CHAPTER 15

Ecological network analysis: an escape from the machine

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Introduction

The scientific community is abuzz over the use of networks to describe complex systems (Watts 1999; Barabási 2002). Recently, the leading journals have reported the rediscovery of the fact that collections of processes and relationships in complex systems often deviate from conventional statistics (Jeong et al. 2000; Montoya and Sole 2002). Many networks of natural systems are said to be "scale-free" in that their elements are distributed according to non-normal power laws (Ulanowicz and Wolff 1991; Barabási and Albert 1999). Others appear to be nested in hierarchical fashion, while still others are dominated by chains of what Almaas and Barabási (2004) have called "hot links" (see also Ulanowicz and Wolff 1991). Because scientists have been conditioned for over 300 years to regard nature as a grand clockwork, the race is now on to elucidate the "mechanisms" behind why the elements of natural systems are arranged in these ways.

Before getting too caught up in the search for mechanisms, it might be wise for investigators to consider if they are pointing their flashlights in the right direction (Popper 1977), for as the late media pundit, Mashall McLuhan (1964) once wrote,

The hybrid or the meeting of two media is a moment of truth and revelation from which new form is born . . . The moment of the meeting . . . is a moment of freedom and release from the ordinary trance and numbness imposed by them on our senses.

By this he meant that when confronted by new ways of seeing things, observers too often are numbed into interpreting what they see according to old, habitual ways. McLuhan's favorite example was that of International Business Machine, Inc, which began its existence building machinery for businesses. The corporation floundered in unexceptional fashion, until it dawned upon someone that the nature of their enterprise was really more like the transfer of information. Thereupon, the company fortune exploded with such vigor that its consequent meteoric rise is studied till today by business students and stockbrokers alike. (Eventually, the association with machinery was hidden within their acronym, IBM, which one now associates more with the technology of computation than with machines per se).

If some readers remain unimpressed by McLuhan's admonition, perhaps they might heed the castigating words of the mathematician, John Casti (2004). Casti builds upon a children's story, "Little Bear," by Else Minarik (1957) wherein the principal character tries to get to the moon by climbing a tree. Casti contends that using the conventional methods of physics to improve one's understanding of complex systems is akin merely to climbing a taller tree. He cites how, when complex systems are approached using conventional tools, they almost invariably give qualitatively *contradictory* prognoses (and not ones that are merely quantitatively inaccurate).

If some readers should find Casti's admonition a little too pessimistic, they would do well to recall how Eugene and Howard Odum, Robert Rosen, Stanley Salthe, this author and others have labored to point out how the dynamics of living systems is qualitatively distinct from that of purely physical systems. In fact, if one examines closely the

fundamental postulates upon which science has operated for the past 300 years, one discovers that each axiom in its turn is violated by one or another ecosystem behavior (Ulanowicz 1999.) Given such disparity, it comes as no surprise that conventional approaches to ecosystems behavior have not yielded any more progress than might come from "climbing a taller tree." Partly out of frustration, a number of investigators have embarked upon a phenomenological search for new ways to quantify ecosystem dynamics and have keyed on quantifying networks as a possibly fruitful approach (Ulanowicz 1986; Wulff et al. 1989; Higashi and Burns 1991). In light of these considerations, it should prove helpful to study in more detail exactly how ecosystem dynamics transcend the usual scientific metaphysic and to explore more fully how quantifying ecosystem networks provides a completely new perspective on the natural world.

Normal science

The problem with writing about the "conventional" approach to science is that no single image exists. Rather, as Kuhn (1962) has suggested, each individual scientist weights differently the various criteria that he or she uses to delimit legitimate science. To deal with such diversity it is helpful to focus on a set of fundamental postulates that once formed a broad consensus about nature around the turn of the nineteenth century (ca. 1800). This "strawman" is not intended to describe the beliefs of scientists today—no one still adheres to the truth of all the classical postulates. On the other hand, virtually every contemporary approach to natural problems still depends upon one or more of these assumptions. The argument made here is that *none* of the postulates remains inviolate within the domain of ecosystem dynamics, and it is the magnitude of such discrepancies that has forced the current phenomenological turn toward describing ecosystems in terms of networks.

