

# The dual nature of ecosystem dynamics

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## ABSTRACT

Mechanistic simulation modeling has not generally delivered on its promise to turn ecology into more of a “hard” science. Rather, it appears that deeper insights into ecosystem functioning may derive from a new set of metaphysical assumptions about how nature functions. Force laws from physics are fundamentally incompatible with the heterogeneity and uniqueness that characterizes ecosystems. Instead, coherence, selection and centripetality are imparted to ecological systems by concatenations of beneficial processes—a generalized form of autocatalysis. These structure-enhancing configurations of processes are opposed by the ineluctable tendency of structure to decay (as required by the second law of thermodynamics). The dual nature of this agonism can be quantified using information theory, which also can be used to measure the potential of the system for further evolution. The balance point for these counter-vailing tendencies seems to coincide with the state of maximal potential for the system to evolve. In an ostensible paradox, the same locus seems to attract stable, persistent system configurations.

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## 1. Checkered success

The success of ecological modeling has been uneven. Among its notable successes are numbered some of the tools which ecological managers rely upon daily to set harvest quotas of fish stocks and game species—especially those constructed around Leslie matrices (Caswell, 1989). Models of single species and/or single processes also have proved useful for prediction and interpolation (Jassby and Platt, 1976), as have models in which physical forces or chemical processes drive the distribution of living organisms, such as happens with many hydrodynamical simulations (e.g., Wang and Johnson, 2000) and water quality models (Biswas, 1981). The latter are variations upon the theme of cellular automata, which also has spawned such disciplines as landscape ecology (Sanderson and Harris, 2000) and individual-based modeling (DeAngelis and Gross, 1992).

Unfortunately, as was remarked over a quarter century ago, as soon as a model encompasses more than one biological process, its robustness and utility decline abruptly (Platt et al., 1981), and there have been few successes over the intervening years to revise this assessment. Nonetheless, multiple process models remain useful for generating and investigating hypotheses about ecological communities. Whether simulation models can be used to test those hypotheses remains questionable. Multiple process models usually behave quite poorly, unless the community being

modeled is driven by a dominant single physical or chemical factor.

One can only wonder why the lack of robust multiple process models? Is it simply a matter of time before modelers discover more appropriate functional prescriptions to mimic the component process (e.g., Patten, 1999), or does the noise inherent in the environment continually drive the simulation astray? Or could it be something even more fundamental—namely, that something is radically wrong with the metaphysical assumptions that underlay mechanical models and the notion of nature as a clockwork is simply a poor metaphor (Jørgensen et al., 2007; Ulanowicz, 2009)?

## 2. A law-driven ecology?

Mechanisms do lie at the heart of ecological modeling, and the tacit assumption has been that the growing catalog of various mechanisms eventually will lead ecologists to formulate law-like generalizations of ecosystem behavior. But do such laws actually exist for ecology (Fox-Keller, 2007; Lewontin, 2000)? The answer remains unclear, but it has already been determined that certain forms of law must be excluded on purely logical grounds (although few seem willing to accept this result). To be more specific, Walter Elsasser (1981) demonstrated that no laws can exist for biology that resemble the force laws of physics. Elsasser's argument begins with the heterogeneity inherent in any collection of biological individuals. Williams (1956), for example, noted that heterogeneity suffuses, if not dominates biology. If one were pressed to do so, one could even discriminate among individual microbes.

Given the individuality among members of a biotic ensemble, one can no longer define a set of organisms in the real world, for

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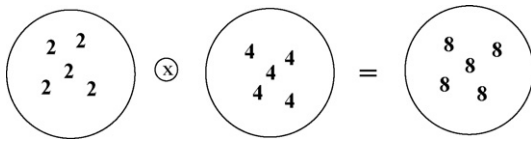


Fig. 1. The result of a fixed operation upon two homogeneous sets. The result is a single homogeneous set.

in the strict mathematical sense, a set can only be a collection of *identical* tokens. Although one usually takes the liberty of calling a collection of organisms a set, the reality is that one can always distinguish among its individual members. Making such distinctions among generic matter, such as the molecules of hydrogen, is impossible. This difference between sets of physical and chemical entities and groupings of biological individuals is far from moot when one learns that Whitehead and Russell (1913) demonstrated in *Principia Mathematica* that the force laws of physics are logically equivalent to operations between true sets. It follows that if one cannot identify true (as opposed to pseudo) sets in ecology, proper laws, like those that govern forces in physics cannot ensue.

The exact logic of Whitehead and Russell lies beyond the scope of this text, but a notion of it can be gained from the following example (Ulanowicz, 2009): homogeneous sets of integers are defined as follows: the first set consists of five tokens of the integer 1, the second contains five tokens of the integer 2, the third contains 3's, etc. Now the set of 2s is made to interact with the set of 4s according to some strict operation. For example, each of the tokens in the first set might be multiplied by a corresponding member of the second. The result would be another homogeneous set of five eights (Fig. 1). The *determinate* result is another single homogeneous set.

