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## 10

# THE PROPENSITIES OF EVOLVING SYSTEMS

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### INTRODUCTION

The fundamental problem with the prevailing scientific worldview is its glaring inadequacy to address living systems. Such an audacious assertion, coming from anyone but the most notable of philosophers, would deserve to be dismissed immediately. But it is, I believe, an accurate summary of a small monograph written recently by one of the preeminent thinkers of our time, Sir Karl Popper (1990).

Popper is perhaps best known for his contributions to logical positivism, although he himself takes credit for "killing" the movement (Popper, 1974). Then there are his engrossing debates with Kuhn, Lakatos and Feyerabend concerning the nature of science. But what has been obscured by these more renowned exploits is Popper's origins as a biologist, and it is to the subject of living systems that he returns in his latest work, *A World of Propensities*. Popper expresses strong misgivings about popular accounts of evolution. Cast as they are solely in terms of proximate and mechanical causes, current narratives on evolution seem inadequate to address its very nature and direction. To grasp the essence of evolution, Popper argues, requires an "evolutionary theory of knowledge," the beginnings of which he proceeds to outline.

While I have never been a disciple of the positivist school of thought, I find much in Popper's latest thinking that lends support to my own inclinations. In fact, I will attempt to show how his recommendations lead quite readily to an alternative image of natural causation that I have espoused elsewhere (Ulanowicz, 1986, 1989, 1990, 1991). Of course, opinions are one thing and quantitative science is quite another. So in good Popperian fashion I will attempt to go even further and provide the reader with mensuration formulae that could be employed by anyone wishing to falsify my very contentions.

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### A WORLD OF PROPENSITIES

To Popper the world is not closed. More precisely, it is not a deterministic clockwork, as Descartes would have had us believe. Rather it is composed of "propensities" – the tendencies that certain processes or events might occur. He gives as an example the estimation of the probability that a given individual will survive until twenty years from the present, say to a particular day in 2016. Given the age, health and occupation of that individual, it is possible to assign a probability for survival until 2016. As the years pass, however, the probability of survival until the set 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.

How does any of this differ from the conventional notion of probability? In two crucial ways: First, Popper holds that there is no such thing as an absolute probability. That is, no probability exists purely in isolation; each is contingent to a greater or lesser extent upon circumstances and interfering events. This is manifestly clear in the cited example of an individual's life course. It is mostly ignored, however, in classical physics, where one deals largely with events that are nearly isolated.

What in physics are called "forces," Popper sees as propensities of events in near isolation. A clear example is the mutual attraction of two heavenly masses for each other. The absence of interfering events in such a case allows for very precise and accurate predictions. When only well-defined forces are at play, the propensity of any effect given its particular cause approaches unity. This certainty is expressed as a deductive relationship between cause and effect. However, as the example of twenty-year survival shows, events are rarely isolated and subject to deductive analysis. Hence, forces are very special and degenerate examples of more general agencies that Popper calls *propensities*.

The problem with contemporary biology is that it attempts to extrapolate backwards from the narrow, deterministic, ethereal realm into that of more common experience. Descartes and Newton gave us the world as universal clockwork, a notion that reigned almost two centuries in physics and still permeates biology (viz. the influence of Newtonian thought upon Darwinism, Weber *et al.*, 1989). The very essence of the scientific method, according to Popper, is to create "at will, artificial conditions that either exclude, or reduce to zero, all the interfering and disturbing propensities."

At this point the reader might object that current theories of evolution hardly seem deterministic. After all, chance and probability play a large role in the neo-Darwinian narrative. However, the probabilities invoked there are of an absolute nature. Furthermore, the role of chance is relegated mostly to mutations that occur at the moment of genetic reproduction. From there the new organism enters a world that is assumed to be Newtonian, until the

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inception of the next generation (Depew and Weber, 1995). Without much exaggeration, the prevailing outlook on evolution is one that splices a causal theory derived at the scale of the heavenly orbs onto the assumption that the world at molecular scales is purely stochastic. The dogma is that cause may originate at these extremes and propagate inward towards the scales of more immediate experience, but we are specifically enjoined from entertaining the notion that causes may arise at intermediate levels.