While descriptions of the scientific method are legion, one rarely encounters attempts to enumerate the fundamental assumptions upon which the method is based. One exception is that of Depew and Weber (1994), who articulated four

fundamental postulates about nature according to which Newtonian investigations were pursued:

Newtonian systems are causally *closed*. Only mechanical or material causes are legitimate.
Newtonian systems are *deterministic*. Given precise initial conditions, the future (and past) states of a system can be specified with arbitrary precision.
Newtonian systems are *reversible*. Laws governing behavior work the same in both temporal directions.
Newtonian systems are *atomistic*. They are strongly decomposable into stable least units, which can be built up and taken apart again.

In addition, Prigogine and Stengers (1984, see also Ulanowicz 1999) alluded to a fifth article of faith, namely that

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

Ecosystem dynamics

Although it might at first seem somewhat removed from the subject of networks, determinism is the most convenient assumption with which to begin the discussion of ecosystem dynamics. Every ecologist is aware of the significant role that the aleatoric plays in ecology. Chance events occur everywhere in ecosystems. Stochasticity is hardly unique to ecology, however, and the entire discipline of probability theory has evolved to cope with contingencies. Unfortunately, few stop to consider the tacit assumptions made when invoking probability theory—namely that chance events are always simple, generic, and recurrent. If an event is not simple, or if it occurs only once for all time (is truly singular), then the mathematics of probabilities would not apply.

It may surprise some to learn that ecosystems appear to be rife with singular events. To see why, it helps to recall an argument formulated by physicist Walter Elsasser (1969). Elsasser sought to delimit what he called an "enormous" number. By this he was referring to numbers so large that they should be excluded from physical consideration, because they greatly exceed the number of physical events that possibly could have occurred since the Big Bang. To estimate a threshold for

enormous numbers Elsasser reckoned the number of simple protons in the known universe to be about 10^{85}. He then noted as how the number of nanoseconds that have transpired since the beginning of the universe have been about 10^{25}. Hence, a rough estimate of the upper limit on the number of conceivable events that could have occurred in the physical world is about 10^{110}. Any number of possibilities much larger than this value simply loses any meaning with respect to physical reality.

Anyone familiar with combinatorics immediately will realize that it does not take very many distinguishable elements or processes before the number of their possible configurations becomes enormous. One does not need Avagadro's number of particles (10^{23}) to produce combinations in excess of 10^{110}—a system with merely 80 or so distinct components will suffice. In probabilistic terms, any event randomly comprising more than 80 separate elements is virtually certain to never have occurred earlier in the history of the universe. Such a constellation is unique over all time past. It follows, then, that in ecosystems with hundreds or thousands of distinguishable organisms, one must reckon not just with occasional unique events, but rather with a legion of them! Unique, singular events are occurring all the time, everywhere! In the face of this reality, all talk of determinism as a universal characteristic is futile, and the argument for reversibility collapses as well.

Despite the challenge that rampant singularities pose for the Baconian pursuit of science, it still can be said that a degree of regularity appears to characterize such ecological phenomena as succession. The question then arises as to the origins and maintenance of such order? An agency that both creates and maintains regularities is embedded in the patterns of processes that are represented by trophic *networks*. In particular, the key to how living systems act differently from purely physical systems appears to reside in the adjunction of autocatalytic loops (or cycles of mutualism, that can be found in ecosystem networks) with frequent aleatoric events (Ulanowicz 1997*a*). Here autocatalysis will be defined as any manifestation of a positive feedback loop whereby the direct effect of every link on its downstream neighbor

is positive. Without loss of generality, one may focus attention on a serial, circular conjunction of three processes A, B, and C (Figure 15.1). Any increase in A is likely to induce a corresponding increase in B, which in turn elicits an increase in C, and whence back to A.

