

THE ORGANIC IN ECOLOGY

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ABSTRACT. Organicism, or the analogy by which various organized living communities are likened to individual discrete organisms, is rejected in many quarters by those who object to the notion of a larger entity forcing the behavior of its smaller constituents. The connections one may draw from organicism to vitalism and oppressive social regimes are all too obvious and unsavory. It is conceivable, however, that organic behavior may exist independently of the nearly deterministic confines of ontogeny. In ecosystems, for example, the configuration of processes among the community appears to influence the fates and behaviors of component populations in a non-deterministic fashion. Popper's generalization of deterministic forces as "propensities," when coupled with the notion of autocatalytic feedback, leads to a wholly natural and quantitative description of such organic behavior. There even exists a perspective from which the organic metaphor for living phenomena satisfies Occam's criterion for simplicity better than the prevailing mechanistic metaphor for evolution. Judiciously reconstituted, organicism affords a highly useful and acceptable natural framework to help guide the scientific investigation of living systems.

KEY WORDS. Autocatalysis, causality, contingency, development, ecosystem, evolution, feedback, neo-Darwinism, Newtonianism, Occam's razor, organicism, organization, propensities, stochasticism.

INTRODUCTION

The persistent tendency to see collections of living entities, such as social systems, economic communities or ecosystems as analogous to living organisms has a long history. Certainly, the metaphor affords some obvious parallels that have been used over the years by innumerable thinkers—among others, Aristotle, Paul of Tarsus, Leibniz, Comte, Spencer, and, more recently, Von Bertalanffy. Nevertheless, the simile is studiously, and sometimes vehemently eschewed by many, either because it not so cryptically hints at vitalism, or because it conjures up examples of any number of totalitarian states that have invoked the likeness to justify their own oppressive agendas. These are most serious criticisms not without at least some justification. The prevailing attitude that they have engendered, however, is akin to a "taboo" that proscribes

any and all further discussion of (and therewith the benefits of any insights into) any legitimate organic features these *organizations* might exhibit.

In considering why so many object to organicism, one is led to ask which of its features appears most odious to its detractors, and the property of *determinism* springs immediately to mind. The lack of freedom is always threatening. It seems not to be determinism per-se that most bothers the opponents of organicism, for most of them have no quibble at all with the physico-chemical reductionism or molecular determinism now so popular in biology. Rather, it seems to be the agency of a larger entity being exercised deterministically upon a smaller component that many find abhorrent in either vitalism or totalitarianism. One is led to wonder, therefore, whether by excising the deterministic from the organic analogy we might arrive at a more palatable and useful metaphor. Might there not be a more amenable middle ground between the rigidity of ontogeny and the utter confusion of stocasticity?

It was in asking himself the latter question that Popper (1990) concluded that to gain the right perspective on evolution, we need first to reconsider our notions of causality—of how form and pattern arise. Following Popper's admonition, we note that it is not too radically removed from current evolutionary thinking to assume that what we call the organic can exist *only because* causal agency is being exercised through an interfering miasma of indeterminacy. Accepting this state of affairs, however, requires that one shift the focal point of organic behavior away from the discrete organism, where development approximates mechanical determinism, and towards living communities that are less rigidly constrained. In distancing our discussion from organisms, we would also prefer not to complicate the picture too much at first by including any elements that hint to teleological directionality or human intentions (although we do not thereby preclude the application of any ensuing conclusions to such systems). Our gaze, therefore, comes to rest on the convenient middle ground of ecosystems.

By historical accident, the first metaphor to become prominent in American ecology was Frederic Clements' (1916) suggestion that ecosystems behave like organisms. Clements directly credited Jan Smuts as his inspiration, but ultimately he was following in the traditions of Leibniz and Aristotle. The organic analogy was advanced in subsequent decades by G. Evelyn Hutchinson and Eugene Odum. The organic metaphor, however, was but one of three that have been invoked over the years by systems ecologists (Hagen 1992). In fact, Clements' analogy was almost immediately countered by his contemporary, Henry Gleason (1917), who suggested that plant communities arise largely by chance and in the absence of any major organizational influences. Such stochasticism was

reminiscent of nominalism and prefigured deconstructivist postmodernism. It has found voice in contemporary ecology through the writings of Daniel Simberloff (1980), Kristin Schrader-Frechette (and McCoy, 1993) and Mark Sagoff (1997), all of whom deride the bulk of ecosystems theory as unwarranted reification of non-existing organizations and agencies. Finally, the most familiar, orthodox and widely-accepted metaphor is that of the ecosystem as machine, or clockwork, which runs according to a Newtonian scenario. This tradition has been kept alive and well by the likes of George Clarke (1954), Howard Odum (1960) and Thomas Schoener (1986).

