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## Chapter 6 ECOSYSTEM INTEGRITY: A CAUSAL NECESSITY

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### 1. Introduction

Ecosystem integrity has become very topical of late. As is usual with emerging concepts, the bulk of what has been written on integrity deals with progressive definitions of the concept. For example, it has been necessary to distinguish between the integrity of an ecosystem and its "health"—another popular notion. Ecosystem health was crafted to quantify how well a system is functioning. Costanza (1992), for example, cites three aspects of ecosystem health—vigor, organization and resilience. The first two components refer to the system in its current state. Only the last property addresses the immediate future of the system.

The intention behind ecosystem integrity has been to focus on the well-being of ecosystems over a longer time span. It necessarily follows that integrity subsumes ecosystems health. Hence, Westra (1994) identifies ecosystem integrity, which she labels  $I_e$ , and ecosystem health, which she labels  $I_h$ .  $I_e$  encompasses most of what is included under the rubric of ecosystem health, and reveals not only how the system is functioning at the present moment, but how it might deal with an array of unforeseen circumstances in the future. That is, integrity addresses a system's entire trajectory of past and future configurations (sensu Holling 1992). The direction in which a system is headed is crucial not only to the meaning of integrity, but it also imports a legitimacy to ethical considerations on how society should interact with its natural surroundings (Westra 1994).

Ecosystem health, because it pertains to relatively brief time spans, fits readily into the accepted framework of scientific ideas. Hence, it is not too surprising that considerable progress has been made towards quantifying  $I_h$ . The larger notion of integrity  $I_e$ , however, entails a secular direction, and endogenous direction (telos) is steadfastly eschewed by the consensus of practicing scientists. Thus, no matter how adroit and succinct we may be in defining integrity, it is obvious from the beginning that the concept does not fit easily into the patterns of thought that have dominated science for the past three centuries. To be more precise, the orthodox, or newtonian worldview is that of a closed universe, wherein only material and mechanical agencies may act. The (Twentieth Century) corollary of this weltanschauung is that if any novelty can arise in the world, it can do so only in the netherworld of atoms and smaller particles or somewhere in the vast reaches of the remote

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cosmos. From these peripheries of the observable world, causes are propagated in closed fashion to intermediate scales, such as that of the ecosystem.

Against such a background ecosystem integrity simply doesn't stand a chance, no matter how well-articulated it may be. At best it will be regarded either as an epiphenomenon or as pure metaphor. More likely, it will, like other purported "emergent" properties, be derided and rejected as a metaphysical or transcendental construct. Most ecologists will draw analogies with Clements' earlier notion of the ecosystem as "superorganism," or with Lovelock's (1979) vision of a transcendent Gaia and dismiss it forthwith. In brief, the incompatibility of ecosystem integrity with contemporary scientific attitudes is such that coexistence is scarcely possible. One or the other must give. Heretical as it may seem, I wish to suggest that it is the conventional picture of the world that today is at risk. We need to reconsider our conceptions of causality—how things happen in the world (Popper 1990). I submit that in an open world that cannot be contained by our closed models, integrity appears not as some mysterious artifact or addendum, but rather as part of the necessary glue that imparts form and order to the observable world.

We embark, therefore, on a reconsideration of the origins of natural events in the living world. I begin by accepting the radical proposal by Popper to expand the indeterminacy of the quantum realm to all scales—his description of an open universe. The problem with opening up the world to such indeterminacy is that the possibility then arises that everything will simply unravel. To avoid this scenario Popper invokes a form of dynamical cohesion, or what he calls "propensities"—a generalization of the conventional notion of force meant to pertain to a probabilistic theatre of events. Unfortunately, Popper's formulation was quite vague, and it lacks a more concrete image of what might lie behind propensities. For this purpose I am suggesting the oft-used example of positive feedback. Unfortunately, however, positive feedback, or more precisely autocatalysis, is considered by most to be a form of mechanism, wholly consistent with the newtonian formulation. Therefore, we need to elaborate these non-mechanical aspects of autocatalysis that differentiate it from conventional agencies. But if autocatalysis is not mechanism, then in exactly what capacity does it function? To close out the argument, we search back into antiquity to rediscover that Aristotle's notions of formal and final causes remain highly applicable to our contemporary description of positive feedback. This marriage of radically new with ancient ideas brackets the evolutionary narrative quite nicely and provides the context wherein integrity now appears as a legitimate and robust attribute of ecosystems—one that yields a direction along which society may predicate an ethical treatment of the natural world (Westra 1994).

