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Life after Newton: an ecological metaphysic

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Abstract

Ecology may indeed be 'deep', as some have maintained, but perhaps much of the mystery surrounding it owes more simply to the dissonance between ecological notions and the fundamentals of the modern synthesis. Comparison of the axioms supporting the Newtonian world view with those underlying the organicist and stochastic metaphors that motivate much of ecosystems science reveals strong disagreements—especially regarding the nature of the causes of events and the scalar domains over which these causes can operate. The late Karl Popper held that the causal closure forced by our mechanical perspective on nature frustrates our attempts to achieve an 'evolutionary theory of knowledge.' He suggested that the Newtonian concept of 'force' must be generalized to encompass the contingencies that arise in evolutionary processes. His reformulation of force as 'propensity' leads quite naturally to a generalization of Newton's laws for ecology. The revised tenets appear, however, to exhibit more scope and allow for change to arise from within a system. Although Newton's laws survive (albeit in altered form) within a coalescing ecological metaphysic, the axioms that Enlightenment thinkers appended to Newton's work seem ill-suited for ecology and perhaps should yield to a new and coherent set of assumptions on how to view the processes of nature. © 1999 Elsevier Science Ireland Ltd. All rights reserved.

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1. Introduction

Ecology has never nestled comfortably among the traditional sciences. The uniqueness of ecology was characterized by Naess, 1988, when he wrote about 'deep ecology' as something that affects one's life and perception of the natural world in a profound way. Numerous others sense that ecology is useful for addressing phenomena in fields that are well-removed from the meadow or savannah. Thus, one encounters books on 'the

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ecology of computational systems' (Huberman, 1988) or discovers whole institutes devoted to the 'ecological study of perception and action' (Gibson, 1979).

It is well and good to laud ecology through poetry or metaphor, but most scientists demand a more rational and systematic comparison of ideas emerging from ecology with those comprising the established modern synthesis. In what follows I will attempt to compare the historical lines of ecosystems thinking against the axioms that undergird the Newtonian treatment of natural phenomena. I will argue that these elements of Newtonianism fail as a framework upon which to hang the manifold facets of the process called life (i.e. life post-Newton.) It appears that a full and coherent apprehension of living systems can be achieved if one reconsiders, in addition to a certain Newtonian element, some ancient Aristotelian concepts in conjunction with the more contemporary notion of a world that is ontologically open, as proposed by Peirce, 1877 and Popper, 1982. The ensuing unitary description of natural dynamics is cast in the mold of Postmodern Constructivism (Griffin, 1996; Ferré, 1996) but nonetheless retains marked similarity to the fundamental laws outlined by Newton in his Principia (life in the image of Newton). The axioms that later thinkers appended to Newton's work, however, do not appear consonant with ecological thinking and perhaps should be replaced by a new set of assumptions.

2. The ecological triptych

Conventional wisdom holds that there exists no single theoretical core to ecological thinking as, say, Maxwell's Laws provide for the study of electricity and magnetism. The reason is that, historically, ecosystems theorists have divided roughly into three camps: (1) organicists; (2) mechanists; and (3) nominalists, or stochastics (Hagen, 1992). The rise of systems ecology early in the 20th Century tracks closely the writings of Frederic Clements, 1916 and his manifold analogies between ecosystems and organisms. The metaphor of ecological community as 'superorganism' is frequently used to characterize Clements' ecology (although a perusal of his writings will reveal he used this neologism only rarely.) Clements credited Smuts, 1926 for his interest in holism, and Clements, in turn, motivated two of ecology's most renowned figures, G. Evelyn Hutchinson and Eugene P. Odum. We note in passing that organic imagery hints broadly of Aristotle, and that Francis Bacon devoted his life to purging Aristotelian thought from natural philosophy.

Organicism appears heterodox to most scientists, because scientific orthodoxy demands a purely mechanical view of the world. Although Darwin did introduce history into biology, he otherwise hewed closely to Newtonian strictures, which he inherited via Thomas Malthus and Adam Smith (Depew and Weber, 1994). In the US, this mechanical view of the living world was bolstered by the technocratic movement of the 1920's and 1930's, which strongly influenced the ecology of Odum, 1960. Clarke, 1954, for example, in his textbook on ecology, went so far as to depict ecosystem populations and processes as the figurative gears and wheels of a machine. Connell and Slatyer, 1977 provide a more recent example of the attempt to portray ecosystem succession as a constellation of basic mechanisms.

Inherent in the mechanical picture of ecosystems is a rigidity and determinism not always found in organisms and other living systems. At the other extreme stand the stochastics, or nominalists, who regard any notion of organization in ecosystems as pure illusion. For some, even ecosystems themselves appear as pure artifice (Engleberg and Boyarsky, 1979; Cousins, 1987). The stochastic vein in ecology runs deep and is at least as old as the holist. Gleason, 1917, for example, published his contention that plant communities are stochastic assemblies at about the same time that Clements, 1916 was advocating that ecosystems approach their climax configurations in virtually deterministic fashion. Stochasticism was slow to catch on in American ecology until the 1950's, when changing political fashions may have herded many into this camp (Barbour, 1996). The nominalist scenario seems to require fewer mathematical applications, so it is perhaps understandable that some of the more gifted ecological writers are attracted to this movement (Simberloff, 1980; Shrader-Frechette and McCoy, 1993; Sagoff, 1997).

Metaphors by definition are not precise, so it is not surprising that ecological descriptions often borrow from more than one of these analogies. Most renditions of ecological succession, for example, include both organismal and stochastic elements. Other fields of inquiry also provide hybrid metaphors. Thus, neo-Darwinian evolution, ecosystem modeling and thermodynamics all include both mechanisms and chance events, whereas developmental biology, cybernetics and teleonomy (sensu Mayr, 1992) combine proportions of organicism with mechanism. An example has yet to appear in ecology of any scientific model that amalgamates all three metaphors (see Salthe, 1993), yet such an admixture would be required of any theory that would coalesce ecology into a unified discipline. Such an overarching paradigm would have seemed unthinkable several decades ago, but recent insights by both philosophers and ecologists have made the goal of a unified theory of ecosystems seem much closer.

3. The Newtonian metaphysic

To begin a systematic comparison of the assumptions behind the three prevailing ecological metaphors, we focus initially upon the most prevalent—the Newtonian or mechanical world view. It is widely accepted that the foundations for the modern view of nature, which had its beginnings with Bacon, Galileo, Hobbes, Gassendi and Descartes, were made fast by Newton's publication of Principia. (Less well-known is how the actual format of Principia, which was largely accidental, set the stage for the materialist/ mechanical revolution that was to follow Westfall, 1993; Ulanowicz, 1995a).