Over the years it is likely that the popularity of each metaphor has been influenced by changing political fashions. Barbour (1996), for example, sees the abandonment of Clements' organicism in favor of a resurgence of interest in Gleason's stochasticism during the 1950's as reflecting the rise of neo-liberalism in American politics during that period. Indeed, the organicism-atomism cleft in sociology has been so deep and acrimonious that it is highly likely that its reverberations in ecology have led many ecologists to seek safe haven in the mechanical view of the world. (The attractiveness of the Newtonian metaphor has been abetted by what Cohen [1971] has termed "physics envy"—this despite the conviction of most physicists that the metaphor is a significantly inadequate representation of the material universe [Capra 1996].) By adhering to the mechanical, one needn't tip one's hand and reveal one's socio-political inclinations. Ostensibly, one maintains social neutrality by regarding organisms in very mechanical terms, as is the fashion of Daniel Dennett (1995) and even Clements himself.

I side with Popper, however, in my belief that a purely mechanical description of growth, development and evolution blinds us to the action of other legitimate natural agencies—among them the organic. In fact, I wish to go so far as to suggest that Popper's insights lead us to a theory that is inclusive of all three metaphors, as I will attempt to describe below. As regards the legitimacy of organic action in ecology, I believe the key lies in the opinion by Depew and Weber (1994) that "Clements had it backwards; ecosystems are not super-organisms, organisms are super ecosystems!" Organic behavior in its most essential form exists outside of pure determinism. Like virtually all earlier organic comparisons, Clements' analogy was too tightly drawn. Organisms are far more highly constrained and ordered than are ecosystems. Ecosystems are not contained within any integument. Their development is ordained only in the loosest sense of the word; their functions are not carried out by predetermined elements, etc. In effect, organicism, as classically defined, misses the mark. Therefore, in order to observe organic behavior unencumbered by determinism, one must look afield of ontogeny and toward ecology.

Despite their relative lack of constraint, ecosystems do develop according to a more-or-less repeatable sequence. The entry of a species into an ecological community does hinge upon the makeup of the system at the time of invasion. Ecosystems do exhibit a form of self-ordering, albeit the agencies behind such ordering do not appear to be as strong and definitive in their actions as one might observe in developmental biology. Although regarding ecosystems in the guise of organisms seems unwarranted, organic action in ecosystems does seem plausible. Perhaps the most reasonable course to follow would be to refer to ecosystems simply as “organic systems.” But is even an attenuated organicism appropriate to ecosystems? What, if anything, allows one to refer to ecosystems as “organic,” rather than as complex machines? To see why ecosystem behavior is other than mechanical, it helps first to codify the assumptions of classical mechanics, as it was practiced at its zenith.

According to Depew and Weber (1994), science during the nineteenth century was overwhelmingly Newtonian in scope. they identified four postulates under which Newtonian investigations were pursued:

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

Newtonian systems are *deterministic*. Given precise initial conditions, the future (and past) states of a system can be specified with arbitrary precision.

Newtonian systems are *reversible*. Laws governing behavior work the same in both temporal directions.

Newtonian systems are *atomistic*. They are strongly decomposable into stable least units, which can be built up and taken apart again.

After consulting with these authors, I have added a fifth article of faith (Ulanowicz, 1997), namely that

Physical laws are *universal*. They apply everywhere, at all times and scales.

Now, early in the nineteenth century, the notion of reversibility had already been challenged by Sadi Carnot’s thermodynamical elaboration of irreversibility, and, several decades later, Darwin’s historical narrative posed even further difficulties. Later, the development of relativity and quantum theories early in the twentieth century worked to subvert the assumptions of universality and determinism, respectively. Nevertheless, many in biology (and especially in ecology) continue to operate under a mechanistic umbrella that differs little from the classical Enlightenment metaphysics I have just outlined. The challenge here is to revise this set of assumptions in a way that brings to bear those elements of the stochastic and, especially, the organic that are relevant to ecosystem behavior, and

to do so in a way that the ensuing metaphysic remains wholly natural and internally consistent. We begin this task by first moving away from strict determinism and reconsidering both the role and the nature of contingencies in ecosystem development.

2. CONTINGENCY, SIMPLE OR COMPLEX?

Reconciling chance with deterministic mechanics is no easy task, and the problem has occupied some of the best minds over the past two centuries. Ludwig von Boltzmann and Josiah Gibbs dominated the effort during latter nineteenth century to construct a statistical mechanics that would salvage Newtonian precepts from the challenge posed by the irreversibility inherent in thermodynamics. Then early in the twentieth century, Ronald Fisher used almost identical mathematics to join the gradualist narrative of Darwin to the discrete phenomena observed by Mendel, resulting in what came to be known as "The Grand Synthesis." I wish to bring to the reader's attention the fact that both these attempts at reconciliation are relevant only to systems of many components that are largely decoupled from one another—hardly the description of an ecosystem.