Now focus shifts to collections of integers grouped by fives according to magnitude. That is, the first group contains the integers 1 through 5; the second, 6 through 10; the third, 11 through 15, etc. Each of these aggregates is inhomogeneous; its members are clearly different each from the other. Now the first group might operate on itself according to the same procedure used in the first example. One possible result would be the integers 4, 5, 6, 8, and 15 (Fig. 2). Noteworthy is that these products are scattered across three separate classes. Other combinations would yield similar *indeterminate* results in the sense that they would scatter among several groups.

The idea here is that operations upon crisp sets yield another crisp set. Operations among heterogeneous groupings, by contrast, scatter among other heterogeneous categories.

Many readers are likely to object that it is hardly news that ecology deals with fuzzy dynamics (Salski et al., 1996). Noisy systems are the rule in ecology, and that's precisely why statisticians are called upon to advise ecologists. Surely, there is no harm in generalizing matters in the hope that statistical attributes of groupings might behave in law-like, predictable fashion! Indeed, regularities in ecological dynamics appear everywhere, and one might be able to follow these dynamics for short intervals using mechanistic relationships between statistical properties. This enterprise, however, is doomed to fail sooner or later—and usually sooner. The notion of mechanisms in ecology remains metaphorical at best.

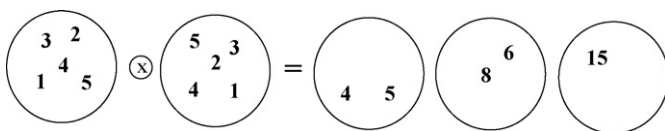


Fig. 2. The same operation as in Fig. 1 carried out between two heterogeneous groups of integers yields results that scatter across several different qualitative classes.

### 3. An ecology beyond statistics?

The reasons why the fit is tenuous go back over a decade before the critique by Platt et al. Elsasser (1969) had elaborated the inapplicability of physical-like laws for biological groupings. He already had provided solid reasons why probability theory ultimately breaks down in ecology: in short, ecosystems are rife with unique events that cannot be treated with known statistical tools. To define a probability requires at least several repetitions of an event, and ecosystems are awash in events that occur once and never again.

If the last statement sounds like fantasy in a universe that is so large and old, Elsasser was quick to provide a quantitative argument to back up his supposition (Ulanowicz, 2004a; Jørgensen et al., 2007). He asked how many distinguishable tokens would have to randomly co-occur before one could say with all reasonable certainty that the particular combination would never again recur by chance? He argued that this threshold is related to the maximal number of simple events that possibly could have occurred throughout the history and extent of the known universe. Most recent estimates agree that there are about  $10^{81}$  simple particles throughout all of known space. Now the simplest physical events one can observe would happen to the simplest of particles over an interval that is characteristic of sub-atomic events (about one nanosecond). Because the universe has been around for some 13–15 billion years, or about  $10^{25}$  nanoseconds, Elsasser therefore concluded that *at the very most*  $10^{81} \times 10^{25}$ , or  $10^{106}$  simple events could have transpired. One can safely conclude that anything with less than one in  $10^{106}$  chances of re-occurring simply is never going to do so, even over many repetitions of the lifetime of our universe. Therefore, one should be very wary about any number greater than  $10^{106}$  or smaller than  $10^{-106}$ , because such frequencies simply cannot apply to any known physical reality. Elsasser calls any number exceeding  $10^{106}$  an *enormous* number.

If one asks how many different types or characteristics are required to assure that a random combination can indisputably be considered unique, it may surprise some that the required number is not extremely large. It is not Avogadro's number (roughly  $10^{23}$ ). It is not one million types, or even 1000. Certifiable uniqueness happens to require only about 75 distinct tokens! This is because the combinations of types scale roughly as the factorial of their number. Because  $75! \approx 10^{106}$ , whenever more than 75 distinguishable events co-occur by chance, one can be certain that they will never randomly do so again.

Elsasser's result is important to ecologists, because it is almost impossible for anyone dealing with real ecosystems to find one that is composed of fewer than 75 distinguishable individuals (e.g., Kolasa and Pickett, 1991). For example, an ecosystem comprised of 10 species, each represented by 40 organisms would yield 400 distinguishable entities. But 400! so overwhelms  $10^{106}$  that an abundance of unique chance events is more than guaranteed.