To review, the three laws that Newton himself formulated can be summarized as:

(1) A body once set in motion continues in straight-line motion until acted upon by another force: This is a statement about what happens to a body when it is isolated from any external influences. It was the revolutionary idea of Descartes to accord primacy to straight-line motion over curvilinear pathways, such as the circle. The Greeks, for example, had regarded the circle as the most natural trajectory for heavenly bodies, because it was considered to be the most perfect geometrical form.

(2) The rate of change of the momentum of a body is proportional to the applied force: This law tells what happens when external agencies intervene. The law is far more phenomenological than most seem willing to admit, and it is central to the definitions of force and mass.

(3) Every action is opposed by an equal and opposite reaction: Like most of his contemporaries, Newton seemed to value conservation quite highly, and one of the ways to impose conservation is to require symmetry.

The mathematical forms of these three laws were sufficient to prescribe all of classical mechanics. It was their rigorous minimalism, more than Newton's three principles, that came to characterize the ensuing 'Newtonianism'. Somewhat surprisingly (given the legion of print that is devoted to the scientific method), one rarely finds the minimalist assumptions behind Newtonianism spelled out in any detail. One exception is by Kampis, 1991 and another is the attempt by Depew and Weber, 1994 to formulate the Newtonian canon in terms of four fundamental postulates. According to these latter authors:

(1) Newtonian systems are *deterministic*. Given the initial position of any entity in the system, a set of forces operating on it, and stable closure conditions, every subsequent position of each particle or entity in the system is in principle specific and predictable. This is another way of saying that mechanical causes are everywhere ascendant.

(2) Newtonian systems are *closed*. They admit of no outside influences other than those prescribed as forces by Newton's theory.

(3) Newtonian systems are *reversible*. The laws specifying motion can be calculated in both temporal directions. There is no inherent arrow of time in a Newtonian system.

(4) Newtonian systems are strongly decomposable or *atomistic*. Reversibility presupposes that larger units must be regarded as decomposable aggregates of stable least units—that which can be built up can be taken apart again. Increments of the variables of the theory can be measured by addition and subtraction.

Closer analysis reveals that implicit in the four items cited by Depew and Weber lies a fifth assumption that should be made explicit, namely,

(5) Newtonian laws are *universal*. They are applicable everywhere, at all times and over all scales (Ulanowicz, 1997). Not only is time considered to be uniform throughout the universe (Matsuno and Salthe, 1995); but, in principle, no complications should arise if laws pertaining to very small dimensions, such as those governing strong intranuclear forces, were to be applied at galactic scales, where gravitation operates.

It should be noted in passing that there are considerable overlaps among the five attributes of the Newtonian metaphysic, i.e. the Newtonian ideal itself is not strongly decomposable.

4. Broader horizons

The advantage in spelling out the framework of the Newtonian world view item-by-item is that we may now proceed to compare these five assumptions with any counterparts that might pertain to the other two ecosystem metaphors:

(1) As for determinism, we recognize immediately that the other viewpoints do not share this Newtonian assumption. Stochasticism is tautologous with chance. Of course, the Newtonian is likely to counter immediately with the belief that such chaos is only apparent and can always be resolved by analyzing the system with greater precision and in finer detail. Ultimately, however, such reductionistic regression leads to a dead-end as one approaches the scale of molecular or subatomic particles, where indeterminism reigns.

Ontogenists might question whether the organic analogy is anything but deterministic. Within certain bounds (Griffiths and Knight, 1998), one can predict how a specific instance of organic development will play out. But one should note that the type of organic development ascribed to ecosystems is decidedly weaker than what is normally observed in ontogeny. As Depew and Weber (1994) put it, 'Clements had it backwards. Ecosystems are not super-organisms; organisms are super-ecosystems.'¹ Certainly, the limits on how accurately one can predict the outcome of ecological succession are far broader than what is possible with ontogeny—too broad, in fact, to allow the claim that such succession is a deterministic process.

(2) Concerning causal closure, the point is almost moot in nominalism. Certainly, nominalism allows no cause other than the material or the mechanical. But the nominalist would go further and question whether it is useful, or even possible, to trace every event to its mechanical/material origins. Chance is, after all, the very crux of nominalism. All of which points directly at the Achilles heel of Newtonianism, namely, that chance is an unwelcome interloper in a Newtonian world. For, if there are only material and mechanical causes at work, a chance event that cannot be subsumed by the law of averages would disrupt the reductionists' scenario, making it impossible to predict higher level phenomena. What, then, keeps the world from coming apart? It took some major backtracking for science to reconcile the idea of chance at the microscopic level with predictable Newtonian behaviors at macroscopic levels. Fisher (1930) pointed out, however, that such reconciliations are predicated on the assumption that 'the reliability of physical material flows not necessarily from the reliability of its ultimate components, but simply from the fact that these components are very numerous and largely independent'. Fact? The real fact is there is no guarantee that components at very small scales act independently of each other-only the desire on the part of some to cling to the Newtonian metaphysic.

It is worth noting that the assumption of independence is favored by individuals who, like most biologists, profess a falsificationist stance regarding scientific propositions. That is, one is expected to pull no punches whatsoever in a continuing attempt to falsify hypotheses. However, cherished Newtonian beliefs appear to be exempt from such

¹ Clements actually referred to ecological communities, as the term "ecosystem" was not coined until 1937 by Tansley.

scrutiny. It is far better to focus upon a narrow range of conditions under which Newtonian postulates can be retained and the rest can be ignored.

If the nominalists preserve the logical coherence of their beliefs by boldly proclaiming all order (except that imposed by observation) to be illusory, what options are available to the organicist, for whom form and function are essential attributes of the systems they study? One possibility would be to borrow from antiquity and explicitly acknowledge form and function as agents behind development. That is, they could return to the ideas of Aristotle, so fervently eschewed by Bacon, and reconsider opening the window of causality to admit once again the existence of natural formal and final causalities (Rosen, 1985, 1991; Ulanowicz, 1990). For these two types of cause are capable of restraining the disordering effects of chance events at lower levels from unbridled propagation up the hierarchy of scales (see Salthe, 1985, 1993; Wimsatt, 1994 for related formulations).

