$T_{..} = \sum_i \sum_j T_{ij}$$

Any rise in system activity occasioned by autocatalytic action (or any other factor) then appears as an increase in $T_{..}$.

Gauging the degree of pruning or streamlining of the network topology requires more elaborate consideration. To recount how the pattern of flows is changing: Those pathways that participate most in autocatalysis increase in their magnitudes, usually at the expense of other processes that are less engaged. Because autocatalytic loops naturally compete for resources (centripetality), those links that are less efficient in augmenting autocatalysis are effectively pruned. (It is not that the links necessarily disappear; they can simply shrink relative to the favored exchanges.) Restated in other words, if a quantum of material currently is embodied in a particular node, and there are several predators upon that population, transfer is more likely to occur to a predator that will return the most resource to its prey via an autocatalytic route. All else being equal, feeding by the competing predators will shrink relative to the most favored exchange. In effect, the probability for transfer to the favored prey will increase, while those to the other predators will fall.

The field of mathematics that quantifies such changes in probabilities is called information theory. Myron Tribus has defined information as anything that causes a change in probability assignment (Tribus and McIrvine 1971). But information cannot be measured directly Instead, one proceeds by first quantifying the degree of indeterminacy inherent in a set of probabilities. (The conventional term used for this property is "uncertainty". The term "indeterminacy" is used here instead to emphasize that the attribute needn't be entirely epistemic in nature. That is, it does not depend entirely upon some outside observer, but is internal to the system [Matsuno 1989].) One begins with the indeterminacy as to which compartment will next donate a quantum of medium. The probability that the next quantum leaves compartment i can be estimated by the quotient $T_{i.}/T_{..}$, where $T_{i.}$ is the sum of all flows leaving i. The associated indeterminacy will be labelled $H(A)$ and its indeterminacy is measured by the familiar Shannon (1948) formula as:

$$H(A) = -\sum_i (T_{i.} / T_{..})\log(T_{i.} / T_{..})$$

Similarly, the indeterminacy as to which compartment a quantum will next enter, $H(B)$, takes the form:

$$H(B) = -\sum_j (T_{.j} / T_{..})\log(T_{.j} / T_{..})$$

In general $H(A) \neq H(B)$.

The idea now is to compare the separate indeterminacies of donations and receptions with that inherent in a particular flow structure, where leaving a particular compartment imposes some degree of constraint upon where the donation can flow. The probability that a quantum both leaves *i and* enters *j* can be estimated as before by the quotient $T_{ij}/T_{..}$. The indeterminacy associated with the constrained flow structure accordingly becomes:

$$H(A,B) = -\sum_i \sum_j (T_{ij} / T_{..})\log(T_{ij} / T_{..})$$

It can be shown that the indeterminacy, $H(A,B)$, which includes the constraints of the flow structure, is always less than (or in degenerate cases equal to) the sum of the separate indeterminacies of donation and reception, $H(A) + H(B)$. The difference, or decrease in indeterminacy, is called the mutual information, $I(A;B)$.

$$I(A;B) = [H(A) + H(B)] - H(A,B)$$

It is a straightforward exercise to demonstrate that

$$I(A;B) = \sum_i \sum_j (T_{ij} / T_{..})\log(T_{ij}T_{..} / T_{i.}T_{.j})$$

In words, the information inherent in the network structure of trophic flows is equal to the decrease in indeterminacy that results from calculating the joint indeterminacy rather than treating the donor and receptor indeterminacies separately. It is rather easy to show that $I(A;B)$ increases as smaller, redundant pathways are pruned from a network structure (Ulanowicz 1986).

The problem with information indices is that they are dimensionless. They do not reflect the physical magnitudes of their associated systems. To impart some measure of physical dimension to information indices, Tribus and McIrvine (1971) have suggested that users of information indices scale them by some characteristic dimension of the physical system. In this case the most intrinsic scale for the extent of the system is the total activity, $T_{..}$. Whence, the information index, $I(A;B)$, is multiplied by $T_{..}$ to yield a scaled variable called the system ascendency, A (Ulanowicz 1980, 1986).

$$A = \sum_i \sum_j T_{ij}\log(T_{ij}T_{..} / T_{i.}T_{.j})$$

Into the measure A has been combined the attributes of system activity and organization. A rise in activity leads to an increase in $T_{..}$; an increase in system development is tracked by a higher $I(A;B)$. Hence, both effects of autocatalysis acting as a formal or final agent are incorporated into a rise in system ascendency. In a very seminal paper, Eugene Odum (1969) listed 24 attributes of ecosystems that might be employed to differentiate whether they were in the early or late stages of succession (ecosystem development.) Odum's properties can be aggregated according to how they characterize major tendencies, such as those toward greater species richness, stronger retention and cycling of resources, and finer trophic specialization. Each of these trends constitutes a separate manifestation of increasing mutual information in trophic networks.