One concludes that singular events are not rare; rather they are legion! They occur everywhere, all the time, and at all scales! (see Chapter 3 in Jørgensen et al., 2007). The theme of this special issue is the emergence of novelties, and we now see that novelties are extremely common. Furthermore, they occur without necessarily violating any physical laws. The known laws of nature continue to constrain evolution, but generally they are incapable of determining actual outcomes in complex systems. To see this one need only consider that in physics there are six fundamental laws of nature (the four force laws and the two laws of thermodynamics). This means that the parametric specification of the laws could cover at most some 6! (or 720) combinations. In a biological situation one might be dealing with some 35 independent factors, so that 35! or  $10^{40}$  combinations are possible. It becomes obvious that the system exhibits massive degeneracy with respect to the confining

laws. That is, a very large number of possibilities can exist for each specification of the laws. Those laws are not violated, but rather are satisfied by a great abundance of alternatives, and the laws are insufficient to specify the exact outcome. Designation of the particular outcome must be accomplished by some other agency.

#### 4. Coherence in ecosystems

Unique events (which elude treatment by conventional probability theory) are thus abundant and occur everywhere in a complex world. In fact, they are so abundant that one begins to worry what holds biotic systems together? Biological systems do, however, cohere and persist, and so the question arises as to how that could be possible? The mechanist would claim that order is being maintained by yet-undiscovered laws, but Elsasser's propositions have rendered that possibility remote. Some agency, looser but still effective, must be at work. A clue to the origin of such cohesion was provided by Gregory Bateson (1972): "In principle, then, a causal circuit will generate a non random response to a random event. . ." Bateson, one of the founders of cybernetics, was dealing with "causal circuits", concatenations of events or *processes* wherein the last element in the chain affects the first—what commonly is known as feedback. Causal circuits, he implied, have the capability to endure, because they can react non-randomly to random stimuli. This inchoate fragment of an idea points the way towards an understanding of the life process and its origins. Furthermore, the phenomenon is capable of fixing the outcome whenever multiplicity has overwhelmed physical law.

Before elucidating how feedback can resolve indeterminacy, it should be emphasized that the links in the circuit do not have to be mechanical by nature. That is, a given input does not have to lead ineluctably to a determinate result. Rather, one can describe the relationship between chance and outcome as a *process*. By "process" here is meant the interaction of random events upon a configuration of constraints that results in a non-random, but indeterminate outcome.

If the combination of "non-random" and "indeterminate" seems confusing and somewhat contradictory, perhaps the example of Polya's Urn (Cohen, 1976) will help to clarify the distinctions. The process described by György Pólya begins with a collection of red and blue balls and an urn containing one red ball and one blue ball. The urn is shaken and a ball is blindly drawn from it. If that ball is the blue one, a blue ball from the collection is added to it and both are returned to the urn. The urn is shaken and another draw is made. If a ball drawn is red, it is replaced along with another red ball into the urn, etc. A first question arises as to whether a long sequence of such draws and additions would cause the ratio of red to blue balls to converge to a limit. It is rather easy to demonstrate that after, say, 1000 draws, the ratio converges to some constant, say 0.54681. That is, the ratio becomes progressively *non-random* as the number of draws grows.

The fact that the system very rarely converges to 0.5000 prompts one to inquire what would happen if the urn were emptied and the starting configuration recreated? Would the subsequent series of draws converge to the same limit as the first? It is easy to demonstrate that it will not. After 1000 draws the second might approach a limit in the vicinity of 0.19732. The Polya process clearly is *indeterminate*. One eventually discovers that the ratio of balls is progressively constrained by the particular series of draws that have already occurred. It gradually becomes clear that the limiting ratio for any long sequence of draws and replacements can be *any* real fraction between zero and one.

The key feature of a process is that it describes what happens most of the time, but not in every instance. It behaves like a "propensity" in the sense of Karl Popper (1990) rather than a force in the mechanistic sense of the word.

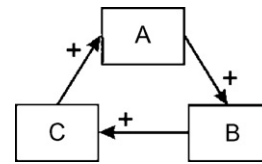


Fig. 3. Schematic of a hypothetical three-component autocatalytic cycle.

Returning then to the causal circuits of Bateson, particular attention is now focused on an interesting subset of feedbacks called "autocatalysis". Autocatalysis is a particular form of positive feedback wherein the effect of every consecutive link in the feedback loop is positive. Without loss of generality, autocatalysis can be illustrated by the simple three-component interaction depicted in Fig. 3. Here the action of process A has a *propensity* to augment the second process B. B in its turn tends to accelerate C in similar fashion, and C has the same effect upon A.

Kauffman (1995) has shown that autocatalytic concatenations become inevitable even in medium dimensional systems.