That formal and final causes occur over longer times and larger scales can be seen from the (unsavory) example of a military battle. The material causes of a battle include the weapons and munitions that the armies employ against each other. The soldiers who use these implements of destruction comprise the efficient causes behind the conflict. The juxtaposition of the armies in the context of the physical landscape constitute two formal agencies that strongly influence the course and outcome of the fray. Lastly, the final causes for the battle appear among the set of social, political and economic events that initiated the war. That the temporal and spatial scales associated with each cause are hierarchically ordered should be obvious and becomes literal when one notes that efficient, formal and final causes are the domains of the private, general and prime minister, respectively. The legitimate interests of these agents map onto progressively broader geographic areas over longer times.

The existence of higher level causes means that a chance event at any level need no longer set organization at larger scales collapsing like some house of cards. As will be argued below, formal and final agencies are capable of exerting topdown selection upon stochastic events below (Salthe, 1985), both mitigating the detrimental consequences of micro events and nurturing those random happenings that enhance functioning. Inevitably, the rehabilitation of formal, and especially final, causalities will elicit strong, but misdirected criticism from those who abhor teleology in biology.

(3) It should be apparent that reversibility has no place in the chaotic world painted by the nominalist. Although, in the organic world view, formal and final agencies can contain the effects of disturbance and restore functioning, it does not necessarily follow that the system always can be returned to its original state. Organic systems are not fully reversible; most chance events leave behind finite alterations in systems structure. Organic systems are historical in nature (Brooks and Wiley, 1986).

(4) Nominalists regard ensembles as atomistic by definition. The antithesis to this view is the organic system, which it is assumed can function (exhibit an intrinsic telos) only by acting as a whole. The Newtonian ideal, as espoused in elementary systems theory, is to break the system into parts, study the behaviors of the parts in isolation and to reconstitute the behavior of the whole from the combined descriptions of such atomistic behavior. This stratagem does not seem to apply to biological systems for several reasons. First, the component processes may simply cease to function once an element is separated from the whole. Even if they should continue, the repertoire of component responses that can be elicited in isolation most likely will not include those most relevant when the unit is imbedded in its organic matrix. Finally, any adaptation that a component might undergo when under the selective influence of the ensemble is simply unknowable whenever the element is observed in isolation (Abrams, 1996).

(5) Universality is antithetical to nominalism (stochasticism), and its relevance to organic systems seems dubious as well. The idea that a law or phenomenon formulated within a particular window of time and space should be applicable all the time and everywhere seems limited to circum-

stances where system parts are rarefied and interact weakly. Only a theoretical physicist would dare to imagine the coupling of quantum phenomena, relevant at atomic scales, with the gravitational forces exerted over light years (Hawking, 1988). Ecology teaches its practitioners somewhat more humility. When objects and processes crowd upon one another, it becomes difficult to project the influence of one event at a particular scale over remote domains of time and space. Too many other elements and processes interfere along the way, and it has just been argued how recourse to atomism is unlikely to salvage matters.

Under these considerations, the most realistic stance for the organicist appears to be the hierarchical approach (Allen and Starr, 1982; Salthe, 1985). While the organic approach is more likely to encompass rules and laws than is nominalism, organic principles seem to pertain to limited ranges of space and time. One must remain wary of any attempt to stretch explanations across scales, as, for example, when the reasons behind all social behavior are sought in genetics, or when the autonomy of human thought processes is purported to arise in the quantum phenomena occurring in molecules of the brain. Although through the hierarchical perspective one perceives an organic world that is more loosely coupled than the Newtonian clockwork universe, the picture is certainly not one without a modicum of order. Whenever a rule or principle wanes in explanatory power as the scale of observation shifts, another is sure to emerge that maintains structure at the new level. Although such a 'granular' view of reality is at odds with the Newtonian vision, it is wholly consistent with the picture of organic causality portrayed above.

5. Enlarging the Newtonian edifice

Ecology is not the sole heterodox discipline in science. Dissatisfaction with the rigidity that Newtonianism forces upon the neo-Darwinian synthesis itself has been expressed by Chomsky, 1996 and also has been voiced by notable developmental biologists, such as Sidney Brenner and Guenther Stent (Lewin, 1984). The late Sir Karl Popper, regarded by many as a conservative philosopher of science, likewise has suggested that practitioners of science need to reconsider their views on basic causality if they are ever to achieve a truly 'evolutionary theory of knowledge' (Popper, 1990). His own opinion was that the universe is causally open: that chance operates, not only in the netherworld of quantum phenomena, but at all levels (Popper, 1982). Popper was no iconoclast, however, and he urged not that we abandon Newtonian forms, but rather that we expand upon them. In his view, Newtonian forces are but a small subset of a more general universe of agents he called 'propensities.' Briefly, a propensity is the tendency for a certain event to occur in a particular context. Propensities are related to, but not identical with, conditional probabilities. Suppose, for example, that one is considering a Newtonian force that relates antecedent A with consequence B. Then every time that A occurs, it is followed by B, without exception. In the language of probabilities, one may say that the conditional probability that B will occur, given that A has happened, is unity (1) or certainty. This is written as

p(B|A) = 1,

where p(B|A) is the conditional probability that Bwill result, given that A has occurred. In the larger non-Newtonian world, we might observe that whenever A happens, B usually ensues—but not always. Whenever the coupling between A and Bis not isolated, interferences can intervene to affect the outcome. Whence, the conditional probability that B will occur, given that A has happened, is usually less than unity. This means that the probabilities for other outcomes, e.g. C, D, E, ... are not zero. In symbols,

p(B|A) < 1 p(C|A) > 0 p(D|A) > 0p(E|A) > 0, ...

As an example, we consider an event frequency table (Table 1) that reports the number of times each 'cause', a_1 , a_2 , a_3 or a_4 is followed by any of

five possible outcomes, b_1 , b_2 , b_3 , b_4 or b_5 . From among the 1000 events recorded in Table 1, one sees that the 'joint probability' that, say a_1 and b_3 occur together is 16 out of 1000 events.

$$p(a_1, b_3) = 16/1000$$

where $p(a_1, b_3)$ is the joint probability that a_1 and b_3 occur together. The joint probability is not the same as the conditional probability, however. To calculate the latter, one must, according to Bayes, normalize the joint probability by the probability, $p(a_1)$, that a_1 occurs under any circumstances, i.e.

$$p(b_3|a_1) = p(a_1, b_3)/p(a_1).$$

One can see from the far right-hand column of Table 1 that $p(a_1) = 269/1000$, so that

$$p(b_3|a_1) = 16/269.$$

From Table 1 it is apparent that whenever a_1 happens, there is a good likelihood that b_2 will follow. Similarly, b_5 is likely to result from a_2 and b_3 from a_4 . The situation is less clear as to what ensues from a_3 , but b_1 and b_4 are more likely to occur than the rest. The events not mentioned $([a_1, b_3], [a_1, b_4], \text{ etc.})$ result from what Popper terms 'interference'. Presumably, if it were possible to isolate phenomena, then each of the 269 times that a_1 happens, it would be followed by b_2 . Similarly, if all phenomena could be strictly isolated, the results might look something like those shown in Table 2. Under isolation, propensities degenerate into mechanical-like forces, e.g. $p(b_2 | a_1) = 1$.