Because these attempts at reconciliation were so narrow in application, biology today remains somewhat "schizophrenic." It resembles a desperate attempt to adjoin two mutually exclusive extremes; that is, narrative constantly is switching back and forth between the realms of strict determinism and pure stochasticity, as if no middle ground existed. It was precisely this regrettable situation that prompted Karl Popper (1990) to voice his concern about our fundamental attitudes toward the nature of causality. True reconciliation, Popper suggested, lies in an intermediate to stochasticity and determinism. He proposed, therefore, a generalization of the Newtonian notion of "force." Forces, he posited, are simple idealizations that exist as such only in perfect isolation. The objective of experimentation is to approximate to the fullest extent possible the isolation of the workings of an agency from interfering factors. In the real world, however, where components are loosely, but definitely coupled, he urges us to speak rather of "propensities." A propensity is the tendency for a certain event to occur in a particular context. It is related, but not identical, to conditional probabilities.

Consider, for example, the hypothetical "table of events" depicted in Table 1, which arrays five possible outcomes: b_1, b_2, b_3, b_4, b_5 , according to four possible eliciting causes: a_1, a_2, a_3 , and a_4 . For example, the outcomes might be several types of cancer, such as those affecting the lung, stomach, pancreas or kidney, while the potential causes might represent various forms of behavior, such as running, smoking, eating fats, etc. In an ecological context, the b 's might represent predation by

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

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

TABLE 1

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

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

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

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

TABLE 2

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

This interconnectedness of propensities highlights an unsung aspect of the role of contingency in systems development—namely, that contingencies are not always simple in nature. Chance events can possess distinct

characteristics and can be rare, or possibly even unique in occurrence. Our tendency, however, is to consider chance events as being almost point like in extent and instantaneous in duration. In fact, we rarely ever think of chance events as anything but simple and generic. Thus, when Prigogine (and Stengers, 1984) writes about macroscopic order appearing via microscopic fluctuations, it is implicit that the latter are generic and structureless. Perturbations, anyhow, happen to come in an infinite variety of forms, and any given system may be very vulnerable to some categories of disturbance and rather immune to others.

Even if disturbances should come in different flavors, a further implicit assumption is that any individual type of disturbance will always occur repeatedly. The repetition of phenomena is, after all, the Baconian cornerstone of normal science. Once one allows that contingencies may be complex, however, one must face up to the possibility that some contingencies might be *unique* for once and all time. In fact, it is even necessary to confront the likelihood that our world might be absolutely rife with one-time events. That such might be the case follows as soon as one ceases to regard contingencies merely as simple point-events, but rather as configurations or constellations of both things and processes. That many, if not most, such configurations are probably unique for all time then follows from elementary combinatorics. For, if it is possible to identify n different things or events in a system, then the number of possible combinations of events varies roughly as n -factorial. It doesn't take a very large n for $n!$ to become immense. Elsasser (1969) called an immense number any magnitude that was comparable to or exceeded the number of events that could have occurred since the inception of the universe. To estimate this magnitude, he multiplied the estimated number of protons in the known universe (ca. 10^{85}) by the number of nanoseconds in its duration (ca. 10^{25}). It is often remarked how the second law of thermodynamics is true only in a statistical sense; how, if one waited long enough, a collection of molecules would spontaneously segregate themselves to one side of a partition. Well, if the number of particles exceeds 25 or so, the *physical* reality is that they would *never* do so.

Because propensities always exist in a context (in accordance with the ecological vision), and because that context usually is not simple, it becomes necessary to consider the reality and nature of complex contingencies. To capture the effects of chance, it won't suffice simply to modulate the parameters of a mechanical model with generic noise (cf. Patten, 1999). In a complex world unique events occur continually. They are by no means rare; they are legion! Perhaps fortunately, the overwhelming majority of one-time events happens and passes from the scene without leaving a trace in the more enduring observable universe. On occasion, however, a singular contingency can interact with a durable system in

such a way that the system readjusts in an *irreversible* way to the disturbance. The system then carries the memory of that contingency as part of its *history*. Again, no amount of waiting is likely to lead to an uncontrived repetition of what has transpired.

The efficacy of Popper's concept of propensity is that it pertains equally well to law-like behavior, generic chance and unique contingencies, all under a single rubric. We note for reference below that, irrespective of the natures of any eliciting interferences, the transition depicted from Table 1 to Table 2 involves proceeding from less constrained to more constrained circumstances. It is the progressive appearance of constraints that we have in mind when we use the term "development." We now ask the questions, "What natural agency might contribute to the transition from Table 1 to Table 2?" or, in a larger sense, "What lies behind the phenomena we call growth and development?" and "How can one quantify the effects of this agency?"