## 2. An Open World

Ecology, sometimes called "the subversive science," is a fertile breeding ground for revolutionary attitudes about nature. Unfortunately, some purported revolutions have been ill-considered, such as Clements' aforementioned suggestion that ecosystems are superorganisms—a claim for which little evidence exists. More recent hypotheses by Lovelock (1979) about the origins of order in the global ecosystem (the Gaia hypothesis) also follow Clements' mistaken ontology, and thereby invite derision by the majority of scientists. It is only when we discover that Clements had his ordinalities reversed that Lovelock begins to make sense. Ecosystems are not superorganisms; organisms are superecosystems (Depew and Weber 1995).

Interestingly enough, not all radical notions in ecology are immediately attacked. An example of a truly exotic perspective that has received relatively little resistance is that of hierarchy theory (Allen and Starr 1982). Hierarchy theory rejects the Newtonian postulate that causes are propagated universally. That is, in a newtonian world, an event at any scale is ramified to all other scales. In the hierarchical view, however, the consequences of an event

at a given scale are attenuated at adjacent levels and become inconsequential at remote scales. This is another way of saying that causality received from other scales is always incomplete (although current descriptions of the theory rarely stress this point). Causal closure begs for something at the focal level to complete the picture. If the focal level happens to be that of the ecosystem, something must arise at that scale to lend integrity to the system. But what?

Popper (1990) suggests why causes do not propagate intact between scales. He cites the "interference" of stochastic and uncontrollable events that have the effect of "opening" the world, causally speaking. That is, he now bids us abandon the notion of a causally closed universe (Popper 1982). To be sure, it is always possible to cite phenomena in relative isolation as examples of strict determinism. But in proportion to the enormous welter of events that make up our world, the strictly mechanical ones comprise but a minor fraction. Of course, mechanisms are useful as ideal limits to which other phenomena conform to greater or lesser degree. The universe in general, however, is open. In accounting for the reasons why some particular event happens, it is often not possible to identify all causes, even if one includes all levels of explanation. There will always remain a small (sometimes infinitesimal) open window that no cause covers. This openness is what drives evolution, and it is only by acknowledging such lacunae that Popper maintains we can embark upon the pathway to a solid "evolutionary theory of knowledge."

Popper's world, though open, is not wholly without form. Those agencies that keep reality from dissolving into total randomness Popper (1990) calls "propensities." In his opinion, we inhabit a "world of propensities." They are the loose glue that keep the world from flying apart. Propensities are the tendencies that certain processes or events might occur within a given context (Ulanowicz 1995a). The subjective "might" connotes a probabilistic aspect to propensities. In fact, Popper's initial example could have come from any textbook on probabilities: Suppose we estimate the probability that a certain individual will survive until 20 years from the present, say to a particular day in 2015. Given the age, health and occupation of that individual, we may use statistics on the survival of past similar individuals to estimate the probability our subject will survive until 2015. As the years pass, however, the probability of survival until the given date does not remain constant. It may increase, if the person remains in good health, decrease if accident or sickness should intervene, or even fall irreversibly to zero in the event of death.