Table 1

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

	b_1	b_2	b_3	b_4	b_5	Sum
a_1	40	193	16	11	9	269
a_2	18	7	0	27	175	227
a_3	104	0	38	118	3	263
a_4	4	6	161	20	50	241
Sum	166	206	215	176	237	1000

Table 2

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

	b_1	b_2	b_3	b_4	b_5	Sum
$\overline{a_1}$	0	269	0	0	0	269
a_2	0	0	0	0	227	227
$\bar{a_3}$	263	0	0	0	0	263
a_4	0	0	241	0	0	241
Sum	263	269	241	0	227	1000

Interestingly, b_4 never occurs under isolated (rarefied or laboratory) conditions. It arises purely as a result of interferences among propensities. That the propensity associated with $p(b_4 | a_3)$ depends entirely upon its proximity to (ability to interact with) other system propensities is an illustration of Popper's assertion that propensities, unlike forces, never occur in isolation, nor are they inherent in an object. They always arise out of a context, which almost invariably includes other propensities. Thus, Popper concludes that the fall of an apple is a decidedly non-Newtonian event. The tendency for an apple to fall and where it might land depend, not just upon the weight of the apple and the gravitational constant, but also upon biochemical conditions in the stem, the speed of the blowing wind, etc.

One concludes that whenever propensities occur in propinguity, interferences and new propensities are likely to arise. Conversely, one must add constraints in order to 'organize' the more indeterminate configuration represented in Table 1 into the more mechanical-like system depicted in Table 2. That is, the transition from the loose configuration into its rigid counterpart is an example of what is meant by 'organization' (Skyrms, 1980; Matsuno, 1986). However, conditional probabilities by themselves do not quantify propensities in any way that bears analogy with Newtonian laws. Popper was quite aware of this lack of connection, and so he noted simply that 'we need to develop a calculus of conditional probabilities.' We will attempt such a calculus presently, but we turn our attention first to elaborating what sort of natural agency conceivably might be behind the transition from the behavior inherent in Table 1 to that shown in Table 2. What causes systems to grow and develop?

6. Autocatalysis: a unitary agency

A clue to one agency behind growth and development comes from considering what happens when propensities act in close proximity to each other. Any one process will either abet (+), diminish (-) or not affect (0) another. The second process in turn can have any of the same three effects upon the first. Out of the nine possible combinations for reciprocal actions, one is very different from all the rest-mutualism (+ , +). There is a growing consensus that some form of positive feedback is responsible for much of the order and structure we perceive in living systems (Eigen, 1971; Haken, 1988; Kauffman, 1995; DeAngelis et al., 1986). Sometimes the positive feedback is considered to take a particular form, such as autopoeisis (Maturana and Varela, 1980) or autocatalysis (Ulanowicz, 1986, 1997). It is this latter form of mutualism that we wish to consider here.

Autocatalysis means any cyclical concatenation of processes wherein each member has the propensity to accelerate the activity of the succeeding link. Suppose, for example, that the action of some process A has a propensity to augment a second process B. B, in turn, tends to accelerate a third process C, which then promotes the initial action A. The consequence of any process, when followed around the cycle, is self-stimulation. An ecological example of autocatalysis exists among the biotic associations formed around aquatic plants belonging to the genus Utricularia (Ulanowicz, 1995b). The surface of the Utricularia plant supports the growth of a fastgrowing film of diatomaceous algae, generically called 'periphyton'. This periphyton is consumed by any number of water-borne heterotrophs referred to as 'zooplankton'. The cycle is completed when the Utricularia captures and absorbs many of the zooplankton in small bladders or utricules that are scattered along its feather-like leaves and stems.

It is important to note two things about autocatalytic loops: (1) The members are not always linked in a rigid fashion, i.e. the action of A does not have to augment that of B at every instant just most of the time. There is simply a *propensity* for A to augment B; (2) The members of the cycles, being biotic elements and processes, are capable of variation. Whereas autocatalysis in simple chemical systems can justifiably be regarded as a mechanism (discrete stoichiometry of the reactions and simple, unchangeable reactants keep the process mostly mechanical in nature), as soon as chance and variation enter the scene, autocatalysis begins to exhibit some behaviors that are decidedly nonmechanical in nature.

Autocatalysis among indeterminate processes gives rise to a form of selection pressure that the ensemble exerts upon its components. If, for example, some characteristic of process B should change in some chance way, and if that change should either increase the catalytic effect of Bupon C or make B more sensitive to catalysis by A, then the change in B will be rewarded and retained. If, however, the change should decrement B's effect upon C or make B less sensitive to A, then B subsequently will receive less support from A and the change is most likely to atrophy. Formally, such selection is unlike what normally is considered under the rubric of natural selection.

In particular, such a selection in autocatalytic systems engenders a centripetal movement of material and energy toward the loop itself. For any change in a constituent process that happens to bring in more material or energy to abet that process will be rewarded. This selection applies to any and all elements of the loop, so that the cycle itself becomes the focus of an inward migration of material and energy that is actively induced by the kinetic configuration.

The centripetal flow of resources represents a siphoning of vital materials away from system members that do not engage as effectively in autocatalysis. There will also be competition between autocatalytic loops. The net result is that the topology of the exchanges connecting system elements is gradually pruned of those members that least effectively participate in autocatalysis. As the same time, flows over the links that remain will increase appreciably, due to the acceleration that is inherent in autocatalysis. An example of the growth and development of a network engendered by autocatalysis is depicted schematically in Fig. 1. In Fig. 1(a), the system begins with many largely equiponderant connections. As autocatalysis prunes the system, however, some of the links shrink or disappear, and an overall greater level of activity is channeled (constrained) along these pathways that most effectively engage in autocatalysis. (Fig. 1(b)).