3. THE ORIGINS OF ORGANIC AGENCY

One clue to an agency behind growth and development appears as soon as one asks what happens when propensities interact. Any one process will either abet (+), diminish (-) or not affect (0) another. Similarly, the second process can have any of the same effects upon the first. Out of the nine possible combinations for reciprocal interaction, it turns out that one interaction, namely mutualism (+,+), possesses very different properties from all the rest. Numerous investigators, including Manfred Eigen (1971), Hermann Haken (1988), Humberto Maturana (and Varela, 1980), Stuart Kauffman (1995) and Donald DeAngelis (1986) have contributed to a growing consensus that some form of positive feedback is responsible for most of the order we perceive in organic systems. I now wish to focus attention upon a particular form of positive feedback, namely, autocatalysis. Autocatalysis is that form of positive feedback wherein the effect of every consecutive link in the feedback loop is positive. When the Newtonian assumptions are satisfied, as happens with autocatalysis among simple chemical reactants, such feedback appears wholly mechanical in nature. As soon as the participants become complicated enough to exhibit some form of indeterminacy, however, several distinctly non-mechanical attributes suddenly appear.

To make clear exactly what form of autocatalysis I am discussing, I direct the reader's attention to the three-component interaction depicted in Figure 1. We assume that the action of process A has a propensity to augment a second process B. I wish to emphasize that my use of the word "propensity" is taken to mean that the response of B to A is not wholly obligatory. That is, A and B are not tightly and mechanically linked. Rather, when process A increases in magnitude, most (but not all) of the

time, B also will increase. B tends to accelerate C in similar fashion, and C has the same effect upon A.

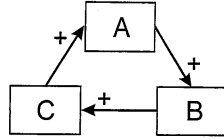


FIGURE 1

Schematic of a hypothetical three-component autocatalytic cycle.

My favorite ecological example of autocatalysis is the community that centers around the aquatic macrophyte, *Utricularia* (Ulanowicz, 1995). All members of the genus *Utricularia* are carnivorous plants. Scattered along its feather-like stems and leaves are small bladders, called utricles (Figure 2a). Each utricle has a few hair-like triggers at its terminal end, which, when touched by a feeding zooplankter opens the end of the bladder and the animal is sucked into the utricle by a negative osmotic pressure that the plant had maintained inside the bladder. In the field the surface of *Utricularia* plants always supports a film of algal growth known as periphyton (Figure 2b). This periphyton in turn serves as food for any number of species of small zooplankton. The autocatalytic cycle is completed when the *Utricularia* captures and absorbs many of the zooplankton.

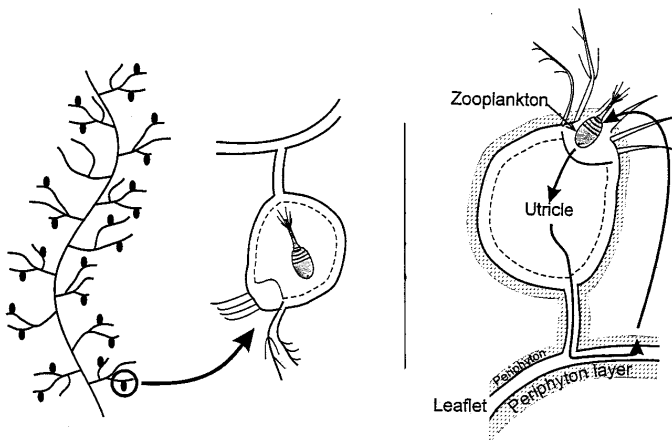


FIGURE 2

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

Autocatalysis among propensities gives rise to at least eight system attributes, which, taken as a whole, comprise a distinctly non-mechanical dynamic. We begin by noting that by our definition autocatalysis is explicitly *growth-enhancing*. Furthermore, autocatalysis exists as a *formal* structure of kinetic elements. More germane to the notion of organic behavior, autocatalysis is capable of exerting *selection* pressure upon its ever-changing constituents. To see this, let us suppose that some small change occurs spontaneously in process B. If that change either makes B more sensitive to A or a more effective catalyst of C, then the change will receive enhanced stimulus from A. Conversely, if the change in B either makes it less sensitive to the effects of A or a weaker catalyst of C, then that change will likely receive diminished support from A. Again we reiterate, all linkages are contingent in nature, not deterministic. We also note that such selection works on the processes or mechanisms as well as on the elements themselves. Hence, any effort to simulate development reductionistically in terms of a fixed set of mechanisms is doomed ultimately to fail.