A didactic example of autocatalysis in ecology is the community that builds around the aquatic macrophyte, *Utricularia* (Ulanowicz 1995). All members of the genus *Utricularia* are carnivorous plants. Scattered along its feather-like stems and leaves are small bladders, called utricles (Figure 15.2(a)) Each utricle has a few hair-like triggers at its terminal end, which, when touched by a feeding zooplankter, opens the end of the bladder, and the animal is sucked into the utricle by a negative osmotic pressure that the plant had maintained inside the bladder. In nature the surface of *Utricularia* plants is always host to a film of algal growth known as periphyton. This periphyton in turn serves as food for any number of species of small zooplankton. The autocatalytic cycle is closed when the *Utricularia* captures and absorbs many of the zooplankton (Figure 15.2(b)).

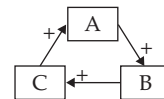In chemistry, where reactants are simple and fixed, autocatalysis behaves just like any other

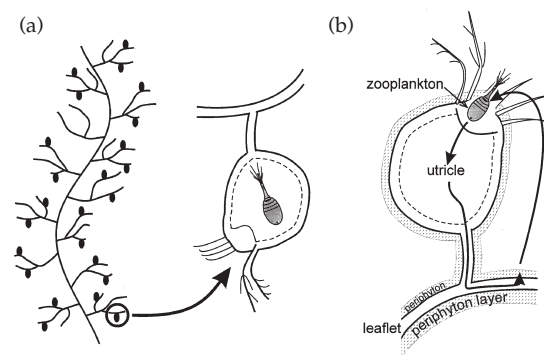**Figure 15.1** A simple example of autocatalysis.

Figure 15.2 (a) *Utricularia*, a carnivorous plant. (b) The cycle of rewards in the *Utricularia* system.

mechanism. As soon as one must contend with organic macromolecules and their ability to undergo small, incremental alterations, however, the game changes. Especially when the effect of any catalyst on the downstream element is fraught with contingencies (rather than being obligatorily mechanical), a number of decidedly nonmechanical behaviors can arise (Ulanowicz 1997a). These emergent attributes of complex systems render the remaining Newtonian postulates inappropriate for ecosystem dynamics (Ulanowicz 2004).

Perhaps most importantly, autocatalysis is capable of exerting *selection* pressure upon its ever-changing, malleable constituents. To see this, one considers a small spontaneous change in process B. If that change either makes B more sensitive to A or a more effective catalyst of C, then the transition will receive enhanced stimulus from A. Conversely, if the change in B either makes it less sensitive to the effects of A or a weaker catalyst of C, then that perturbation will likely receive diminished support from A. That is to say that there is a preferred *direction* inherent in autocatalysis—that of increasing autocatalytic participation. This preferred direction can be interpreted as a breaking of symmetry, and such asymmetry, like the singular events just discussed, also transcends the assumption of reversibility. Furthermore, with such increasing autocatalytic engagement, or mutual adaptation, elements lose their capability of acting on their own; or, should they remain capable of persisting in isolation, it would be with behavior radically different from that exhibited as part of the autocatalytic scheme. That is, the full cycle manifests an *organic* nature that is refractory to the assumption of atomism.

To see how another very important attribute of living systems can arise, one notes in particular that any change in B is likely to involve a change in the amounts of material and energy that are required to sustain process B. As a corollary to selection pressure one immediately recognizes the tendency to reward and support any changes that serve to bring ever more resources into B. Because this circumstance pertains to any and all members of the feedback loop, any autocatalytic cycle becomes the epi-center of a *centripetal* flow of resources toward which as many resources as

possible will converge (Figure 15.3). That is, an autocatalytic loop embedded in a network *defines itself* as the focus of centripetal flows.