7. Quantifying growth and development

It is paramount among the advantages of Newtonian science that it is strictly quantitative. If Newtonian dynamics are to be extended success-



Fig. 1. 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).

fully to an open universe, the effects of autocatalysis just described must be given concrete mathematical expression. Toward this end, we note how the terms 'growth' and 'development', although their meanings overlap considerably, nonetheless emphasize different aspects of a unitary process. 'Growth' highlights the increase in system size or activity, whereas 'development' lays more stress upon the increase in system organization.

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

$$T = \sum_{i} \sum_{j} T_{ij}$$

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

Quantifying the intensive process of development is somewhat more complicated. The object here is to quantify the transition from a very loosely coupled, highly indeterminate collection of exchanges to one in which exchanges are more constrained along the most efficient pathways. We begin, as did Boltzmann, 1872, who anticipated information theory by quantifying the indeterminacy, h_{ij} , of category j,

 $h_i = -k \log p(B_i),$

where $p(B_j)$ is the marginal probability that event B_j will happen, and k is a scalar constant. Roughly speaking, h_j is correlated with how surprised the observer will be when B_j occurs. If B_j is almost certain to happen, $p(B_j)$ will be a fraction near 1, and h_j will be quite small. Conversely, if B_j happens only rarely, $p(B_j)$ will be a fraction very near zero, and h_j will become a large positive number. In the latter instance, the observer is very surprised to encounter B_{i_j} Constraint removes indeterminacy. Therefore, the indeterminacy of a system with constraints should be less than what it would be in unconstrained circumstances. Suppose, for example, that an a priori event A_i exerts some constraint upon whether or not B_j subsequently occurs. The probability that B_j will happen in the wake of A_i is by definition the conditional probability $p(B_j | A_i)$, so that the (presumably smaller) indeterminacy of B_j under the influence of A_i (call it h_j^*), will be measured by the Boltzmann formula as

 $h_i^* = -k \log p(B_i | A_i)$

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

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

= k log[p(B_j|A_i)/p(B_j)].

We note here for future reference that the constraint that A_i exerts upon B_j is formally equal to the constraint that B_j exerts on A_i . Using Bayes' Theorem, we see that

$$h_{ij} = k \log[p(B_j|A_i)/p(B_j)]$$

= $k \log[p(B_j, A_i)/p(A_i)p(B_j)]$
= $k \log[p(A_i|B_j)/p(A_i)] = h_{ii}$

Hence, one may speak of the mutual constraint that A_i and B_j exert on each other.

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

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

In order to apply A to evaluate constraint in ecosystems, it remains to estimate $p(A_i, B_i)$ in terms of measurable quantities. If we focus upon trophic exchanges, a convenient interpretation of A_i is 'a quantum of medium leaves compartment *i*' and of B_j , 'a quantum enters compartment *j*'. The T_{ij} may be regarded as entries in a square events matrix, similar to Tables 1 and 2. The joint probabilities can be estimated by the quotients T_{ij}/T , and the marginal probabilities become the normalized sums of the rows and columns

$$p(A_i) \sim \left(\sum_j T_{ij}\right)/T$$

and

$$p(B_j) \sim \left(\sum_i T_{ij}\right)/T$$

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

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

(Note: In estimating probabilities by palpable flows, one avoids the criticism leveled against Popper's propensities that one cannot infer cause from probability. At a minimum, there will always exist a material cause linking i to j.)

That A indeed captures the extent of organization created by autocatalysis can be see from the example in Fig. 2. In Fig. 2(a), there is equiprobability that a quantum will find itself in the next time step in any of the four compartments. Little is constraining where medium may flow. The average mutual constraint in this kinetic configuration is appropriately zero. One infers that some constraints are operating in Fig. 2(b), because medium that leaves any compartment can flow to only two other locations. These constraints register as k units of A. Finally, Fig. 2(c) is maximally constrained. Medium leaving a compartment can flow to one and only one other node.

The reader may be puzzled as to why we continue to measure constraint in units of k. The conventional practice in information theory is to designate the base to be used in calculating the logarithms (usually 2, e or 10) and set the value of



Fig. 2. (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.

k = 1. The units of A would then appear as 'bits', 'napiers' or 'hartleys', respectively. The problem with this convention is that the calculated value conveys no indication as to the physical size of the system. The goal here, however, is to capture both the extensive and intensive consequences of autocatalysis in a single measure. One convenient way of incorporating size is to give physical dimensions to k (Tribus and McIrvine, 1971), i.e. we set k = T, and the dimensions of A will contain the units used to measure the exchanges. For example, if the transfers in Fig. 2 had been measured as $g/m^2/d$, and the base of the logarithm was 2, then the values of A would be expressed in the units g-bits/m²/d.

To signify that the scaled measure is now qualitatively different, we choose to rename A. Accordingly, it will be called the system 'ascendency' (Ulanowicz, 1980). It measures both the size and the organizational status of the network of exchanges that occur in an ecosystem. In an attempt to characterize what it means for an ecosystem to develop, Odum (1969) catalogued ecosystem attributes that were observed to change during the course of ecological succession. His list of 24 properties can be subgrouped as pertaining to speciation, specialization, internalization or cycling—all of which tend to increase during system development. However, increases in these same four features of network configurations lead, ceteris paribus, to increases in ascendency. Whence, Odum's phenomenology can be quantified and condensed into the following principle:

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

The reader may correctly object that real ecosystems are never free of perturbations, and under many natural conditions a rise in systems ascendancy hardly even seems probable. That is because ascendancy tells only half of the story. A complementary narrative that quantifies the freedom and indeterminacy of a given network can be formulated with the help of other variables from information theory in terms of what has been called the systems 'overhead'. Components of the system overhead play very important roles in the evolution and sustainability of ecosystems, but elaboration on this topic would only distract from the search here for generalized Newtonian images. Those interested in the persistence of ecosystems are encouraged to read about the significance of adaptability in ecosystems (Conrad, 1983) and about the importance of overhead (Ulanowicz and Norden, 1990; Ulanowicz, 1986, 1997).

8. Propensities as generalized forces

Returning to the notion of propensity, the reader may recall how propensity was explicitly folded into the definition of autocatalysis. We now ask whether it is possible to extract an expression for propensities from the resulting formulae for ascendency? As a first step in this search, it is helpful to rewrite the last formula with T substituted for k:

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

The reader should note in this last formula that the ascendency is the sum of exactly *m* terms, where *m* is the number of individual transfers, T_{ij} . That is, to calculate *A* one multiplies each flow, T_{ij} , by a corresponding logarithmic factor and sums over *m* such products.