Popper is decrying this disjointed view of reality and urges us to rethink our attitudes toward causality. He is suggesting that there is something between the "all" of Newtonian forces and the "nothing" of stochastic infinitesima. "Propensities" spontaneously appear at any level of observation because of interferences among processes occurring *at* that level. This hypothesis highlights Popper's second distinction of propensities from common probabilities. Propensities are not properties of an object, rather they are *inherent in a situation*. The reality of propensities derives from the circumstances or the context in which processes occur. The mutual attraction of two heavenly bodies occurs in a context that is almost vacuous – not so the fall of an apple from a tree. "Real apples are emphatically not Newtonian apples," according to Popper. 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 a biochemical process that weakens the stem, etc.

It makes no sense to Popper to speak of a propensity in abstraction from its surroundings, which in turn are affected by other propensities. Sidney Brenner, in trying to map genetic sequences onto the characteristics of phenotypes, said it very convincingly (Lewin, 1984):

At the beginning it was said that the answer to the understanding of development was going to come from a knowledge of the molecular mechanisms of gene control . . . [but] the molecular mechanisms look boringly simple, and they do not tell us what we want to know. We have to discover the principles of organization, how lots of things are put together in the same place.

Popper provides a major clue how to begin to understand the principles of organization: "We need a calculus of relative or conditional probabilities as opposed to a calculus of absolute probabilities."

## A CALCULUS OF CONDITIONAL PROBABILITIES

Popper posits the tantalizing notion of propensity as a generalization of the concept of force, but he does not explicitly show how to quantify propensities. Precisely what calculus of conditional probabilities pertains when "lots of things are put together in the same place"? But if we follow

Popper's lead in a very literal way, we discover that much of his calculus already has been developed.

Conditional probabilities have probably been encountered by most readers. In a system consisting of multiple processes, one might identify a suite of potential "causes", call them  $a_1, a_2, a_3, \dots, a_m$ . Similarly, one may cite a list of observable "effects", say  $b_1, b_2, b_3, \dots, b_n$ . One could then study the system in brute empirical fashion and create a matrix of frequencies that contains as the entry in row  $i$  and column  $j$  the number of times (events) that  $a_i$  is followed immediately by  $b_j$ . A table showing the hypothetical number of times that each of four causes was followed by one of five outcomes is shown in Table 10.1. For the sake of convenience exactly 1,000 events were tabulated. This allows us to use the frequencies of joint occurrence to estimate the *joint probabilities* of occurrence simply by moving the decimal point to the left. For example, of all the events that occurred, in 19.3 per cent of the cases cause  $a_1$  was followed by effect  $b_2$ , and in 2 per cent of the cases  $a_4$  was followed by  $b_4$ , etc. We denote these joint probabilities as  $p(a_i, b_j)$ .

Listed in the sixth column are the sums of the respective rows. Thus,  $a_1$  was observed a total of 269 times,  $a_2$ , 227 times, etc. Similarly, the entries in the fifth row contain the sums of their respective columns. Effect  $b_4$  was observed 176 times,  $b_5$ , 237 times, etc. These marginal sums are estimators of the *marginal probabilities* of each cause and effect. Thus, 26.3 per cent of the times a cause was observed, it was  $a_3$ , or 17.6 per cent of the observed effects were  $b_4$ . We denote the marginal probabilities by  $p(a_i)$  or  $p(b_j)$ .

A *conditional probability* is the answer to the question: "What is the probability of outcome  $b_j$  given that 'cause'  $a_i$  has just occurred?" The answer is easy to calculate. For example, if  $i = 2$  and  $j = 5$ , then  $a_2$  occurred a total of 227 times, and in 175 of those instances the result was  $b_5$ . Therefore, the conditional probability of  $b_5$  occurring, given that  $a_2$  has happened, is estimated by the quotient  $175/227$  or 77 per cent. In like manner, the conditional probability that  $b_4$  happens, given that  $a_1$  has just transpired, is 4.1 per cent, etc. If we represent the conditional probability

Table 10.1 Frequency table of the hypothetical number of joint occurrences that four "causes" ( $a_1 \dots a_4$ ) were followed by five "effects" ( $b_1 \dots b_5$ )

	$b_1$	$b_2$	$b_3$	$b_4$	$b_5$	Sum
$a_1$	40	193	16	11	9	269
$a_2$	18	7	0	27	175	227
$a_3$	104	0	38	118	3	263
$a_4$	4	6	161	20	50	241
Sum	166	206	215	176	237	1,000

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Table 10.2 Frequency table as in Table 10.1, except that care was taken to isolate causes from each other

	$b_1$	$b_2$	$b_3$	$b_4$	$b_5$	Sum
$a_1$	0	269	0	0	0	269
$a_2$	0	0	0	0	227	227
$a_3$	263	0	0	0	0	263
$a_4$	0	0	241	0	0	241
Sum	263	269	241	0	227	1,000

that  $b_j$  happens given that  $a_i$  has occurred by  $p(b_j|a_i)$ , then we see the general formula  $p(b_j|a_i) = p(a_i, b_j)/p(a_i)$ .