A key feature of autocatalysis is that it exerts a selection pressure upon all of its components as well as on any of their attendant mechanisms. Any change in a characteristic of a component that either makes it more sensitive to catalysis by the upstream member, or a better catalyst of the element that it catalyzes, will be rewarded. Other changes will at best be neutral, but more likely will be decremented by the feedback. Through such selection, the integrity of the autocatalytic cycle can be maintained through the repair of the effects of disturbances that may impinge upon it (Ulanowicz, 2009). Furthermore, the entire cycle records its history in the collective behaviors of its component elements and the structures of the processes linking them.

In particular, this selection will reinforce changes that bring more material or energy into a participating element (Ulanowicz, 1997), resulting in what can be called (in Newton's word) "centripetality" (Fig. 4).

Centripetality is an enormously important feature of life that eludes description by mechanical models, encumbered as they are by their inability to change component mechanisms in a sufficiently general way. Furthermore, centripetality imparts a direction and an identity to the circuit that generally escapes mechanical description (Chapter 4 in Jørgensen et al., 2007). It also plays a key but tacit role in the Darwinian scenario—that of "striving". The various species of organisms are engaged in ubiquitous struggle—competing with each other. But what accounts for the drive behind this competition? One now sees that striving is the outcome of an autocatalytic configuration of processes. It stands at the very core of evolution (Russell, 1960). While orthodox Darwinism places competition at the center of evolution, it now becomes apparent that competition, to the contrary, is actually *subsidiary* to centripetality (which, as was shown, rests upon *mutuality*). Competition at any scale simply could not exist were it not for mutual beneficence at some lower level.

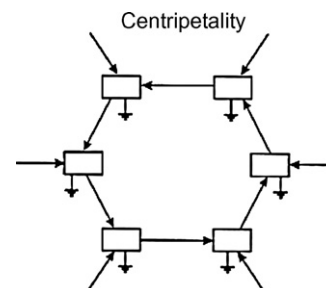


Fig. 4. Autocatalysis induces centripetality.

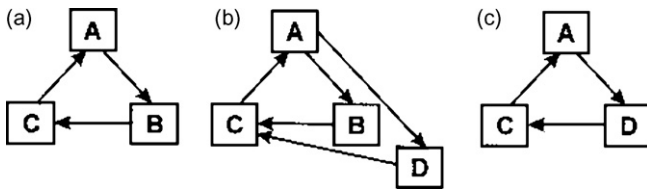


Fig. 5. Centripetality induces competition.

To illustrate how autocatalysis engenders competition, it is helpful to regard the sequence in Fig. 5 (Ulanowicz, 1997). In Fig. 5b element D appears spontaneously in conjunction with A and C. If D is more sensitive to A and/or a better catalyst of C, then the ensuing dynamics of centripetality will so favor D over B, that B will either fade into the background or disappear altogether (as in Fig. 5c). That is, selection pressure and centripetality can guide the replacement of elements.

Some readers may object to the description of autocatalysis as non-mechanical, because many of the foregoing scenarios *seem* amenable to mechanical simulation—and in some contrived circumstances they may be. Crucial, however, is the fact that, in light of Elsasser's emphasis on how combinatorics overwhelm complex systems, it becomes impossible to state apriori all the possible *complex* events that could perturb an element or a relationship, much less to specify the direction in which it might move the system. Stuart Kauffman (2008) calls the ensemble of such complex possibilities the “adjacent possible”, and he is at pains to demonstrate how such evolutionary “preadaptations” remain impossible to specify.

## 5. The yin and yang of ecology

By now the reader may have noticed that two countervailing tendencies are at play in the development of any dissipative structure. In one direction a continuous stream of perturbations works to erode any existing structure and coherence. Meanwhile, this drift is opposed by the workings of autocatalytic configurations, which drive growth and development and provide repair to the system. This tension has been noted since Antiquity. Diogenes related that Heraclitus saw the world as a continuous tearing down and building up. With the Enlightenment, however, science opted for a more Platonic view of nature as monistic equilibrium.

Outside of science, Hegel retained Heraclitus' view of the fundamental tension, but with significant amendment. He noted that, although the two tendencies may be antagonistic at the level of observation, they may become mutually obligatory at the next higher level. Hegel's view is resonant with the picture of ecosystem dynamics portrayed here. Indeed, the second law does dissipate what autocatalysis has built up, but it has been noted that singular chance is also necessary if systems are truly to evolve over time and develop novel emergent characteristics. Looking in the other direction, complex, evolved systems can be sustained only through copious dissipation.

The problem with this agonistic view of the natural world is that, unlike the mechanistic (Platonic) convention, dialectic-like dynamics cannot be adequately represented as algorithms. To repeat again, mechanistic simulation models are inadequate to the task of describing ecosystems over the longer run, because the selfsame selection exhibited by autocatalysis can unpredictably replace not only components, but their accompanying mechanisms as well. Not only does the notion of mechanism defy logic, it seems also to poorly match the dynamics that actually are at play.