It is important to note as how autocatalytic selection pressure is exerted in top–down fashion—that is, action by an integrated cluster of processes upon its constituent elements. Centripetality, in its turn, is best described as an agency that acts at the focal level. Both selection and centripetality violate the restriction of causal *closure,* which permits only mechanical actions at smaller levels to ramify up the hierarchy of scales. In autocatalytic selection, causal action resembles the final causality of Aristotle, which was explicitly excluded from Newtonian discourse, while centripetality bears all the trappings of Aristotelian formal cause (by virtue of the agency being exerted by a *configuration* of processes), which concept likewise atrophied in the wake of Newton.

Centripetality also guarantees that whenever two or more autocatalytic loops exist in the same network and draw from the same pool of finite resources, *competition* among the loci will necessarily ensue. In particular, whenever two loops share pathway segments in common, the result of this competition is likely to be the exclusion or radical diminution of one of the nonoverlapping sections. For example, should a new element D happen to appear and to connect with A and C in parallel to their connections with B, then if D is more sensitive to A and/or a better catalyst of C, the ensuing dynamics should favor D over B to the extent that B will either fade into the background or disappear altogether (Figure 15.4). That is, the
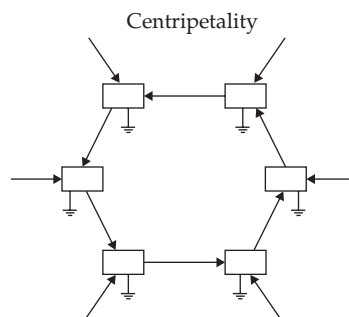

Figure 15.3 Centripetal action as engendered by autocatalysis.
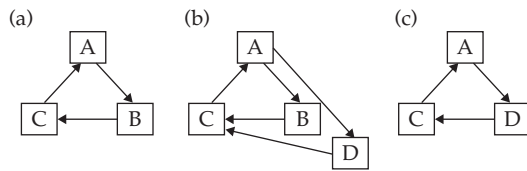
Figure 15.4 The selection of new element D to replace B.

selection pressure and centripetality generated by complex autocatalysis (as embedded in the macroscopic network of processes) is capable of influencing the replacement of elements.

The reader will note the above emphasis upon a causality that arises out of a *configuration of processes,* and which is able to influence significantly which objects will remain and which will pass from the scene. Unlike the conventional attitude that all events are the consequences of actions by objects, the reverse now becomes possible: objects themselves can become the products of constellations of processes. In other words, networks themselves can become legitimate agents of change. Hence, to describe network dynamics, it is no longer mandatory that one search for constituent mechanisms that are facilitated by objects residing in the nodes. One is now free to develop what might be called *process ecology* (Ulanowicz 2004).

Finally, it is worthwhile to note how autocatalytic selection can act to stabilize and regularize behaviors across the hierarchy of scales. Unlike with Newtonian universality, a singular event anywhere rarely will ramify up and down the hierarchy without attenuation. The effects of noise at one level are usually subject to autocatalytic selection at higher levels and to energetic culling at lower levels. Nature as a whole exhibits regularities, but in place of the universal effectiveness of all natural laws, one discerns instead a *granularity* about the real world. That is, models of events at any one scale can explain matters at another scale only in inverse proportion to the remoteness between them. Obversely, the domain within which irregularities and perturbations can damage a system is usually circumscribed. Chance does not necessarily unravel a system, which is held together by the (flexible) lattice of network interactions itself.

A new metaphysic

It begins to appear as though Casti was not exaggerating after all. As Popper (1990) suggested, a wholly new perspective on how things happen in nature may be required in order to achieve an adequate understanding of development and evolution. The topsy-turvy realm of ecological dynamics must seem strange indeed to those educated as biologists always to look to smaller scales for the causes behind phenomena, but in hindsight the appeal of reductionism now seems but a chimera.