It is well to pause at this point and consider what sort of system might have given rise to the frequencies in Table 10.1. Unless the observer was unusually inept at identifying the  $a_i$  and  $b_j$ 's, then the system did not behave in strictly mechanical fashion. We see that most of the time  $a_1$  gives rise to  $b_2$ ,  $a_2$  to  $b_5$  and  $a_4$  to  $b_3$ . But there is also a lot of what Popper calls "interference" – situations like those in which  $a_4$  yielded  $b_1$ , that were occasioned either by some external agency or by the interplay of processes within the system. One also notices that there is ambiguity as to the outcome of  $a_3$ .

If it were possible to isolate individual processes and study them in laboratory-like situations, then something like a mechanical description of the system might ensue. For example, we might discover that if we take great care to isolate processes,  $a_1$  always yields  $b_2$ ,  $a_2$  gives  $b_5$ ,  $a_3$  invariably results in  $b_1$  and  $a_4$  in  $b_3$ . The same frequency counts for a collection of isolated processes could look something like that in Table 10.2. Knowing  $a_i$  immediately reveals the outcome  $b_j$  in mechanical, lockstep fashion. As Popper noted, the conditional probabilities of force-effect pairs are all unity, or certainty. What is also interesting in Table 10.2 is that  $b_4$  is never the outcome of an isolated cause. One surmises that in the natural ensemble,  $b_4$  is purely the result of interaction phenomena.

There is assuredly nothing new about conditional probabilities. Bayes defined them in the eighteenth century. What is decidedly of more recent origin is Popper's sought-after "calculus of conditional probabilities," i.e., information theory. Now the word "calculus" probably associates freely in the minds of most readers with Newton's or Leibniz's methods for studying changes in algebraic quantities. One uses the operations of differential calculus to quantify the rate of change of an algebraic function at a given point. What too few realize is that the relationship of information theory to probability theory is strictly analogous to that which differential calculus bears to algebra. Information theory was created to quantify the results of a change in probability assignment. In fact, Tribus and McIrvine (1971)

proposed as the definition of information, "anything that causes a change in probability assignment." Seen in this way information theory bears an organic relation to probability theory. This fact is tragically ignored by so many ecologists and economists, who regard probability theory as their bread and butter, but perceive information theory as something unrelated and totally useless. (One could go even further and regard probability theory as deriving from information theory, as Li and Vitanyi (1992) did.)

What should be clear from the way I introduced conditional probabilities is that they represent revisions in probability assignments. For example, delete any knowledge of "causes," and the probability that one observes outcome  $b_5$  is identical to its marginal probability, or 23.7 per cent. However, knowing that  $a_2$  has just occurred allows us to revise that estimate (upwards in this case) to a 77 per cent chance that  $b_5$  will now happen. The same knowledge about  $a_2$  induces us to amend the probability that  $b_2$  will transpire downward from 20.6 per cent to 3 per cent, etc.

It remains to relate the calculated change in probability assignment to the degree of information which it conveys. The difficulty in so doing is that information cannot be directly quantified. Rather, it can be gauged only indirectly in terms of the disappearance of its opposite, or what is variously called "uncertainty" or "surprisal."

A connection between the probability of an event occurring and the subjective response such happening evokes (surprise) is made mathematically via the logarithmic operator. More precisely, one's surprise at a particular outcome is assumed to be proportional to the negative logarithm of the probability that that outcome will transpire. Thus, if  $p(b_j)$  is the a priori probability that  $b_j$  will occur, then our surprisal when it happens is measured by  $-\log p(b_j)$ . This measure accords with intuition insofar as whenever one is absolutely certain that  $b_j$  will occur (i.e.,  $p(b_j) = 1$ ), then one's surprisal is identically zero. Conversely, if  $p(b_j)$  is very small (near zero), one is very surprised whenever it does turn up. In the latter case  $-\log p(b_j)$  is high.