## 6. Quantifying agonism

Adopting a more positive attitude, one now asks how to describe quantitatively this universal “conversation” between structure-building and dissipation? Obviously, science needs to put a little more distance between itself and the Platonic, mechanistic metaphor of the clockwork (Goerner, 1999). Because order persists within living systems that are immersed in a noisy world by virtue of the action of their constituent autocatalytic processes, it is only reasonable to turn attention towards description in terms of processes—or more specifically, towards the description of ecosystems dynamics as configurations of processes (Platt et al., 1981).

The study of linked processes is not a theme foreign to ecology, even outside simulation modeling. Almost 70 years ago Raymond Lindeman (1942), a student of G. Evelyn Hutchinson, attempted to describe quantitatively the trophic processes occurring in the ecosystem of Cedar Bog Lake in terms of a flow network. A rich literature of the analysis on such quantitative flow networks has ensued (e.g., Hannon, 1973; Finn, 1976; Levine, 1980; Fath and Patten, 1999; Ulanowicz, 2004b).

To summarize some of the relevant results of ecological network analysis, one designates the flow from taxon  $i$  to another taxon,  $j$ , as  $T_{ij}$ . If one then denotes the source of exogenous inputs to the system as component zero and the sink that receives all outputs and dissipations as taxon  $n+1$ , one can thereby identify and label all the trophic flows in an ecosystem.<sup>1</sup> Proceeding in this manner, Ulanowicz (1979, Hirata and Ulanowicz, 1984; Ulanowicz and Norden, 1990) has used information theory to quantify the organization inherent in any network of  $T_{ij}$ 's as the system's ascendancy,  $A$ , or,

$$A = \sum_{i,j} T_{ij} \log \left( \frac{T_{ij} T_{..}}{T_{i.} T_{.j}} \right), \quad (1)$$

where it can be shown that  $A$  is inherently non-negative, i.e.,  $A \geq 0$ .

The chief advantage of using information theory to describe organization is that it allows one also to quantify the opposite (or complement) to information in similar fashion. Whence everything that is disordered, incoherent and dissipative in the same network can be captured by a related, non-negative variable called the system's overhead,  $\Phi$ ,

$$\Phi = - \sum_{i,j} T_{ij} \log \left( \frac{T_{ij}^2}{T_{i.} T_{.j}} \right). \quad (2)$$

Furthermore, a system's ascendancy and overhead sum to yield its overall capacity for development,  $C$ ,

$$C = A + \Phi$$

$$C = - \sum_{i,j} T_{ij} \log \left( \frac{T_{ij}}{T_{..}} \right). \quad (3)$$

Because  $0 \leq A/C \leq 1$ , this ratio (call it  $a$ ) provides a convenient (and normalized) measure of the degree of system order. The actual pattern of order is the result of two opposing tendencies: In an inchoate system (one with low  $a$ ), there are manifold opportunities for autocatalytic cycles to form, and those that arise create internal constraints that increase  $A$  (and thereby abet  $a$ ). This tendency for  $a$  to grow via autocatalysis exists at all values of  $a$ . The role of overhead,  $\Phi$ , however, changes as the system progresses toward higher

<sup>1</sup> A dot in place of a subscript is a shorthand for summation over that index. For example,  $T_{..} = \sum_{i,j} T_{ij}$  represents the sum of all measureable activities occurring in the system.



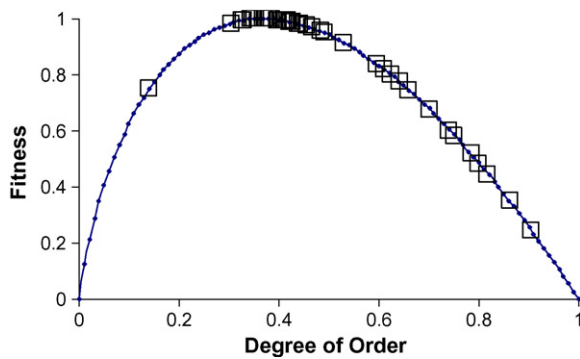


Fig. 6. The degrees of order and their corresponding magnitudes of fitness for the 48-sample weighted ecosystem flow networks used by Zorach and Ulanowicz (2003).

*a*. In inchoate systems (low *a*), it is  $\Phi$  that provides the opportunities for new cycles to form. In doing so it abets the tendency to increase autocatalysis. However, in systems that are already highly developed ( $a \approx 1$ ), the dominant effect of  $\Phi$  becomes the disruption of established feedback loops, resulting in a sudden loss of organized performance. (The system resets to much a lower *a*.) So at high *a*,  $\Phi$  strongly opposes further increase in *a*. Presumably, a critical balance between the countervailing roles of  $\Phi$  exists near the value of *a* at which the qualitative role of  $\Phi$  reverses.