To anyone with a passing familiarity of irreversible thermodynamics, the procedure just described should be very familiar. It is exactly how one calculates the total dissipation in an ensemble of processes. For, very near to thermodynamic equilibrium, the theory of irreversible thermodynamics postulates that, for each observable process or flow, one may identify a conjugate 'thermodynamic force'. For example, mass diffusion is assumed to flow 'downhill' along any spatial gradient in the chemical potential of the medium in question. Similarly, thermal conduction flows down a gradient in temperature of the conducting medium, electrical current follows a gradient in voltage, chemical reaction occurs in response to a difference in Gibbs free energy, etc. It is assumed that these 'forces' all can be cast in appropriate dimensions such that the product of each flow times its conjugate 'force' yields a product with the dimensions of power (Onsager, 1931). The sum of all such products pertaining to each process in a system yields what is known as the power (or dissipation) function, which is believed to characterize the overall dynamics of the system. Prigogine (1945), for example, has hypothesized that, very near to equilibrium, any ensemble of processes takes on the particular configuration that results in the smallest value of the dissipation function.

Unfortunately, there are problems with the formulation of thermodynamic forces (Ulanowicz, 1997). For one, the forces are defined opposite to Newton's original conception. Because they relate to near equilibrium conditions, they pertain more to the first law conditions of non-intervention. In far-from-equilibrium systems, such as biological entities, the 'forces' remain elusive and even may be impossible to identify. Nonetheless, there remains great appeal in the notion that the community power function is a significant indicator of overall system status. As was noted, ascendency has the form of a power function (James Kay, personal communication). In fact, if the medium used to calculate the ascendency is energy, the index takes on the dimensions of 'power-bits'. All of which suggests that the logarithmic factors in the formula for ascendency may stand as formal analogs to the thermodynamic forces. However, Popper has criticized the concept of 'force' as too narrow in scope. This leads us to speculate that the logarithmic factors represent the 'generalized forces', i.e. the 'propensities' conjugate to their respective flows.

Popper, 1990 appealed for the development of 'a calculus of conditional probabilities'. We note here that it is conditional probabilities, not marginal or unconditional probabilities, that are most germane to the meaning of information (Tribus and McIrvine, 1971). Hence, I wish to suggest that information theory already satisfies Popper's desiderata for a calculus of conditional probabilities (Ulanowicz, 1996). Accordingly, we may calculate the propensity p_{ij} , for flow from *i* to *j*, according to the formula

$$p_{ij} = \log \left[\frac{T_{ij}T}{\left(\sum_{k} T_{ik}\right) \left(\sum_{l} T_{lj}\right)} \right].$$

It is worth noting that deriving an explicit formula for Popper's propensities renders his concept fully operational whenever all the T_{ij} 's in a system are known. For example, Ulanowicz and Baird, 1999 estimated the transfers of carbon, nitrogen and phosphorus among the major taxa of the ecosystem inhabiting the mesohaline reach of Chesapeake Bay and utilized the resulting propensities to identify those exchanges that most influence the nutrient dynamics of that community.

9. In the image of Newton

This discovery of a convenient thermodynami-

cal analogy opens one's eyes to still further analogs. We recall that the measure of constraint which a donor (A_i) exerts on its receptor (B_j) is equal in value to that which the receptor imposes upon the donor. That is, Newton's third law (symmetry) has its counterpart in our probabilistic reformulation. (Note: the propensities p_{ij} themselves are *not* symmetric with respect to donor and recipient, any more than the force with which one boxer striking a second is obliged by Newton's third law to equal the force with which the second might simultaneously strike the first.)

Still further analogies appear. Reconsideration of the formula for A in light of the new identification of propensities reveals that the community ascendency takes the form of a flow-weighted average propensity for the system as a whole. Since A is itself a propensity, Odum's phenomenological principle can be restated as,

In the absence of major perturbations, there is a propensity for the flow-weighted ecosystem propensity to increase in value.

The 'propensity of a propensity' relationship appearing in the restated principle is reminiscent of Newton's second law, which deals with the time rate of change of momentum. Momentum, in its turn, is a time rate of change of position, i.e. the second law treats the rate-of-change of a rate-of-change (Ulanowicz, 1998). If at first this resemblance should seem a bit far fetched, then one should pause to consider the contexts of Newton's first and second laws. As mentioned earlier, the first law tells what happens in the absence of external influence-the rate of change of the rate of change is identically zero. With mechanical systems, no input means no change. This differs from ecological phenomenology, which indicates that, in the absence of external disturbance, the propensity of the system propensity assumes a positive value. An organic system can exhibit change from within. This is a radical departure from Darwin, who, as intellectual grandson of Newton, took great pains to locate selection pressure outside the developing system (Depew and Weber, 1994).

Newton's second law states that, in response to an external interference, the system will follow the disturbance, i.e. the response is positive. In the biological realm, after any immediate negative impact that a disturbance might have on an organic system, the system response looks at first glance qualitatively indistinguishable from how it behaves when the ensemble is unperturbed, i.e. there is again a propensity for the system to increase in ascendency. But closer scrutiny of the usual behaviors in perturbed and unperturbed situations reveals that the dynamics in each case differ significantly.

The scales of the responses with and without intervention usually differ markedly. What happens after intervention (the analog to the second law) is likely to occur rapidly and in such a way that the interference is absorbed locally and with minimal dissipation (Lubashevskii and Gafiychuk, 1995). Quite often, the operative control is via localized negative feedback. This response has been labeled 'self-regulation' (Gafiychuk and Ulanowicz, 1996) and is depicted as a Venn diagram in Fig. 3. The system A had adapted to some extent to its environment, B, as represented by the intersection between A and B. Suddenly, the environment changes from B to B', and some structural constraint is irretrievably lost, as indicated by the dotted region on the diagram. Adaptation ensues, and ascendancy increases, however, by progressively greater overlap with the new environment, as indicated by the striped area on Fig. 3.





Fig. 3. Venn diagram depicting the process of self-regulation. System A had accommodated to environment B to an extent indicated by the overlap of the two circles. Intervention brings about a changed environment, represented by B'. Some modes of accommodation are irretrievably lost (dotted area), whereas regulation proceeds by expanding the stippled area (and the ascendency) as much as feasible.





Fig. 4. Venn diagram depicting the process of semi-autonomous development: (a) System A and environment B at a given time; (b) System at later time has developed to harmonize more with its environment, as indicated by increased overlap between A and B.