If surprisal prior to knowing anything about the  $a_i$  is set to  $-\log p(b_j)$ , then it follows that surprisal after the particular  $a_i$  is revealed should become  $-\log p(b_j|a_i)$ . Any decrease in surprisal would be equal to the difference between the a priori and a posteriori surprisals, i.e.,

$$-\log p(b_j) - [-\log p(b_j|a_i)]$$

or, more simply,

$$\log [p(b_j|a_i)/p(b_j)].$$

Every combination of  $i$  and  $j$  makes such a contribution, some of which may be negative in value. However, when each term is weighted by the joint probability that  $i$  and  $j$  occur in combination, the weighted terms all sum to

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yield a nonnegative overall measure of information contained in the system of processes,

$$I = \sum_{i=1}^n \sum_{j=1}^n p(a_i, b_j) \log[p(b_j|a_i)/p(b_j)].$$

The formal name for the quantity  $I$  is the *average mutual information*.  $I$  increases in systems that are highly defined and that approximate mechanical behavior, and decreases as interference and ambiguity increase. For example, the value of  $I$  for Table 10.1 is 0.96 bits, whereas it increases to 2.00 bits for the more highly articulated system in Table 10.2.

## A NEW VIEW OF CAUSALITY

A calculus of conditional probabilities already exists, and it can be used to differentiate between strictly mechanical and more complex behaviors. But we have yet to capture the full import of Popper's propensities. He lays great emphasis, for example, on skewed behavior, such as might be exhibited in a pair of loaded dice or an uneven roulette wheel. As mentioned, he cites the need for a new view of causality, implying that the Newtonian categories of material and efficient causes are somehow insufficient for describing evolving systems. However, there seems to be little in our derivation of the "calculus of conditional probabilities" that would seem to justify his attitudes. We therefore ask whether there is anything special that could happen when "lots of things are put together in the same place" that might impart a preferred direction to evolutionary behavior?

When a process occurs in proximity to another, there are three qualitative effects each could have on the other. It could augment the other process (+); it could decrement it (-); or it could have no effect whatever (0). When one considers the reciprocal effect of the other process on the given one, there are nine pairs of possible interactions, e.g. (+-), (-0), (- -), etc. I wish to concentrate on the peculiarities of one type of interaction, namely, mutualism (++).

When manifested in a system of chemical reactions, mutualism is called "autocatalysis," a term which I shall retain as applying to more generic systems (e.g., ecosystems, economic networks, etc.). Autocatalysis is not limited to interaction pairs, but also can pertain to cycles with one or more intermediaries. For example, Figure 10.1 is a schematic representation of a four-member autocatalytic loop. An increase in the activity of any member in this loop engenders increments in the activities of all other "downstream" elements (including itself). Thus, an increase in the activity of A leads to a growth in the level of activity B, which in turn causes the rate of C to rise, and so forth, until the effect propagates back to its origin, A, i.e., it becomes self-reinforcing.

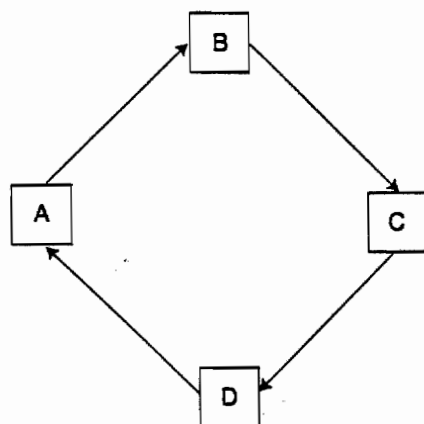


Figure 10.1 A four-member autocatalytic configuration (two intermediaries)

Most unfortunately, conventional wisdom regards autocatalysis simply as a mechanism. This outlook reflects the deterministic mentality that Popper justifiably takes to task. Autocatalysis is not mechanical in nature. It possesses intriguing properties, several of which are quite incompatible with the concept of mechanism (Ulanowicz, 1989).

To start with, autocatalytic configurations, almost 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 greater than what it would be if the compartments were decoupled.