## 7. The fitness of ecosystems for evolution

The degree of organization (*a*) is a key indicator of the ability of the system to self-organize. If the degree is too low ( $a \approx 0$ ), the efficacy of the existing constraints is lost among the noise of perturbations (Atlan, 1974). If *a* is too high ( $\approx 1$ ), however, the system will become brittle or “frozen”, and the dominant, inflexible pathways of feedback can fall victim to perturbations (Holling, 1986). For a system to remain alive and react to the external world, it clearly must avoid these endpoints, but that opens the question of how systems distribute themselves along the interval? To address this question some index of the ability of a system to evolve is needed. Accordingly, one defines the fitness of a system for change (*F*) to be the product of the degree of system order (*a*) times the Boltzmann measure of its disorder ( $-k \log[a]$ ),<sup>2</sup>

$$F = -ka \log(a). \quad (4)$$

To investigate how the degrees of order for real ecosystems are distributed, a set of weighted networks of trophic exchanges in 48 different ecological communities (Zorach and Ulanowicz, 2003) are plotted along the fitness arc, as shown in Fig. 6.

One observes that most systems cluster around the maximal fitness ( $a = 1/e$ ), with some bias towards higher values of *a*. Robert Christian (personal communication) noted that all the systems with higher values of *a* corresponded to communities that had been represented in terms of only very few constituent elements ( $n = 4$ –8). Such depictions are likely to be wanting in richness and detail.

## 8. The return of law to ecology?

Those systems that were described in greater detail yielded values of *a* and  $\Phi$  that clustered closer around the point of maximal

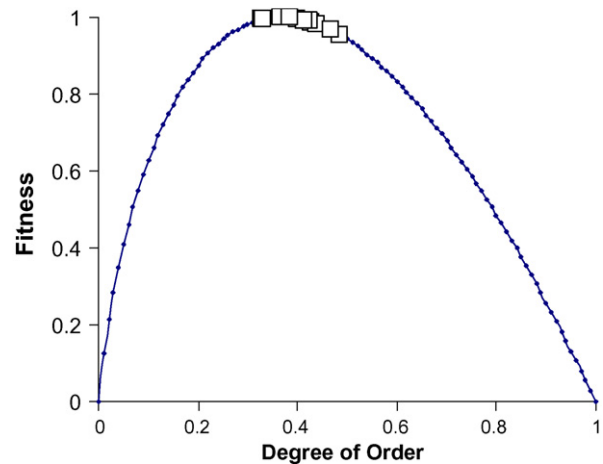


Fig. 7. The degrees of order and corresponding magnitudes of fitness for the subset of 17 ecosystem flow networks in Fig. 6 that each possess >12 compartments.

fitness ( $1/e$ ). Fig. 7, for example, shows the distribution of the subset of 17 systems for which  $n > 12$ . The minimal value of the fitness for this subset was  $F = 0.954$ .

The data in Fig. 7 reveals a striking natural tendency for systems to gravitate towards configurations of maximal fitness for change. From a purely phenomenological viewpoint, one could say that ecosystems tend to gravitate towards configurations that possess maximal fitness for evolution.

In fact, there are several remarkable features about the maximum in Fig. 7. The first is revealed by calculating the sensitivity of the fitness with respect to each individual flow. Applying the chain rule of differentiation yields:

$$\frac{\partial F}{\partial T_{ij}} = F' \frac{\partial a}{\partial T_{ij}}$$

or

$$\frac{\partial F}{\partial T_{ij}} = \frac{F'}{C} \left\{ \log \left[ \frac{T_{ij} T_{..}}{T_{i.} T_{.j}} \right] + a \log \left[ \frac{T_{ij}^2}{T_{i.} T_{.j}} \right] \right\}, \quad (5)$$

where  $F'$  is the derivative of *F* with respect to *a*, i.e.,

$$F' = -ea \left[ \frac{\log(a)}{\log(e)} + 1 \right].$$

One notices that at  $a = (1/e)$ ,  $F' = 0$ , so that Eq. (5) becomes  $\partial F / \partial T_{ij} = 0$  for each and every flow,  $T_{ij}$ . At  $a = (1/e)$ , all flows contribute equally towards sustaining the system in this propitious state. In other words, the system is acting as a coherent whole in endowing itself with fitness. The subject of coherent domains in physics and their possible relevance to ecology is addressed by Brizhik et al. (this issue) elsewhere in this forum, and the phenomenology just discussed lends credence to their conjecture that such domains exist in ecosystems. It remains to be seen, however, whether such coherence is maintained in ecosystems by quantum-like phenomena or whether they are linked in macroscopic fashion. Regardless of the means, whenever the system is not in the state of maximal, coherent fitness, Eq. (5) can be employed to calculate the relative degree to which a unit increase in each link would advance the system towards maximum fitness (Ulanowicz et al., 2008).