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

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

our mothers were to see us for the first time in ten years, she would recognize us immediately.

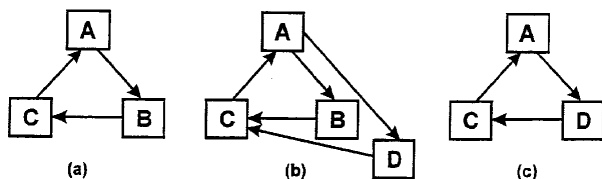


FIGURE 3

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

Autocatalytic selection pressure and the competition it engenders together define a preferred direction for the system—namely, that of ever more effective autocatalysis. In the terminology of physics, such direction is the result of *symmetry-breaking*. One should not confuse this rudimentary directionality with full blown teleology, however. It is not necessary, for example, that the system strives towards some pre-ordained endpoint. The direction of the system at any one instant is defined by its state at that time, and the state changes as the system develops. Hence, I have used the term “telos” to denote this *weaker* form of directionality and to distinguish it from the far rare and more complex behavior known as teleology.

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

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

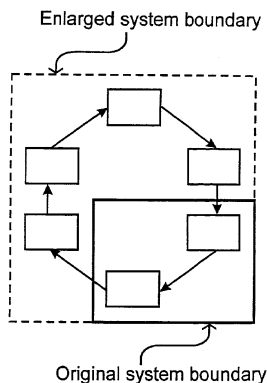


FIGURE 4

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

4. CAUSALITY RECONSIDERED

It is important to note that selection pressure that arises from autocatalysis is exerted by larger composites upon smaller constituents. Top-down influence is an essential, defining feature of organic systems, and has been familiar to ecologists for a while now in the context of trophic interactions. Such phenomena would nevertheless appear mysterious under the Newtonian metaphysic, which permits only those influences originating at smaller realms of time and space to exert their effects at larger and longer scales. By way of contrast, the prevailing view on natural causalities prior to Newton had been formulated by Aristotle, who favored organic similes and explicitly recognized the existence of downward causation. In line with Popper's suggestion, we have been urged by Robert Rosen (1985), among others, to reconsider Aristotle's organic conceptions of causality as legitimate and appropriate to the description of living phenomena.

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

Encouraged by the simplicity of Newton's *Principia* and perhaps influenced by the politics of the time, early Enlightenment thinkers acted decisively to excise formal and final causalities from all scientific description. Yet there appear to be especial reasons why Aristotle's schema provides a more satisfactory description of ecological dynamics, and those reasons center around the observation that efficient, formal and final causes are hierarchically ordered—as becomes obvious when we notice that the domains of influence by soldier, officer and prime minister extend over progressively larger and longer scales.

The Achilles heel of Newtonian-like dynamics is that it cannot in general accommodate true chance or indeterminacy (whence the "schizophrenia" in contemporary biology). Should a truly chance event happen at any level of a strictly mechanical hierarchy, all order at higher levels would be doomed eventually to unravel. On the other hand, the Aristotelian hierarchy is far more accommodating. Any spontaneous efficient agency (simple or complex) at any hierarchical level is subject to selection pressures from formal autocatalytic configurations above. These configurations in turn experience selection from still larger constellations in the guise of final cause (Salthe, 1985). The result of such top-down pressure is that the influence of most irregularities remains circumscribed. Unless the larger structure is particularly vulnerable to a certain type of perturbation (which happens relatively rarely), the effects of most perturbations are quickly damped. Hence, the results of any particular event appear to follow neither universal laws nor self-similar fractal rules. Rather, they seem confined to a particular subregion of a world that is "granular" in hierarchical appearance (Allen and Starr 1982).

5. FORMALIZING ORGANIC DYNAMICS

Popper suggested that we should no longer be satisfied with the prevailing image of rigid mechanisms set opposite to complete disorder, with nothing in between. He urged us to consider a middle ground, wherein propensities interacting with each other give rise to non-rigid structures that nonetheless retain their coherence over time, i.e., the world of the truly organic. We now see how, once the focus on organic behavior is shifted from near-determinism towards contingency, that the objections to organic behavior begin to fade. No longer does the overall system *inexorably* drive the components. It does, nonetheless, influence the behaviors of their parts, as well as how they will be replaced. Furthermore, an Aristotelian framework of causalities allows an observer to focus more clearly on the (formal) agency that exerts statistical pressure towards organic system coherence—namely, autocatalytic configurations of processes.