Although the growth characteristics of autocatalysis are widely accepted it often is not recognized that an autocatalytic configuration also exerts *selection pressure* upon the characteristics of all its constituents. If a random change should occur in one member such that its catalytic effect upon the next compartment is accelerated, then the effects of that alteration will return to the starting compartment as a reinforcement of the new behavior. The opposite also holds – should a change in an element decrement its effect on downstream elements, it will be reflected upon itself in negative fashion. Thus, inherent within autocatalysis is an *asymmetry* that ratchets all participants to ever greater levels of performance. It is just such skewedness that accounts for Popper's loaded dice. In Newton's scheme every action has an equal and opposite reaction. In the world-at-large, autocatalytic configurations impart a definite sense (direction) to the behaviors of systems in which they appear.

Matters become even more unconventional when one realizes that an autocatalytic loop can define itself as the focus of a *centripetal* flow of material and resources. To see how this could happen, one need only consider the particular case where a change in a compartment accidentally



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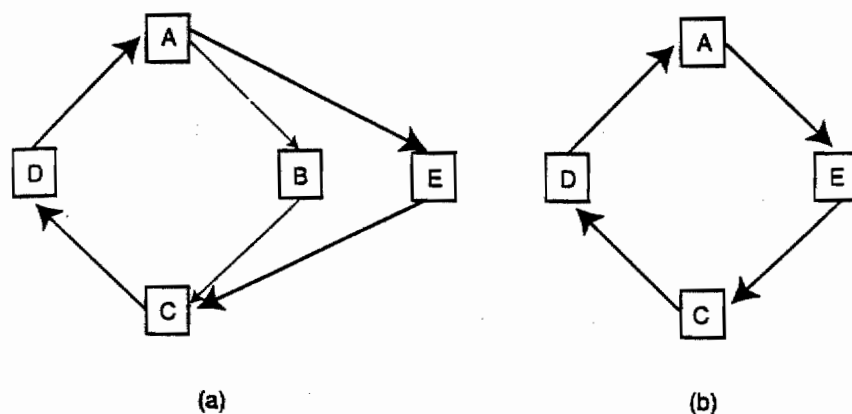


Figure 10.2 The replacement of B by E in the loop shown in Figure 10.1

brings more necessary resources into it, thereby allowing it to operate at an elevated level. By the argument in the preceding paragraph, such acquisition will be rewarded. Because this selection pressure favoring the acquisition of resources applies to all members of the configuration, the loop will become an attractor of material and energy from the world around it. Taken as a unit, the autocatalytic cycle is not simply reacting to its environment, it also actively creates its own domain of influence.

The evolutionary propensities of autocatalysis also delimit the ways in which the participants in the process configuration may be replaced. For example, if A, B, C, and D are four sequential elements comprising an autocatalytic loop, and if some element E: (1) appears by chance, (2) is more sensitive than B to catalysis by A, and (3) provides greater enhancement to C than does B; then E either will grow to dominate B's role in the loop, or will displace it altogether (Figure 10.2). Alternatively, if B should happen suddenly to disappear for whatever reason, it is, in Popper's own words, "always the existing structure of the . . . pathways that determines what new variations or accretions are possible."

By simple induction, one may proceed from replacement of B by E to the successive replacements of C, D, and A by, say, F, G, and H, until the final configuration, E-F-G-H, contains *none* of the original elements. In this sense the action of the autocatalytic loop over the long term becomes immaterial of its particular constituents. Even more importantly, the duration of the autocatalytic form is usually *longer* than that of its constituents. Lest this sound too bizarre, the reader should realize that one's own body is composed of cells (with the exception of neurons) that, on the average, did not exist seven years ago. The residences of most chemical constituents in the body are usually of even shorter duration. Yet most readers will be recognized by friends they haven't met in the last ten years.

By now it should be clear that autocatalysis is no passive mechanism. The emergence of selection pressure, centripetality and persistence, taken together, bespeak of a degree of autonomy from material constitution and mechanical constraint. Attempts to predict the life course of an autocatalytic configuration by ontological reduction to material constituents and mechanical operation are doomed over the long run to failure. If one persists in maintaining that only material and mechanical causes are legitimate for explanation, then one will remain trapped in Tolstoy's conundrum, "... the cause of the event is neither in the one nor in the other. ... Or in other words, the conception of a cause is inapplicable to the phenomena we are examining."