What Popper wishes to convey with this simple example is that there is no such thing as an absolute probability. All probabilities are contingent to a greater or lesser extent upon circumstances and interfering events. While this is manifestly clear in the example just mentioned, it is mostly ignored in classical physics, where one deals largely with events that are nearly isolated. In classical physics events are either independent or rigidly coupled in mechanical fashion—if A occurs then B follows in lock-step fashion. B is forced to follow A.

What, then, in physics are called "forces," Popper regards as the propensities of events in near isolation. The classical (and motivating) example is the mutual attraction of two heavenly masses for each other. The virtual absence of interfering events in this case allows for very precise and accurate predictions. With only a well-defined force at play, the probability of a given effect subsequent to its eliciting force approaches unity. Propensities in the limit of no interfering agencies degenerate (in the mathematical sense of the word) into forces.

Propensities are those agencies that populate the causal realm between the "all" of newtonian forces and the "nothing" of stochastic infinitesima. They can appear spontaneously at any level of observation because of interferences among processes occurring at that level. This circumstance highlights Popper's second difference between propensities and common probabilities. Propensities are not properties of an object; rather they are inherent

in a situation. Propensities always exist among, and are mutually defined by, other propensities. There are no isolated propensities in nature, only isolated forces or nothingness.

While it may be permissible to talk about the force of attraction between two heavenly bodies in a context that is almost vacuum, Popper maintains that one cannot apply the same reasoning to the fall of an apple from a tree. "Real apples are emphatically not newtonian apples!" he opines. When an apple will fall depends not only upon its newtonian weight, but also upon the blowing wind, and the whole process is initiated by biochemical events that weaken the stem, etc. Exactly what happens and when is conditional upon any number of other events. For this reason Popper appeals, "We need a calculus of relative or conditional probabilities as opposed to a calculus of absolute probabilities."

### 3. Dynamical Cohesion

As Popper describes them, his propensities remain mysterious as to their origins. What sort of agencies are these propensities? Can one give an example of how they might arise in a given context?

We begin our search for ordering agencies by considering what sort of interactions might ensue when two processes occur in proximity to each other. There are three qualitative effects the first process could have on the second: it could be beneficial (+); it could be detrimental (-); or it could have no effect (0). The latter process in its turn could have any of these same effects on the former. Whence, there are nine pairs of possible interactions, e.g., (+), (-), (0), etc. I wish to argue that one of these combinations gives rise to behavior that is qualitatively very different from the other eight possibilities. In fact, I would go so far as to assert that it has the potential for generating decidedly non-mechanical behaviors and for imparting cohesion or integrity to systems that contain mutualistic dynamics.

Mutualism (++) is a special case of positive feedback. Positive feedback can arise according to any number of scenarios, some of which involve negative interactions (e.g., two negative interactions taken serially can yield a positive overall effect). "Mutualism" we shall take as "positive feedback comprised wholly of positive component interactions." Mutualism need not involve only two processes, and when more than two elements are involved, it becomes "indirect mutualism."

A schematic of indirect mutualism among three processes or members is presented in Figure 1. The plus sign near the end of the arrow from A to B indicates that an increase in the rate of process A has a strong propensity to increase the rate of B. Likewise, growth in process B tends to augment that of C, which in its turn reflects positively back upon process A. In this sense the behavior of the loop is said to be "autocatalytic," a term borrowed from chemistry that means "self-enhancing." An increase in the activity of any member of the triad will tend to increase the activities of the others as well.

In keeping with Popper's idea of an open universe, we do not require that A, B and C be linked together in lock-step fashion, only that the propensities for positive influence be stronger than cumulative decremental interference. Also, there is the issue of the phasing of the influences. It is conceivable that the timing of sequential positive effects could result in overall negative feedback. Such configurations are simply excluded from our definition of autocatalysis.