Finally, it is noteworthy that information has been defined by Tribus and McIrvine (1971) as “anything that causes a change in probability assignment”. This is another way of saying that information is to probability as differential calculus is to algebra. Under this analogy (4) would correspond to a second derivative of probabilities. That real systems cluster around  $\partial F / \partial T_{ij} = 0$  hints, therefore,

<sup>2</sup> The reader might wonder why  $(1 - a)$  was not chosen as the measure of disorder. Boltzmann's choice quantifies the fact that the combinatorics of nature bias reality in the direction of disorder (the second law of thermodynamics.) More about this presently.

at conservative behavior in probability space. That is, only a limited range of phase space is available to living systems (see “window of vitality” in Zorach and Ulanowicz (2003)).

Analytical proof that  $a = [1/e]$  (or  $\partial F/\partial T_{ij} = 0$ ) is an attractor point for living systems has yet to be provided. A heuristic numerical operation is available; however, that conveniently illustrates some of the dynamics at play. The reader may recall that the notion of process was defined above as “the interaction of random events upon a configuration of constraints that results in a non-random, but indeterminate outcome.” Furthermore, the Boltzmann formulation ( $-\log[a]$ ) was chosen to be the metric of choice to quantify disorganization, chance or “noise”. One may regard this measure as an “operator” in the mathematical sense of the word, which, when it acts upon the system organization,  $a$ , projects the system into its next configuration. Mathematically, this can be represented by the sequence,

$$[-\log(a_i)]^\circ a_i \rightarrow a_{i+1}, \quad (6)$$

where the symbol ( $^\circ$ ) is interpreted as “operates upon” (multiplies),  $a_i$  is the degree of order at time  $i$ , and  $a_{i+1}$ , that during the following time interval.

It is straightforward to prove that, whenever the starting value  $a_0 < (1/e)$ , the sequence converges (usually in short order) to  $a = (1/e)$ . For example, when  $a_0 = 0.2$ , the resulting sequence is: 0.200000, 0.321888, 0.364877, 0.367867, 0.367879, 0.367879, ...

If, however,  $a_0 > (1/e)$ , the initial transition takes the form of a “catastrophe” that abruptly decrements the degree of order to below  $(1/e)$ , from whence successive states will converge, as in the first sequence, to  $(1/e)$ . For example, when  $a_0 = 0.8$ , the ensuing sequence is: 0.800000, 0.178515, 0.307596, 0.362646, 0.367842, 0.367879, 0.367879, ...

It is not difficult to demonstrate that the more  $a_0$  exceeds  $(1/e)$ , the smaller the ensuing  $a_1$ ; that is, the more drastic becomes the collapse.

Many ecologists will immediately recognize this dynamic. It strongly resembles the well-known “Figure 8” hypothesis that Holling (1992) patterned after Schumpeter’s (1942) notion of “creative destruction”. Holling described the sequence whereby an impacted ecosystem recovers its robustness slowly, but eventually “overshoots” its most propitious configuration. The overshoot then renders the system vulnerable to catastrophic collapse, which starts the cycle all over again.

It is worth noting that when,  $a_0 = (1/e)$ ,  $[-\log(a_0)] \cdot a_0 = a_0$ . Hence, at the attractor point itself, noise plays the role of an idempotent operator. That is, it acts on the system status to recapitulate itself. This recursion has important implications for sustainability theory, because it indicates that systems in nature could sustain themselves indefinitely at  $(1/e)$  without supplementary work. It appears to be the point of natural sustainability. It is not that systems cannot exist when  $a > (1/e)$  (as with many artificial systems, e.g., agriculture or economics), but that additional work is required to maintain metastable configurations, and the greater the overshoot, the more maintenance necessary to keep them there.

Of course, noise and determinism do not readily mix, so that one should not expect systems to zero in on  $a_0 = (1/e)$ . Rather, one should anticipate some scatter around the attractor, which is what one observes among the data in Fig. 7. The data, in fact, seem skewed towards the upper side of the attractor point, but remain along the flat portion of the curve, where overshoot and recovery do not imply drastic changes in fitness.

By definition, a process is non-random but indeterminate. Data reveal that systems are drawn non-randomly towards a particular value of  $a$ , but is such attraction determinacy at work? The answer is a definite “no”, because any given value of  $a$  pertains to a manifold infinity of particular network configurations—just as an infinity of molecular configurations correspond to any particular value of a

thermodynamic variable, such as entropy. There remains, therefore, an enormous latitude for any configuration that maps into  $a = (1/e)$  to continue to change and evolve, even though its overall degree of organization remains relatively fixed. The reader will recall that the measure of fitness was conceived as the potential to evolve. It follows that a maximum in this attribute should provide greatest potential for further evolution.