A system in relative isolation (all living systems must remain open to some degree) will undergo 'development' in a way that is qualitatively different from recovery from intervention. It will develop slowly over time and usually involve positive feedbacks that span most of the system. Usually, development is accompanied by progressively more overall dissipation (Ulanowicz and Hannon, 1987). In terms of Venn diagrams, this slower transition resembles that shown in Fig. 4.

10. An ecological metaphysic

Just as Schroedinger used the form of Newton's second law as a point from which to embark upon an entirely unmechanical view of the sub-microscopic world, we have just discerned formal connections between the laws that Newton himself exposited and at least one version of contemporary ecosystems science. It does not follow, however, that the assumptions that were added by later practitioners of Newtonian science translate as well into the biological realm, Darwin and his successors notwithstanding. If one wishes to understand the development of biological systems in full hierarchical detail and is not content with the abrupt juxtaposition of pure stochasticity and determinism found in neo-Darwinism (Ulanowicz, 1997), then one must abandon the assumptions of closure, determinism, universality, reversibility and atomism and replace them by the ideas of openness, contingency, granularity, historicity and organicism, respectively. That is, one must formulate a new metaphysic for how to view living phenomena. By way of summarizing the foregoing exposition, I propose below a set of rough counterparts to the five elements of the Newtonian metaphysic elaborated earlier (albeit in a different order):

- 1. Ecosystems are ontically *open*: Indeterminacies, or 'genetic events' can arise anytime, at any scale. Mechanical, or efficient causes usually originate at scales inferior to that of observation and propagate upwards; formal agencies appear at the focal level; and final causes arise at higher levels and propagate downward (Salthe, 1985; Ulanowicz, 1997).
- 2. Ecosystems are *contingent* in nature: Biotic actions resemble propensities more than mechanical forces.
- 3. The realm of ecological phenomena is *granular* (Allen and Starr, 1982) in the hierarchical sense of the word: An event at any one scale can affect matters at other scales only with a magnitude that diminishes as the scale of the effect becomes farther removed from that of the eliciting event. It follows that genetic events at lower levels do not propagate unimpeded up the hierarchical levels, because they become subject to constraint and selection by formal and final agencies extant at higher levels.
- 4. Ecosystems are *historical* entities: Genetic events often constitute discontinuities in the behaviors of systems in which they occur. As such, they engender irreversibility and degrade predictability. The effects of genetic events are retained in the material and kinetic forms that result from adaptation. The interactions of propensities in organic systems create a more likely direction or telos in which the system develops.
- 5. Ecosystems are *organic*: Genetic events often appear simultaneously at several levels. Propensities never exist in isolation from their context, which includes other propensities. Propensities in communication grow progressively more interdependent, so that the observation of any part in isolation (if possible) reveals ever less about its behavior when acting within the ensemble.

None of the foregoing statements is entirely new to ecology. Most have appeared in the literature, either singly or in combination with several others. The intention here has been to portray each element as part of a complete and coherent framework for viewing the ecological world. It is possible the metaphysic could pertain as well to the broader biological and social sciences.

It is appropriate to note in closing that the indefinite article appears in the title of this essay modifying the word 'metaphysic'. Nobody is pretending to have developed 'the' metaphysic for ecology, much less for all higher-level phenomena. Other combinations may be possible; however, the encouraging feature of the perspective just formulated is that it appears to reconcile disparate schools of ecological thought into one overarching, coherent structure. As a unified vision, it offers the promise for a fecund, new outlook that will elicit more penetrating insights into ecosystem behaviors.

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References

- Abrams, P., 1996. Dynamics and interactions in food webs with adaptive foragers. In: Polis, G., Winemiller, K. (Eds.), Food Webs: Integration of Patterns and Dynamics. Chapman Hall, New York, pp. 113–121.
- Allen, T.F.H., Starr, T.B., 1982. Hierarchy. University of Chicago Press, Chicago, p. 310.

- Barbour, M.G., 1996. American ecology and American culture in the 1950's: Who led whom? Bull. Ecol. Soc. Am. 77 (1), 44–51.
- Boltzmann, L., 1872. Weitere studien über das wärmegleichtgewicht unter gasmolekülen. Wien. Ber. 66, 275–370.
- Brooks, D.R., Wiley, E.O., 1986. Evolution as Entropy: Toward a Unified Theory of Biology. University of Chicago Press, Chicago, p. 335.
- Chomsky, N., 1996. Powers and Prospects. South End Press, Boston, p. 244.
- Clarke, G.L., 1954. Elements of Ecology. Wiley, New York, p. 534.
- Clements, F.E., 1916. Plant Succession: An Analysis of the Development of Vegetation. Carnegie Institution of Washington, Washington, DC, p. 340.
- Connell, J.H., Slatyer, R.O., 1977. Mechanisms of succession in natural communities and their role in community stability and organization. Am. Nat. 111, 1119–1144.
- Conrad, M., 1983. Adaptability: The Significance of Variability from Molecule to Ecosystem. Plenum, New York, p. 383.
- Cousins, S., 1987. Can we count natural ecosystems? Br. Ecol. Soc. Bull. 18, 156–158.
- DeAngelis, D.L., Post, W.M., Travis, C.C., 1986. Positive Feedback in Natural Systems. Springer, New York, p. 290.
- Depew, D.J., Weber, B.H., 1994. Darwinism Evolving: Systems Dynamics and the Geneology of Natural Selection. MIT Press, Cambridge, MA, p. 588.
- Eigen, M., 1971. Selforganization of matter and the evolution of biological macromolecules. Naturwiss 58, 465–523.
- Engleberg, J., Boyarsky, L.L., 1979. The noncybernetic nature of ecosystems. Am. Nat. 114, 317–324.
- Ferré, F., 1996. Being and Value: Toward a Constructive Postmodern Metaphysics. SUNY Press, Albany, New York, p. 406.
- Fisher, R.A., 1930. The Genetical Theory of Natural Selection. Oxford University Press, Oxford, UK, p. 272.
- Gafiychuk, V.V., Ulanowicz, R.E., 1996. Self-development and distributed self-regulation in dissipative networks. Ref. No. CBL 96-010, Chesapeake Biological Laboratory, Solomons, Maryland.
- Gibson, J.J., 1979. The Ecological Approach to Visual Perception. Houghton Mifflin, Boston, p. 332.
- Gleason, H.A., 1917. The structure and development of the plant association. Bull. Torrey Bot. Club 44, 463–481.
- Griffin, D.R., 1996. Introduction to SUNY series in constructive postmodern thought. In: Being and Value: Toward a Constructive Postmodern Metaphysics. SUNY Press, Albany, New York.
- Griffiths, P.E., Knight, R.D., 1998. What is the developmental challenge? Philos. Sci. 65 (2), 253–258.
- Hagen, J.B., 1992. An Entangled Bank: The Origins of Ecosystem Ecology. Rutgers University Press, New Brunswick, NJ, p. 245.
- Haken, H., 1988. Information and Self-Organization. Springer, Berlin, p. 196.