In order for reductionism to work, the simplest and most enduring elements must all be at the very bottom of the spatio-temporal scales, so that the more complicated and less durable objects can be built up from them. Such is the case with the nested hierarchy of quarks, mesons, electrons, atoms, and chemical compounds. When one reaches the ecosystem, however, one encounters a significant inversion of these assumptions. The ecosystem per se is not as well-organized as the individual organisms that comprise it (Ulanowicz 2001). Furthermore, the network constituents (and mechanisms) come and go, while the configuration of ecosystems processes endures (and some would even say, preceded the current forms of its constituents (Odum 1971)).

Such inversion notwithstanding, no one should regard the causal agency inherent in networks as a triumph for Holism as it was once depicted. Certainly, no one is contending that configurations of processes *fully determine* the fate and nature of each constituent. One must always bear in mind that singular events loom significantly in the dynamical picture. In the overwhelming number of cases, however, singular events occur and disappear, leaving no trace upon the overall system makeup. Occasionally, they will exert detrimental effects upon autocatalytic action, and the system will respond by reconfiguring itself so as to ameliorate such disturbance. In a very small number of instances, a singular event can serve to enhance the autocatalytic functioning of the system and will become incorporated as an enduring (historical) change to the larger network structure (which thenceforth will exert somewhat different selection pressure upon subsequent singular events).

The realm of ecosystem behavior is certainly different from that of classical mechanical dynamics. Instead of a world that is closed, atomistic, reversible, deterministic, and universal; one now perceives a domain that is (respectively) open, organic, historical, contingent, and granular.

A network dynamic

If the reader studies closely the scenario described above, he or she will discern the interplay of two antagonistic tendencies. In one direction there is what might be called a *probabilistic drift* that ratchets the system in a direction of ever-greater autocatalytic activity. Opposing this drift is the entropic tendency resulting from the unpredictable occurrences of singular events, which, on one hand, act to disrupt system organization, but on the other could also provide a source for diversity and novel behaviors. Fortunately, these two tendencies can both be tracked as changes in quantitative network properties.

The probabilistic drift toward greater organization has long been characterized as "increasing network ascendency" (Ulanowicz 1980, 1986, 1997*a*). The ascendency of a network is defined as the product of its total activity (as measured by the sum of all the arc weights) times the average mutual information inherent in the linkage structure (Rutledge et al. 1976; Hirata and Ulanowicz 1984). This mutual information of the flow structure measures, on the average, how definitively transfers act in the system. That is, if a transfer is but one of a number of similar, parallel processes, it contributes little to the mutual information; but if a process plays a unique role in sustaining another node or subgraph, then the contribution of that key link to the mutual information becomes significant. Zorach and Ulanowicz (2003) showed how this latter attribute is captured by the network's mutual information, which turns out to be the logarithm of the effective number of *distinct roles* embedded in the network.

To quantify the ascendency, one must know the magnitude, T_{ij}, of each flow from arbitrary node i to any other node j. The total activity then becomes the sum of all the T_{ij}, or $T..$, where a dot in place of a subscript indicates summation over that index.

Hirata and Ulanowicz (1984) showed how the ascendency can then be expressed as

$$A = \sum_{i,j} T_{ij} \log\left[\frac{T_{ij}T..}{T_{.j}T_{i.}}\right] \geq 0,$$

and Zorach and Ulanowicz (2003) showed how the geometric mean number of roles in the network can be estimated as b^A, where b is the base used to calculate the logarithms in the formula for A.

In opposition to this drift toward increasing ascendency is the spontaneous tendency to increase what has been called the network "overhead," Φ. Overhead is the encapsulation of all ambiguity, incoherence, redundancy, inefficiency, and indeterminacy inherent in the network (Ulanowicz and Norden 1990). It can be quantified by an information-theoretic property called the "conditional entropy," which is complementary to the mutual information that was used to quantify the ascendency. In terms of the T_{ij}, Φ can be written as

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

As with the ascendency, Zorach and Ulanowicz (2003) have demonstrated how the logarithm of the geometric mean of the network link-density, L_D, is equal to one-half of the overhead. That is, $L_D = b^{\phi/2}$. (Link-density is the effective number of arcs entering or leaving a typical node. It is one measure of the connectivity of the network.)