Many examples of indirect mutualism in ecology are subtle and require much elaboration. One I discovered by chance personal encounter is somewhat more straightforward (Ulanowicz 1995b). Inhabiting freshwater lakes over much of the world, and especially in subtropical, nutrient-poor lakes and wetlands are various species of aquatic vascular plants belonging to the genus *Utricularia*, or the bladderwort family. Although these plants are sometimes anchored to the lake bottom, they do not possess feeder roots that draw nutrients from the sediments. Rather, they absorb of their sustenance directly from the surrounding

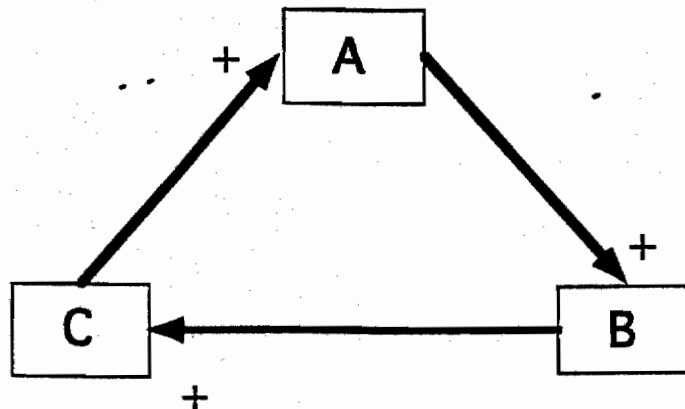
water. One may identify the growth of the filamentous stems and leaves of *Utricularia* into the water column with process A in Figure 1.

Upon the leaves of the bladderworts invariably grows a film of bacteria, diatoms and blue-green algae that collectively is known as periphyton. There is evidence that some species of *Utricularia* secrete mucous polysaccharides (complex sugars) to bind algae to the leaf surface and to attract bacteria (Wallace 1978). Bladderworts are never found in the wild without their accouterment of periphyton. Apparently, the only way to raise periphyton without its film of algae is to grow *Utricularia* seeds in a sterile medium (Bosserman 1979). If we identify process B with the growth of the periphyton community, it is clear that, bladderworts provide an areal substrate which the periphyton species (not being well adapted to growing in the pelagic, or free floating mode) need to grow. Some species may even provide other subsidies to the periphyton film.

Enter component C in the form of a community of small, almost microscopic (ca. 0.1mm) motile animals, collectively known as "zoophytes," that feed upon the periphyton film. These zoophytes can be from any number of genera of cladocerae (water fleas), copepods (other microcrustacea), rotifers and ciliates (multi-celled animals with hairlike cilia used in feeding). In the process of feeding upon the periphyton film, these small animals occasionally bump into hairs attached to one end of small bladders, or utricla, that give the macrophyte its family name. When moved, these trigger hairs open a hole in the end of the bladder, the inside of which is maintained by the plant at negative osmotic pressure with respect to the surrounding water. The result is that the animal is sucked into the bladder, and the opening quickly closes behind it. Although the animal is not digested inside the bladder, it does decompose, releasing nutrients that can be absorbed by the surrounding bladder walls. The cycle of Figure 1 is now complete.

It is appropriate at this juncture to ask how prevalent is autocatalysis in the ecological realm? Other familiar examples of indirect mutualism include symbiosis of algae-zoophytes in coral reefs and the homeostatic regulation of nutrients in the euphotic zone of the open oceans by the "microbial loop" of picoplanktonic organisms (Stone and Weisburd 1992). Interestingly, all three examples pertain to oligotrophic, or nutrient poor environments. One might hastily conclude, therefore, that autocatalysis is relegated to the margins of ecosystem behavior. Such judgement ignores, however, the observation that oligotrophy appears to be

Figure 1. *Utricularia* and Indirect Mutualism (see text for discussion).



an endpoint for ecological succession, rather than its starting point (Baird et al. 1991). That is, the trend in ecological succession is to sequester as many available resources as possible within the system biomass. Unless sources of nutrients are extremely abundant, this tendency ultimately drives the available abiotic resources towards very low values, i.e., the system eventually becomes oligotrophic. A more correct conclusion, therefore, would be that autocatalysis characterizes the endstate towards which systems, left on their own, naturally converge. One recognizes, therefore, that autocatalysis and system integrity are inextricably entwined as the natural ends for living systems. As such they deserve special consideration whenever we propose to intervene in the natural course of events.