A final issue relates to thermodynamic equilibrium. Does not  $a \rightarrow (1/e)$  represent a convergence to equilibrium? Ecologists are justifiably wary of equilibrium theories (Gil Friend, personal communication). But as with determinacy, this misgiving is likewise misplaced, because the system at maximum fitness fails the test for thermodynamic equilibrium. That is, if the system at the attractor were to be isolated, it would undergo subsequent change. Systems at true equilibrium will remain the same after being isolated. Obviously, all living systems that cluster around the attractor would die and decay after isolation.

## 9. Nature as a balancing act

To summarize the dynamics: only two states of thermodynamic equilibrium are possible ( $a = 0$  and  $a = 1$ ). Whenever a source of external energy acts upon coupled entities, equilibrium states cease to be the most probable configurations. The system will then move to some intermediate value of  $a$ , and the system fitness will gravitate eventually towards the maximum at  $a = (1/e)$ . At this maximum the system achieves a balance of sorts between its countervailing tendencies.

Reversing the scenario, if external sources of free energy are removed from the system (it becomes isolated), matters will devolve towards the polar extremes ( $a = 0$  and  $a = 1$ ) both of which represent true equilibrium. It is significant that the end state is not unique, because under Boltzmann’s assumptions, which pertained to a rarified ideal gas composed of homogeneous atoms which did not interact, the only possible end state was  $a = 0$ . On the basis of Boltzmann’s results, cosmologists concluded that the physical cosmos will ultimately reach a state they called “heat death”—the uniform distribution of weak, long-frequency radiation throughout the universe. Ulanowicz (in press) has suggested, however, that portions of decaying systems may converge instead into “perpetual harmonies” (at  $a = 1$ ), and that it was just such a convergent process that yielded the stable atoms and molecules that serve as the starting point for the materialist ideology. Of course, it is difficult to imagine how biological systems might somehow culminate in equilibrium structures, but the fact that living systems converge towards coherence leaves open such possibility.

The significant departure of ecosystem dynamics from the mechanical paradigm necessarily has its practical implications. One notes how systems that cluster around  $F = 0$  are those likely to be most sustainable under the prevailing inputs of energy and resources. As living systems that are “self-entailing” (Rosen, 1999), no further subsidies should be necessary. The appearance of new resources would likely cause a system to deviate from the most probable degree of order, but the ensuing configuration would then be at risk in at least two regards: for one, a supply of auxiliary resources must be sustained to retain the system in its less probable state. Secondly, the further the system is artificially separated from a sustainable configuration, the more likely is a catastrophic “avalanche” or sudden collapse of the system to a more disordered state ( $a < [1/e]$ ). In this regard, relation (5) provides a tool, not only for assessing how far a system is removed from a sustainable configuration, but also for identifying which elements of the system should be tuned and by which relative magnitudes in order to turn the system towards a more sustainable, persistent state (Ulanowicz et al., 2008).

What, then, are the consequences of dialectic-like ecological dynamics for ecological modeling in general? While the new insights do not render mechanical simulation modeling useless, they do appreciably circumscribe its utility. Mechanical scenarios can still help one diagnose why a system may be misbehaving and afford some insight into possible diagnosis/remedy. The time horizon for such assessment is usually quite short, however, and one cannot expect the diagnosis to remain appropriate for any significant duration, because the radically different dynamics just described must eventually intervene.

# 10. Science is like a muscadine grapevine

Doubtless, many will balk at this critique of the mechanical paradigm. Most view the progress of science akin to the simile that Daniel Dennett (1995) used to describe natural evolution. Dennett likened evolution to “cranes built upon cranes”. That is, the foundational crane is used to lift to its top new materials that can be used to assemble yet another crane. The process can then be repeated so that the tower of cranes grows progressively taller.

This mechanical simile is a poor fit to the life sciences, however, where the organic metaphor of growing muscadine grapevines is likely to prove more appropriate (Ulanowicz, 2004c). Muscadine grapevines begin as a single vine that becomes a trunk supporting an arborescence of vines leaves and grapes. Later, however, the plant drops from its lower members adventitious roots, some of which sink deep into the ground and thicken. Still later, the original trunk often dies and rots away, as sustenance is taken over by the later connections.

An extended column of cranes can eventually become unstable and come crashing down like the tower of Babel. Not so the muscadine vine, where the replacement of original members by younger, more efficacious connections occurs naturally. The mechanical paradigm has served science admirably through the early stages of the enterprise. It has nourished the accumulation of a significant body of knowledge, but this very knowledge now suggests that the time has come to replace the original foundations (Ulanowicz, 2009). Such is evolution; such is the march of knowledge; and such is progress in ecosystems science.

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