From the above considerations on autocatalysis we can abstract two major facets of its actions: Autocatalysis serves to increase the activities of

all participating constituents; and it prunes the network of interactions so that those links that most effectively contribute to autocatalysis come to dominate the system. These facets of behavior are extensive (size-dependent) and intensive (size-independent), respectively. Schematically this transition is depicted in Figure 5. The upper figure represents a hypothetical, inchoate four-component network before autocatalysis has developed, and the lower one, the same system after autocatalysis has matured. The magnitudes of the flows are represented by the thickness of the arrows. To the right appear the matrices that correspond to the pattern of flows. One recognizes that the differences between the matrices in Figure 5 resemble those between Tables 1 and 2 above, and we recall how that transition was associated with the appearance of progressive constraints.

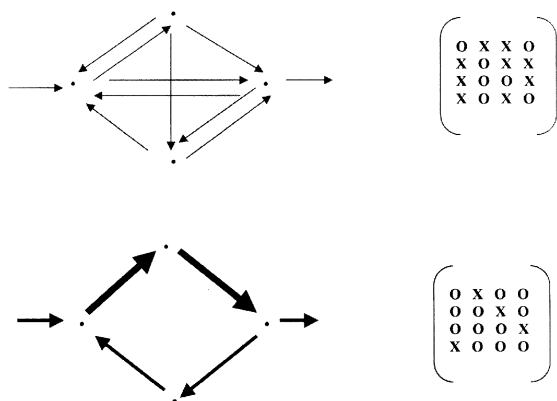


FIGURE 5

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

There is not sufficient space to detail how these two facets of autocatalysis may be quantified (Ulanowicz, 1986). Suffice it here merely to relate the results in simple prose. We begin by designating the sum of the magnitudes of all system processes, or what in economic theory is called the "total system throughput," as the measure of the total system extent or activity. Growth thereby becomes an increase in the total system throughput, much as economic growth is reckoned by any increase in Gross Domestic Product.

As for the "pruning," or development effected by autocatalysis, it will be related to changes in the probabilities of flow to different compart-

ments. Knowing the magnitudes of all the flows in the system, one can use these flows to estimate the conditional probability that a quantum of material or energy in any one taxon will flow to any other specific taxon in its next transfer (Ulanowicz and Norden, 1990). Knowing these conditional probabilities allows us to calculate an index from information theory called the "average mutual information," or AMI. One notes that the meaning of information overlaps strongly with the notion of "constraint," so that one may also view the AMI as a measure of the average constraint that guides the flows between the compartments of the ecosystem. Development then becomes any increase in the AMI, which reflects increasing internal constraint within the ecosystem, as exemplified above by the transition from Table 1 to Table 2.

To demonstrate how an increase in AMI actually tracks the "pruning" process, I refer the reader to the three hypothetical network configurations shown in Figure 6. In configuration (a) it is maximally indeterminate whether medium from any one compartment will next flow. The corresponding AMI is identically to zero. The possibilities in network (b) are somewhat more constrained. Flow exiting any compartment can proceed to only two other compartments, and the AMI rises accordingly. Finally, flow in schema (c) is maximally constrained, and the AMI assumes the maximal value possible for a network of dimension 4.

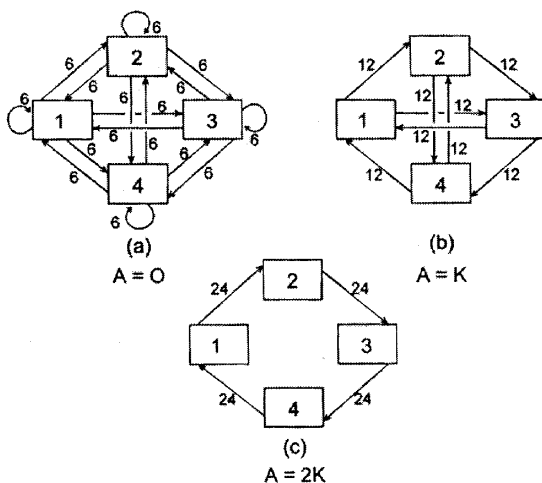


FIGURE 6

(a) The most equivocal distribution of 96 units of transfer among four system components. (b) A more constrained distribution of the same total flow. (c) The maximally constrained pattern of 96 units of transfer involving all four components.

Autocatalysis is a unitary process in the sense that it is a single agency that produces both extensive and intensive results. We can incorporate both these factors of growth and development into a single index by multiplying them together to define a measure called the system *ascendency*. In his seminal paper, "The strategy of ecosystem development," Eugene Odum (1969) identified 24 attributes that characterize more mature ecosystems. These can be grouped into categories labeled species richness, dietary specificity, recycling and containment. All other things being equal, a rise in any of these four attributes also serves to augment the ascendency. It follows as a phenomenological principle that "in the absence of major perturbations, ecosystems exhibit a propensity to increase in ascendency." Increasing ascendency is a quantitative way of expressing the tendency for those system elements that are in catalytic communication to reinforce each other to the exclusion of non-participating members. The internal coherence thereby achieved is a cornerstone of organic behavior.