Because the example of indirect mutualism provided by *Utricularia* is so colorful, it becomes too easy to get lost in the mechanical-like details of how it, or any other example of mutualism, operates. For it is important in biological systems that the components of any system maintain some plasticity or indeterminacy. Such is obviously the case with the periphyton and zooplankton communities, as their compositions change with various habitats. Plasticity applies as well over the longer time scale to *Utricularia* itself, which has evolved into numerous species, and even exhibits a degree of polymorphism over rather short intervals (Knight and Frost 1991). Such plasticity or adaptability contrasts with the usual situation in chemistry, where the reactants in any autocatalytic process are fixed, thereby contributing to the stereotypical image of autocatalysis as a "mechanism."

#### 4. Non-Mechanical Attributes

Although autocatalysis as mechanism may well pertain to most chemical examples, I wish to argue that such identification is wholly inappropriate as soon as the elements that constitute the autocatalytic loop become adaptable. In general, autocatalysis is not a mechanism. Taken as a whole, autocatalytic systems exhibit properties that transcend the much-overused metaphor of nature-as-machine (Ulanowicz 1989).

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

Of course, even conventional wisdom acknowledges the growth enhancing characteristic of autocatalysis. Far less attention is paid, however, to the selection pressure which the overall autocatalytic form exerts upon its components. For example, if a random change should occur in the behavior of one member that either makes it more sensitive to catalysis by the preceding element or accelerates its catalytic influence upon the next compartment, then the effects of such alteration will return to the starting compartment as a reinforcement of the new behavior. The opposite is also true. Should a change in the behavior of an element either make it less sensitive to catalysis by its instigator or diminish the effect it has upon the next in line, then even less stimulus will be returned via the loop.

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

Perhaps the most intriguing of all their attributes is the way autocatalytic systems affect the transfers of material and energy between their components and the rest of the world. Figure 1 does not portray such exchanges, which generally include the import of substances with higher exergy (available energy) and the export of degraded compounds and heat. The degradation of exergy is a spontaneous process mandated by the second law of thermodynamics. But it would be a mistake to assume that the autocatalytic loop is itself passive and merely driven by the gradient in exergy. Suppose, for example, that some arbitrary change



happens to increase the rate at which materials and exergy are brought into a particular compartment. This event would enhance the ability of that compartment to catalyze the downstream component, and the change eventually would be rewarded. Conversely, any change decreasing the intake of exergy by a participant would ratchet down activity throughout the loop. The same argument applies to every member of the loop, so that the overall effect is one of centripedality, to use the term coined by Sir Isaac Newton. The autocatalytic assemblage behaves as a focus upon which converge increasing amounts of exergy and material that the system draws unto itself.

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

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

In like manner one could argue that C could be replaced by some other component E, and A by F, so that the final configuration D-E-F contains none of the original elements. (Simple induction will extend this argument to an autocatalytic loop of  $n$  members.) Important to notice in this case is the fact that the characteristic time (duration) of the larger autocatalytic form is longer than any of its constituents. Persistence of active form beyond present makeup is hardly an unusual phenomenon. One sees it in the survival of corporate bodies beyond the tenure of individual executives or workers; of plays, like those of Shakespeare that endure beyond the lifetimes of individual actors. But it also is at work in organisms as well. One's own body is composed of cells that (with the exception of neurons) did not exist seven years ago. The residencies of most chemical constituencies (even of those comprising the neural synapses by which are recorded long-term memory in the brain) are of even shorter duration. Yet most people would be recognized by close friends they haven't met in the last ten years.