Popper was right, we do need a new conception of causality if we are to accommodate propensities such as are engendered by autocatalysis. To see why radical change is necessary, it helps to regard causality in a hierarchical framework. For example, in the Newtonian world we are used to observing a system at a particular level and explaining its behavior in terms of its material and mechanical components, i.e., the "bottom-up", or reductionistic approach of conventional systems analysis. Although it is usually not accorded the same emphasis, we are also familiar with the "top-down" influence that may be exerted on a system via its "boundary conditions," e.g., its environment (which often is dominated by the experimenter).

Absent from our conceptual inventory is the possibility that causation can appear *at* the focal level of observation. However, this is exactly how autocatalysis operates! Its agency is inherent in the configuration of processes *at* the scale of observation and does not derive from other levels. Of course, an autocatalytic system continues to be constrained and influenced from above and below, but I hasten to emphasize that at the same time it is the origin and locus of influence that subsequently can propagate both up and down the scale of events.

The reader will note that the agency of autocatalysis derives not from the entities composing a system, but rather from the spatial and temporal juxtaposition of processes that transpire among the elements, i.e., the kinetic *form* of the system. For this reason I have elsewhere called this agency a "formal cause." In so doing I borrowed from the lexicon of Aristotle, although I hasten to point out that the formal agency of autocatalysis differs appreciably from the formal cause posited by Aristotle.

### QUANTIFYING PROPENSITIES

Most of the ideas advanced by Popper in his latest monograph now have been elaborated. It remains to bring them all together for the purpose of defining "propensity" in clear and quantitative terms. To do this it becomes necessary to point out that we have been implicitly regarding systems as networks of connecting processes. To be sure, any system has identifiable material components, such as individual cells, organisms, populations,

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species, economic sectors, or whatever. But more importantly, these entities affect one another over threads of communication that constitute processes, e.g., exchanges of material or energy, exchanges of money, spatial displacements, exchanges of explicit information, etc. The focus in evolutionary thinking must be upon networks of processes. As Popper so delightfully put it, "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 processes, of highly active (energy-coupled) chemical pathways."

The problem with networks of processes is that often they are very difficult to quantify. For one, the sheer multitude of exchange processes usually makes the accumulation of sufficient data a formidable task. Then some exchanges simply don't lend themselves to easy mensuration — like the effect a bird's colors and morphology have upon its prey, predators and comensals. For this latter reason it is best to limit further discussion to networks of palpable exchanges, like those of energy, material or cash. In considering only palpable media the assumption is made that the effects of other, harder to measure properties are implicit in those flows we do measure. For example, the color of a population of birds could affect how successful its members are at capturing prey and how often they are eaten in turn. Both of these processes constitute palpable rates of exchange. This reduction bothers some ecologists who eschew the expression of intangibles in such "brute" terms (Engelberg and Boyarsky, 1979). Economists seem to have fewer scruples about expressing the world of human activities as a matrix of material transactions!

The relative availability of data in the fields of economics and ecology is likewise disparate. Input-output tables of commodity flows among hundreds of economic sectors abound. By contrast, quantified networks of ecological exchanges are few and usually treat communities with but several compartments, although networks of ecosystems with twenty to forty elements are beginning to appear (see Baird and Ulanowicz, 1989).

The key question to ask about networks of exchanges is how might autocatalysis tend to affect patterns of exchange among system elements? From the foregoing discussion we see its effects are basically twofold: First, autocatalysis tends to increase the aggregate amount of system activity. To quantify this effect, we let  $T_{ij}$  represent the measured transfer of medium from compartment  $i$  to compartment  $j$ . Then the aggregate community activity in an  $n$ -compartment system can be expressed as

$$T = \sum_{i=0}^n \sum_{j=1}^{n+1} T_{ij}$$

where the index value 0 (zero) identifies the source of imports from outside the system, and the value  $n + 1$  designates the destination of exports out of the system. In the parlance of economic input-output analysis  $T$  is called the "total system throughput." It is a sibling variable to the gross com-

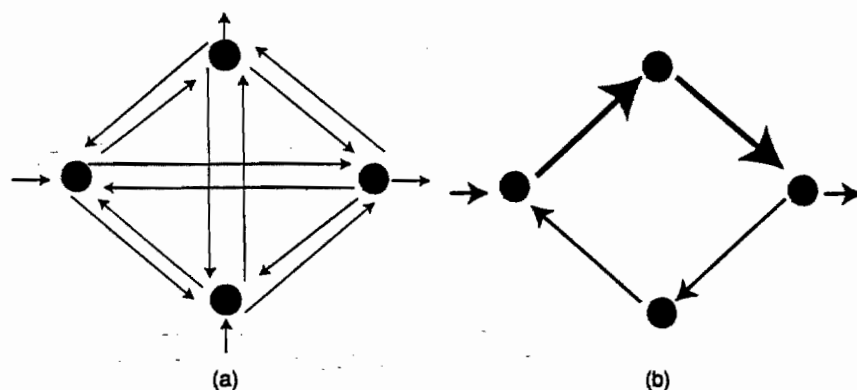


Figure 10.3 A schematic representation of the effects of autocatalysis: (a) before; (b) after.