5. SYMMETRY CONSIDERATIONS

Of particular interest as regards symmetry is the average mutual information that constitutes one of the two factors of the system ascendency. The word "mutual" is included in its name to signify its symmetry with respect to inputs and outputs. One look at the formula for A, and it immediately becomes evident that the quantity remains unchanged when inputs are switched with outputs. That is,

$$I(A;B) = I(B;A).$$

This same property is evident among the other forms of indeterminacy. One can see from (*) that $H(A,B) = H(B,A)$. The difference between the joint indeterminacy and the mutual information has been called the system "overhead", Φ (Ulanowicz 1980. It is also the Rokhlin metric of ergodic theory, Petersen 1983). That is,

$$\Phi(A,B) = H(A,B) - I(A;B)$$

It is obvious that the system overhead is likewise symmetric (Ulanowicz and Norden 1990). We are led, therefore, to the rather interesting observation that our exercise has yielded results that are just the reverse of Boltzmann's. Boltzmann began with a microscopic universe of particles that interacted in a purely reversible (temporally symmetric) manner. By aggregating in a manner formally analogous to standard practice in information theory, he arrived at a temporally asymmetric description at the macro-level. We have begun with a "microscopic" description of ecosystems that is highly irreversible (temporally asymmetric) and have obtained wholly symmetric macroscopic variables.

Not that there are no clues to the direction of time within the information variables just described. It was noted above, for example, how $H(A) \neq H(B)$. Defining what are called the "conditional indeterminacies"

$$H(A|B) = H(A,B) - H(B)$$

and

$$H(B|A) = H(B,A) - H(A),$$

we note that

$$\Phi(A,B) = H(A|B) + H(B|A)$$

where

$$H(A|B) \neq H(B|A).$$

That is, the overhead can be decomposed into terms that are not symmetrical with respect to the reversal of A and B. Recall that we have used the convention that A represents inputs and B, outputs, so that the conventional ordering of time is $B \rightarrow A$, i.e., an output from one component becomes the input to another. Because the second law of thermodynamics requires a dissipatory output from each living component, and because systems tend to concentrate upon the few input sources that can be tapped most efficiently, in the overwhelming number of cases it will happen that $H(B|A) > H(A|B)$. This is another way of saying that the multiplicity or indeterminacy (degrees of freedom) among outputs exceeds that among inputs. If the reverse should occur, i.e., if $H(A|B) > H(B|A)$, then one of two conclusions may be drawn: Either (a) the observer has concentrated upon a small living subsystem that is being subsidized by dissipation in some larger system, or (b) the direction of time should be reversed (i.e., time proceeds as $A \rightarrow B$.)

Unlike in classical thermodynamics, which deals with enormous numbers of almost non-interacting particles, in ecology and the social sciences one deals with *middle number* systems — typically from ten to a few thousand partially (but not necessarily rigidly) interacting components. In thermodynamics, the probability of the second law being contravened is vanishingly infinitesimal. With middle number systems, there is a very small, but finite chance that $H(A|B) > H(B|A)$ for a real system. An example of such inversion might occur in ecology if an observer were to define the ecosystem to be a collection exclusively of omnivores. Omnivores constitute relatively small fractions of any real community, so that expanding the scale of observation to encompass more of the natural interactions will soon restore the inequality, $H(B|A) > H(A|B)$.

6. CONCLUDING REMARKS

Looking at the decomposition of the indeterminacy,

$$H(A,B) = H(A|B) + H(B|A) + I(A;B)$$

we are led to the following conclusion:

The constraints that define the form and order of a dissipative system $[I(A;B)]$ are symmetrical by nature. It is perhaps yet another manifestation of Newton's genius that he apprehended the mutuality inherent in any constraint that binds two objects or agents. This is not to say that all connections between agents are purely symmetrical. Indeed, one member of the pair may be more constrained by the link than the other. In such case, our calculus assigns the degree of freedom possessed by the latter to the conditional indeterminacy. Only the constraint common to both participants contributes to the *mutual* information.

Some have questioned the utility of the mutual information as an indicator of causality, precisely because it is symmetric with respect to A and B. But that very same criticism could be summoned as well against the laws of mechanics. Yet there is usually no problem assigning cause and effect in mechanical situations. The trick to doing so resides in making reference to some cue outside the purely mechanical realm, i.e., to some irreversible phenomenon. The same considerations apply when the components of a system are no longer rigidly coupled. The magnitude of the constraints active in (formal) causality can be gauged by the symmetrical mutual information. The clue to the direction of that causality does not reside in the ordered structure itself, but rather on the acausal periphery. The direction of causality is set by the casual (and therefore asymmetric) phenomena that contribute to the conditional indeterminacies.

It should also be remembered that the mutual information is symmetric only at the level of the whole system. If one breaks the measure down into its individual components, each generated by a particular flow, the symmetry immediately vanishes. If, for example, there is a flow from i to j, but none from j to i, then the $i \rightarrow j$ flow will make a contribution (positive or negative) to the overall mutual information, but none will be made in the reverse direction. This situation, of course, does not allow one to infer that j does not affect i. We have seen in the definition of autocatalysis how j could feedback into i via some indirect route. The effect of such autocatalysis is to foster symmetry among community interactions, just as the same agency drives the increase in the community ascendency (a symmetrical system property.)

We are finally in a position to charactenze the phenomenon of ecosystem development. It been descnbed above as any increase in the mutual information inherent in the trophic flow network structure. But that measure is symmetrical with respect to interactions at the level of the whole system. We conclude, therefore, that ecosystem development can properly be regarded as symmetry arising.

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