I should hasten to emphasize in the strongest terms possible that increasing ascendency is only half of the organic story. Ascendency accounts for how efficiently and coherently the system processes medium. Using the same type of mathematics, one can compute as well an index, called the system overhead, that is complementary to the ascendency (Ulanowicz and Norden, 1990). Overhead quantifies the degrees of freedom, interferences, inefficiencies and incoherencies present in the system. Although these latter properties may encumber overall system performance at processing medium, they become absolutely essential to system survival whenever the system incurs a novel perturbation. At such time, the overhead becomes the repertoire from which the system can draw to adapt to the new circumstances. Without sufficient overhead, a system is unable to create an effective response to the exigencies of its environment.

The configurations we observe in nature appear, therefore, to be the results of two agonistic tendencies (ascendency vs. overhead) working off of each other in a relationship that resembles a dialectic. Although the attributes appear to be in conflict, some degree of both is necessary if the existence of organic structure is to survive. Others may wish to view the interaction as an analog of the "ying-yang" agonism, where the active agency of autocatalysis, as measured by an increasing ascendency, works opposite to a passive, but necessary background of disorder, inefficiency and ambiguity, that is gauged by the system overhead.

6. UNDER OCCAM'S RAZOR

Doubtless, some readers will regard the organic description of evolutionary dynamics to be unnecessarily complicated in comparison to the very simplistic neo-Darwinian scheme. Neo-Darwinians would immediately invoke Occam's razor to reject the notion of organic behavior outright. But

I wish to counter with the question "Which description is actually more simple?" Howard Pattee (personal communication) emphasizes how any description of change in nature must consist of two elements: the dynamics by which those elements interact and the boundary conditions or context within which the dynamics transpires.

Charles Darwin consciously followed the prevailing Newtonian approach towards describing nature by explicitly making external all the agencies that elicit change under his rubric of "natural selection" (Depew and Weber, 1994). The remaining dynamics become rather easy to codify and describe. Natural selection remains, however, an enormously complicated "boundary condition" that at times is described in almost transcendental tones. We implicitly are urged to keep our eyes focused intently on the simple dynamical description and to pay no attention to the overwhelming complexity within which that dynamic occurs. Subsequent emendations to Darwinian thought have not altered his basic Newtonian separation and focus.

According to Pattee, however, any natural description should be judged in its entirety. By this standard, neo-Darwinism does not fare well under Occam's razor. By contrast, self-organization theory (of which the current organic narrative is an example) seeks to *include* far more agency into its dynamics. The result is necessarily a slightly more complicated description of the operative dynamic. The cost of such complication, however, is more than repaid by the degree to which it simplifies the boundary value problem. A significant amount of biological order, which under the Darwinian scheme had to be explained by arbitrary and innumerable manifestations of "natural selection," now are consolidated as the consequences of dynamics that are *internal* to system description. Kauffman (1995) called this class of phenomena "order for free," in the sense that the given pattern did not have to be encoded into the genome of the organism.

Regarding the overall problem description, the jury is still out as to whether neo-Darwinism or self-organization theory better satisfies Occam's criterion, but proponents of the latter description have every reason to be optimistic that the scales are beginning to tip in their favor.

Apropos simplicity of description, one may well ask which metaphor more simply and appropriately pertains to *biological* phenomena—the mechanical or the organic? The answer should be tautologically obvious, but mechanists would have us think otherwise. Daniel Dennett (1995), for example, bids us imagine the progressive complexity of biological entities as analogous to "cranes built upon cranes," whereby new features are hoisted on to the top of a tower of cranes to become the top crane that lifts the next stage into place. He specifically warns against invoking what he

calls “skyhooks,” by which he means agencies that create order but have no connection to the firmament.

Once one is convinced that the organic metaphor does have a legitimate place in scientific narrative intermediate to the mechanical and the stochastic, then organic analogs for biological phenomena become the simplest and most natural possible. This point was brought home to me via one of the few “Eureka!” experiences that have ever happened to me. I was working distractedly in my garden, pondering why I thought Dennett’s analogy was inappropriate, when my eye was drawn to a muscadine grapevine that has grown on the corner of my garden fence for the last twenty-five or so years. In the initial years after I had planted it, the lead vine had become a central trunk that fed an arboreal complex of grape-bearing vines. Eventually, the lateral vines had let *down* adventitious roots that met the ground some distance from the trunk. Then in the last few years, the main trunk had died and rotted away completely, so that the arboreal pattern of vines was now being sustained by the new roots, which themselves had grown to considerable thickness.