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

The appearance of centripedality and the duration of form beyond that of constituents make it particularly difficult to maintain any hope that a strict reductionist, analytical approach to describing organic systems will succeed in the end. Although the system requires material and mechanical elements, it is evident that some behaviors, especially those on a longer time scale, are, to a degree, autonomous of lower level events. Attempts to predict the

course of an autocatalytic configuration by ontological reduction to material constituents and mechanical operation are doomed over the long run to failure.

It is important to note that the autonomy of a system may not be apparent at all scales. If, for example, one's field of view does not include all the members of an autocatalytic loop, the system will appear linear in nature, i.e., one can identify an initial cause and a final result. The subsystem possibly would appear wholly mechanical in its behavior. However, once the observer expands the scale of observation enough to encompass all members of the loop, then autocatalytic behavior with its attendant centripedality, persistence and autonomy emerges as a consequence of this wider vision.

To recapitulate, our study of indirect mutualism has revealed that autocatalytic systems can possess at least seven properties. Autocatalysis induces (1) growth and (2) selection. It exhibits (3) an asymmetry that can give rise to the (4) centripetal amassing of material and available energy. The presence of more than a single autocatalytic pathway in a system presents the potential for (5) competition. Autocatalytic behavior is (6) autonomous to a degree of its microscopic constitution. It (7) emerges whenever the scale of observation becomes large enough.

### 5. Expanded Causality

In our consideration of autocatalytic systems, we see how agency can arise quite naturally at the very level of observation. This occurs via the relational form that processes bear to one another. Furthermore, there is an asymmetry inherent in autocatalytic systems, and a direction is defined by the centripedality they exhibit. Neither of these observations fits well into newtonian descriptions of events. Rather, they are reminiscent of an earlier narrative of how things happen — one made by Aristotle.

Aristotle's image of causality was more complicated than the one subsequently promulgated by the founders of the Enlightenment (Rosen 1985). He taught that a cause could take any of four essential forms: (1) material, (2) efficient, or mechanical, (3) formal, and (4) final. Any event in nature could have as its causes one or more of the four types. The textbook example for parsing causality into the four categories concerns the building of a house. Behind this process, the material causes are obviously the stone, mortar, wood, etc., that are incorporated into the structure, and as well the tools that are used to put these elements together. The workers whose labor brings the material elements together comprise the efficient cause.

The formal cause behind the construction of a house is not as clear-cut as the first two. Aristotle posited abstract forms towards which developing entities naturally progressed. Thus, he thought the form of the adult chicken was immanent in the fertilized egg, and it was this endpoint that attracted all earlier forms of the growing chicken into itself. This notion does not translate well outside the realm of ontogeny, so that the closest one can come to the formal cause for building a house is the image of the completed house in the mind of the architect. Usually, this image takes on material reality as a set of blueprints that orders the construction of the building. The final cause for building the house is the need or desire for shelter on the part of those who will occupy it.

Blueprints or an image in an architect's mind provide rather equivocal examples of formal cause. I have suggested instead (Ulanowicz 1995a) that one consider a military battle, which, despite its unsavory image, nonetheless lends a more appropriate example of formal cause. The material causes of a battle are the weapons and ordnance that individual soldiers use against their enemies. Those soldiers, in turn, are the efficient causes, as it is they who actually swing the sword, or pull the trigger to inflict unspeakable harm upon each other. The officers who are directing the battle concern themselves with the formal elements, such as the juxtaposition of their armies *vis-à-vis* the enemy in the context of the physical landscape. It



is these latter forms that give shape to the battle and serve as agents of the third type. In the end, the armies were set against each other for reasons that were economic, social and/or political in nature. Together they provide the final cause or ultimate context in which the battle is waged.

In addition to lending more concrete reality to formal cause, the example of a battle also serves better to highlight the hierarchical nature of Aristotelean causality. All considerations of political or military rank aside, the soldier, officer and head of state all participate in the battle at different scales. It is the officer whose scale of involvement is most commensurate with those of the battle itself. In comparison, the individual soldier usually affects only a subfield of the overall action, whereas the head of state influences events that extend well beyond the time and place of battle.