- Hawking, S.W., 1988. A Brief History of Time: From the Big Bang to Black Holes. Bantam, New York, p. 198.
- Huberman, B.A. (Ed.), 1988. The Ecology of Computation. North-Holland, Amsterdam, pp. 342
- Kampis, G., 1991. Self-modifying Systems in Biology and Cognitive Science: A New Framework for Dynamics, Information, and Complexity. Pergamon Press, Oxford, p. 543.
- Kauffman, S., 1995. At Home in the Universe: The Search for the Laws of Self-Organization and Complexity. Oxford University Press, New York, p. 321.
- Lewin, R., 1984. Why is development so illogical? Science 224, 1327–1329.
- Lubashevskii, I.A., Gafiychuk, V.V., 1995. A simple model of self-regulation in large natural hierarchical systems. J. Env. Syst. 23 (3), 281–289.
- Matsuno, K., 1986. From physics to biology and back, I. Rev. Biol. 79, 269–285.
- Matsuno, K., Salthe, S.N., 1995. Global idealism/local materialism. Biol. Philos. 10, 309–337.
- Maturana, H.R., Varela, F.J., 1980. Autopoiesis and Cognition: The Realization of the Living. Reidel, Dordrecht, p. 141.
- Mayr, E., 1992. The idea of teleology. J. Hist. Ideas 53 (1), 117–177.
- Naess, A., 1988. Deep ecology and ultimate premises. Ecologist 18, 128–131.
- Odum, E.P., 1969. The strategy of ecosystem development. Science 164, 262–270.
- Odum, H.T., 1960. Ecological potential and analogue circuits for the ecosystem. Am. Sci. 48, 1–8.
- Onsager, L., 1931. Reciprocal relations in irreversible processes. Phys. Rev. A. 37, 405–426.
- Peirce, C.S., 1877. The fixation of belief. Pop. Sci. Mon. 12, 1–15.
- Popper, K.R., 1982. The Open Universe: An Argument for Indeterminism. Rowman and Littlefield, Totowa, NJ, p. 185.
- Popper, K.R., 1990. A World of Propensities. Thoemmes, Bristol, p. 51.
- Prigogine, I., 1945. Moderation et transformations irreversibles des systemes ouverts. Bull. Cl. Sci. Acad. R. Belg. Cinque E Ser. 31, 600–606.
- Rosen, R., 1985. Information and complexity. In: Ulanowicz, R.E., Platt, T. (Eds.), Ecosystem Theory for Biological Oceanography. Canadian Bulletin of Fisheries and Aquatic Sciences 213, Ottawa, pp. 221–223.
- Rosen, R., 1991. Life Itself: A Comprehensive Inquiry into the Nature, Origin and Foundation of Life. Columbia University Press, New York, p. 285.
- Sagoff, M., 1997. Muddle or muddle through?: Takings jurisprudence meets the Endangered Species Act. William and Mary Law Rev. 38 (3), 825–993.

- Salthe, S.N., 1985. Evolving Hierarchical Systems: Their Structure and Representation. Columbia University Press, New York, p. 343.
- Salthe, S.N., 1993. Development and Evolution: Complexity and Change in Biology. MIT Press, Cambridge, MA, p. 357.
- Shrader-Frechette, K.S., McCoy, E.D., 1993. Method in Ecology: Strategies for Conservation. Cambridge University Press, Cambridge, p. 328.
- Simberloff, D., 1980. A succession of paradigms in ecology: essentialism to materialism and probabilism. Synthese 43, 3–39.
- Skyrms, B., 1980. Causal Necessity: A Pragmatic Investigation of the Necesscity of Laws. Yale University Press, New Haven, p. 205.
- Smuts, J.C., 1926. Holism and Evolution. MacMillan, New York, p. 362.
- Tribus, M., McIrvine, E.C., 1971. Energy and information. Sci. Am. 225, 179–188.
- Ulanowicz, R.E., 1980. An hypothesis on the development of natural communities. J. Theor. Biol. 85, 223–245.
- Ulanowicz, R.E., 1986. Growth and Development: Ecosystems Phenomenology. Springer, New York, p. 203.
- Ulanowicz, R.E., 1990. Aristotelean causalities in ecosystem development. Oikos 57, 42–48.
- Ulanowicz, R.E., 1995a. Beyond the material and the mechanical: Occam's razor is a double-edged blade. Zygon 30 (2), 249–266.
- Ulanowicz, R.E., 1995b. Utricularia's secret: The advantages of positive feedback in oligotrophic environments. Ecol. Model 79, 49–57.
- Ulanowicz, R.E., 1996. The propensities of evolving systems. In: Khalil, E.L., Boulding, K.E. (Eds.), Evolution, Order and Complexity. Routledge, New York, pp. 217–233.
- Ulanowicz, R.E., 1997. Ecology, the Ascendent Perspective. Columbia University Press, New York, p. 201.
- Ulanowicz, R.E. 1998. Theoretical and philosophical considerations why ecosystems may exhibit a propensity to increase in ascendency. Pp 177–192. In: Mueller, F. (Ed.), Eco Targets, Goal Functions and Orientors. Springer, Berlin.
- Ulanowicz, R.E., Baird, D., 1999. Nutrient controls on ecosystem dynamics: the Chesapeake mesohaline community. J. Mar. Syst. 19: 159–172.
- Ulanowicz, R.E., Hannon, B.M., 1987. Life and the production of entropy. Proc. R. Soc. Lond. B. 32, 181–192.
- Ulanowicz, R.E., Norden, J., 1990. Symmetrical overhead in flow networks. Int. J. Syst. Sci. 21 (2), 429-437.
- Westfall, R.S., 1993. The Life of Isaac Newton. Cambridge University Press, Cambridge, p. 328.
- Wimsatt, W.C., 1994. The ontology of complex systems: Levels of organization, perspectives, and causal thickets. Pp. 207–274. In: Matthen, J., Ware R.X., (Eds.), Biology and Society: Reflections on Methodology. Can. J. Phil.