Experience shows that the effective numbers of roles and the connectivities of real ecosystems are not arbitrary. It has long been known, for example, that the number of trophic roles (levels) in ecosystems is generally fewer than 5 (Pimm and Lawton 1977). Similarly, the effective link-density of ecosystems (and a host of other natural systems) almost never exceeds 3 (Pimm 1982; Wagensberg et al. 1990). Regarding this last stricture, Ulanowicz (2002) suggested how the May–Wigner stability criterion (May 1972) could be reinterpreted in information-theoretic terms to identify a threshold of stability at $e^{e/3}$, or ca. 3.015 links per node.

Both limits appear quite visibly when one plots the number of roles versus the effective connectivity of
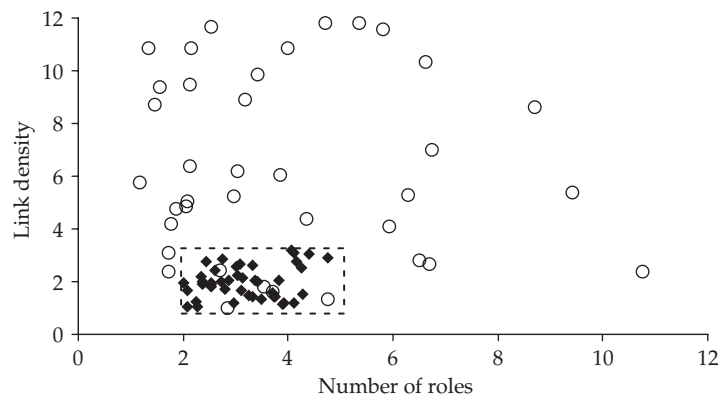
Figure 15.5 Combinations of link densities and numbers of roles pertaining to random networks (open circles) and actual ecosystems networks (solid squares). The "window of vitality" is indicated by the dotted lines.

a collection of 44 estimated ecosystem flow networks (Figure 15.5). Whereas the pairs of numbers generated by randomly constructed networks are scattered broadly over the positive quadrant, those associated with actual ecosystem networks are confined to a small rectangle near the origin. Ulanowicz (1997b) has labeled this rectangle the "window of vitality," because it appears that the entire drama of ecosystem dynamics plays out within this small theatre: as mentioned above, the *endogenous* tendency of ecosystems is to drift toward the right within this window (i.e. toward ever-increasing ascendency, or higher system performance). At any time, however, singular events can appear as exogenous perturbations that shift the network abruptly to the left. (Whether the link-density rises or falls during this transition depends upon the nature and severity of the disturbance). In particular, whenever the system approaches one of the outer edges of the window, the probability increases that it will fall back toward the interior. Near the top, horizontal barrier (LD = ~3.015 links per node) the system lacks sufficient cohesiveness and disintegrates spontaneously. As the system approaches the right-hand frame (# roles = 4.5 to 5.0), it presumably undergoes something like a "self-organizing catastrophe" (Bak 1996) as described by Holling (1986, see also Ulanowicz 1997a).

As one follows the historical dance of an ecosystem within the window of vitality, it is important to hold firmly in mind that any description of a trajectory solely in terms of mechanisms and the actions of individual organisms will perforce remain inadequate. Rather, the prevailing agencies at work are the tendency of configurations of processes (subgraphs) to increase in ascendency acting in opposition to the entropic tendency generated by complex, singular events. It is only by focusing on these larger actors that one can discover, as Karl Popper (1990) once put it,

we are not things, but flames. Or a little more prosaically, we are, like all cells, *processes of metabolism*; nets of chemical processes . . . (Italics by Popper.)

That is, by embarking upon a serious examination of the nature of ecological networks, ecologists are not simply climbing trees; they are attempting to go *beyond* rocket science!

Acknowledgments

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