munity (or national, as the case may be) output. Hence, one effect of autocatalysis is to increase  $T$ , the "size" or extent of the system.

The other visible effect of autocatalysis is to streamline the topology of interconnections (processes) in a way that abets those transfers that more effectively engage in autocatalysis at the expense of those showing little or no participation. In effect, as autocatalysis progresses, the network will tend to become dominated by a few intense flows. Schematically, this tendency is depicted in Figure 10.3.

In order to quantify these topological changes, one should notice that the exchange  $T_{ij}$  can be arrayed as the entry in row  $i$  and column  $j$  of a two-dimensional matrix. Then the effect of pruning connections and augmenting those remaining will be depicted as something like the transition from Table 10.1 to Table 10.2. Because flows represent aggregate discrete transfers, or events, it is only natural to estimate probabilities in terms of measured flows (viz. Rutledge *et al.*, 1976). Toward this end, we identify  $p(a_i, b_j)$  with the probability that a quantum of some medium leaves  $i$  and enters  $j$ . Because  $T$  is the aggregate of all such system transfers, we can estimate  $p(a_i, b_j)$  by  $T_{ij}/T$ . Similarly,  $p(b_j)$ , the probability that a quantum enters element  $j$ , will be estimated by  $(\sum_p T_{pj})/T$ . Finally, the conditional probability  $p(b_j|a_i)$ , that a quantum enters  $j$  after having left  $i$ , is approximated by  $T_{ij}/(\sum_k T_{ik})$ . Substituting these estimators into the definition of the average mutual information yields

$$I = \sum_{i=0}^n \sum_{j=1}^{n+1} (T_{ij}/T) \log(T_{ij}T/[\sum_p T_{pj}][\sum_k T_{ik}]).$$

That is, the average mutual information,  $I$ , quantifies the degree to which autocatalysis (and possibly other agencies) have organized the flow structure.

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The reader will notice that  $I$  is an intensive and dimensionless quantity, i.e., it depends on the system topology but not on its physical extent. However, it has been argued above that the effects of autocatalysis are both extensive and intensive – it tends to increase both the size and the organization of the flow structure. Therefore, following the lead of Tribus and McIrvine (1971), who urge information theorists to attach physical dimensions to their indices, we scale  $I$  by  $T$  to yield a network property called the system ascendancy,

$$A = T \times I = \sum_{i=0}^n \sum_{j=1}^{n+1} T_{ij} \log(T_{ij}T / [\sum_p T_{pj}][\sum_k T_{ik}]).$$

To summarize, autocatalysis is hypothesized as a formal agency that imparts a preferred direction to evolving systems. That is, in the absence of major perturbations, *autonomous systems tend to evolve in a direction of increasing network ascendancy.*

Evolution as increasing ascendancy, which appeared here as a deductive consequence of several assumptions concerning autocatalysis, originally was formulated as a phenomenological description that encapsulated diverse trends in ecological succession (Ulanowicz, 1980). Specifically, more developed ecosystems are usually comprised of a larger number of elements (species), which, in the aggregate, exchange more material and energy among themselves over less equivocal routes. Furthermore, as ecosystems undergo succession, they decrease both their losses to the external world, as well as their dependencies on imported resources (Odum, 1969). Taken individually, these changes all result in increases in a system's network ascendancy. Elsewhere, I have argued that increasing ascendancy also portrays development in economic systems (Ulanowicz, 1986).

A word of caution: Although natural progression appears to give rise to increasing ascendancy, it does not follow that a system's robustness should be equated to its ascendancy. With increasing ascendancy may come greater vulnerability to external perturbations. Furthermore, disorder and redundancy, elsewhere called system overhead (Ulanowicz, 1980), actually can contribute to system persistence. Overhead may act as a reservoir of potential adaptations available for the system to implement in response to novel perturbations.