No need for skyhooks here! The entity always remains in contact with the firmament, and bottom-up causalities continue to be a necessary part of the narrative. Yet it is the later structures that *create* connections that eventually replace and displace their earlier counterparts. Top-down causality, the crux of organic behavior, but totally alien to mechanistic reductionistic discourse, fits the developmental situation perfectly. Evolution is like a muscadine grapevine. As strange as that analogy might seem at first, it fits the description far better than Dennett’s mechanical construct. In trying to concoct mechanical metaphors for what is a more inherently and legitimately organic phenomena, mechanists unnecessarily complicate the picture and lead us astray from the most natural perspective on the living world.

7. THE ECOLOGICAL PERSPECTIVE

Let us now take stock of our organic, ecological worldview as I have interpreted it. As for the underlying metaphysic, we can conclude that the classical Newtonian motif is inadequate in each of its five postulates:

1. Ecosystems are not causally closed. They appear to be *open* to the influence of contingency and non-mechanical agency. Spontaneous events may occur at any level of the hierarchy at any time. Efficient (or mechanical) causes usually originate at scales inferior to that of observation, and their effects propagate upwards. Formal agencies appear at the focal level; and final causes exist at higher levels and propagate (in organic fashion) downwards (Salthe, 1985; Ulanowicz, 1997).

2. Ecosystems are not deterministic machines. They are *contingent* in nature. Biotic agencies resemble propensities more than mechanical forces.
3. The realm of ecology is *granular* rather than universal. Models of events at any one scale can explain matters at another scale only in inverse proportion to the remoteness between them. Obversely, the domain within which irregularities and perturbations can damage a system is usually circumscribed. Chance does not necessarily unravel a system.
4. Ecosystems, like other biotic systems, are not reversible, but *historical*. Irregularities (either simple or complex) often engender discontinuities, which degrade predictability into the future and obscure hindcasting. The effects of past discontinuities are often retained (as memories) in the material and kinetic forms that result from adaptation. Time takes a preferred direction or telos in ecosystems—that of increasing ascendancy.

Finally, and most important to this essay,

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

The ecological worldview is not entirely revolutionary; further, by following Popper's *evolutionary* leads we retain connections with the orthodox and the classical. Unfortunately, it remains beyond the scope of this paper to demonstrate exactly how Popper's propensities are imbedded in the expression for the ascendancy (Ulanowicz, 1996). Furthermore, because propensities are generalizations of Newtonian forces, it can be shown how the principle of increasing ascendancy resembles a generalization of Newtonian law upwards into the macroscopic realm, in a way similar to how Schrödinger's wave equation originated as an extension of Newton's second law downwards into the netherworld of quantum phenomena (Ulanowicz, 1999).

The final question I wish the reader to consider is whether science is being well-served by those whose understandable zeal for simplicity has led them to mistake minimalism for simplicity. For we learn in elementary statistics that two types of mistakes regarding hypotheses are possible: One can accept a false hypothesis (an alpha error), or one can reject a true hypothesis (a beta error). Should one be over-cautious in avoiding either of these errors, the likelihood of committing the other will grow inordi-

nately. In seeking to obviate all semblances of the organic from the description of living phenomena, mechanists appear to have committed a beta-type error. To paraphrase an opinion commonly attributed to Albert Einstein, "Explanations should be as simple as possible, and no simpler."

Again, the major problem with classical expressions of organicism has been that the organic was miscast in strictly deterministic, mechanical terms. Even early ecologists, like Clements, could conceive the organic in only this fashion. It is difficult to blame them, when the most obvious manifestations of organic behavior, organisms themselves, lie at one extreme of the range of organic behavior and *do* develop in close analogy to rigid predeterminism. But the crux of organic behavior is neither mechanism nor determinism. These are only peripheral limits towards which organic behavior, if left unimpeded, could drift. The kernel of organic systems lies rather in the coherence and direction that systems level configurations of processes impart to their components.

This "ecological" form of organicism seems far less threatening a notion than its earlier counterpart. To convince oneself of this, one need only to consider the absurdity of a dictator trying to describe his/her totalitarian state in terms of an ecosystem with its loose connections and manifold feedbacks. As regards any similarity of ecological organicism with vitalism, we note as how the concept does not involve any "*élan-vital*" independent of material substrate. Like the muscadine grape, autocatalytic configurations of processes are inexorably connected with their material resources.

Finally, it should be noted that the ecosystem as organic metaphor is already abroad in scientific discourse. One encounters, for example, books on "the ecology of computational systems" (Huberman, 1988) or entire institutes devoted to the "ecological study of perception and action" (Gibson, 1979). It would appear that by following Popper's lead on propensities, we have arrived at a legitimate role for the organic in ecology that provides as well a useful metaphor for phenomena in the wider realms of biology and the social sciences.

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