That is, formal cause should act most frequently at what is called the "focal" level of observation. Efficient causes tend to exert their influence over only a small subfield, although their effects can be propagated up the scale of action. The entire catastrophe transpires under constraints set by the final agents. The three contiguous levels of observation constitute the fundamental triad of causality (Salthe 1993), all three elements of which should be apparent to the observer of any physical events. It is normally (but not universally) assumed that events at any hierarchical level are contingent upon (but not necessarily determined by) material elements at lower levels.

## 6. The Full Causal Picture

In light of the foregoing, autocatalysis seems to exhibit aspects of both formal and final causes, *sensu* Aristotle. An expanded view of causality in nature can now be cast in metaphorical terms: One imagines the full suite of natural phenomena as a background over which one tries to place a curtain of causality. Newtonian description provides enough curtain to cover only part of the background. In heeding Rosen, many now believe that formal and final causality will provide enough cloth to cover the remainder. Popper, however, warns us that the cloth is not entirely whole. There exist at all levels small holes in the cover, thru which novel events may emerge unexpectedly. That the curtain doesn't come apart is due to the preponderance of cloth between the holes. We now acknowledge the connecting fabric consists not only of material and mechanical threads, but of formal and final ones as well.

Philosophical imagery is all well and good, but one must also address practical considerations, such as how one can identify an ecosystem with a high degree of integrity. Fortunately, the possibility for such distinction follows from our identification of integrity with autocatalysis and self-organization. That is, an ecosystem with strong integrity is one that is relatively insensitive to its physical inputs. Whenever the response of the ecosystem to changing inputs can be tested without doing irreparable harm to the system, one should be able to assess the relative level of system integrity. For example, one expects that the productivity and structure of the *Utricularia* system is, up to a point, rather insensitive to fluctuations in dissolved abiotic nutrients. The advantage of positive feedback to this macrophytic system waxes and wanes in compensatory fashion as nutrient levels rise and fall within the oligotrophic range (Ulanowicz 1995b). Once a threshold in nutrient level is exceeded, however, the entire system can collapse and be displaced by another biotope (one dominated by *Typha* in the Everglades) that responds more directly to fluctuations in available nutrients.

Such a "black-box" test for integrity tells us about the entire ecosystem, but provides us with little information as to which species could be manipulated or removed from the system without considerable loss of integrity. An empirical search for key species, if at all feasible, would be extremely demanding of time and research resources. One possible shortcut might be to elaborate the full suite of trophic transfers of key nutrients within the ecosystem. The

structure of cycling within the resultant network should highlight the major pathways of internal recycling (Ulanowicz 1983), and thereby provide clues as to the major players in the maintenance of system integrity.

The reader should be cautioned that any analysis to identify potentially manipulatable or expendable species, such as the cycle method just cited, is fraught with grave dangers. Given the considerable indeterminacy that is a necessary part of any ecosystem, coupled with the pervasive uncertainty of ecological methods, techniques and information, it is highly unlikely that ecologists will be able to predict with reasonable certainty future ecosystem states. Promoting ecological integrity, then, seems to require a precautionary approach, or a shifting of the burden of proof on to those who propose that their activities will not impair integrity (see e.g., Lemons 1995).

In conclusion, we regard ecological integrity as very much a part of the overall fabric of nature. It is not some mysterious or elusive construct that some are trying to tack on to a clockwork universe. Ecosystems may be defined only insofar as they are capable of behaving as an integrated whole, like the *Utricularia* system (Norton and Ulanowicz 1991). Without the integrity afforded by indirect mutualism, ecosystems would not exist, nor for that matter could life as we know it continue. Integrity is an essential attribute of all living systems. To ignore it could be disastrous, to destroy it wantonly would be immoral.

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