It would not be incorrect to say that evolving systems exhibit a propensity toward higher ascendancies. However, one can be even more precise. Ascendancy is, after a fashion, a surrogate for overall system efficiency – an index of system performance. If the constituent flows are measured in terms of energy, then the resulting  $A$  has the physical dimensions of power. In fact, it was first formulated as a rough analogy to the thermodynamic Helmholtz work function (Ulanowicz, 1980, 1986).

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Power functions play a prominent role in the thermodynamics of irreversible processes. For example, Onsager (1931) showed how the entropy production of a system always could be written as the sum of terms, each of which is the magnitude of a constituent flow times its conjugate thermodynamic "force." Consider, for example, several electrolytes moving in a solution under the influence of a voltage gradient. The first set of conjugate products would be the diffusive flux of each species times the negative of its gradient in chemical potential (diffusive "force"), and the second would be the electrical flux of each ion times the negative of the imposed electrical gradient (the coulombic force). One need only sum all such products to calculate the system's rate of dissipation. The same formal procedure with a change in sign applies as well to power *production* or "work" functions.

Elsewhere, I have remarked how ascendancy is, in formal terms, a power function (Ulanowicz, 1986). The system ascendancy is the sum of products, each of which consists of a flow magnitude times a logarithmic term. In a formal sense one could identify the logarithmic term with the thermodynamic "force" that the system context exerts upon the resultant flow. However, I have never been comfortable with the notion of generalized thermodynamic forces, mostly because they cannot be formulated (or even identified!) for anything but the simplest of physical systems.

Popper now affords the overarching perspective: Those agencies we identify as forces are but a small and degenerate subset of a larger class of actors – propensities! More generally speaking, things are not always compelled (forced) to happen, but there is a greater or lesser tendency that they transpire. When "lots of things are put together in the same place," there is a propensity for or against particular events to occur.

We are led formally to identify the logarithmic terms in the ascendancy with the propensities for their conjugate process to occur. Rather than formulate the propensities in terms of flows, it is better to define them more generally in terms of joint and conditional probabilities. Accordingly, we let  $P_{ij}$  be the propensity for event  $i$ - $j$  to occur within the context of the given system.  $P_{ij}$  may be written as any one of three equivalent expressions:

$$\begin{aligned} P_{ij} &= \log[p(b_j|a_i)/p(b_j)] \\ &= \log[p(a_i, b_j)/p(a_i)p(b_j)] \\ &= \log[p(a_i|b_j)/p(a_i)]. \end{aligned}$$

Thus, all one needs to calculate the propensities in a system is a table of joint occurrences that categorizes a sufficient number of observations on its behavior.

This definition of propensity also makes intuitive sense. If  $a_i$  and  $b_j$  are completely independent, then  $p(a_i, b_j) = p(a_i) \times p(b_j)$ , and  $P_{ij} = 0$ . A value of  $P_{ij} > 0$  means that the associated process has that particular propensity to

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happen *in the given system context*. For any prescribed system configuration the count of  $P_{ij} < 0$  is usually small, especially in systems that are the result of natural evolution. The processes with negative  $P_{ij}$  do not coordinate well with the prevailing system kinetics. There is a degree of selection pressure against their happening. That they nevertheless occur is due either to chance disturbance, or to a particular limiting factor that has not been included in the system description. (For example, a particular predator-prey interaction may have a negative propensity when interactions are measured in terms of carbon flows; however, this may mask the possibility that this prey provides essential nitrogen to the predator. As mentioned earlier, processes with low or negative propensities may become major players in a system's adaptation to unforeseen changing external conditions.)

### AN EMERGING EVOLUTIONARY SYNTHESIS

Popper may have been unaware of the extent to which his desiderata already are part of emerging evolutionary theory. His sought-after "calculus of conditional probabilities" is extant in current information theory, which may be used to facilitate a quantification of propensities that accords well with observable trends in evolving systems.

Some readers might object (in good Popperian tradition) that the principle of increasing ascendancy and its attendant calculus of propensities are seeming tautologies. Just how tautologous they really are is a matter of hierarchical perspective. Rather than contend the issue, however, I am content to point out that, tautologous or not, ascendancy makes quantitative that which heretofore was only descriptive. The same critics could as well argue that the laws of thermodynamics are only tautologies, but it is hard to deny their power in making explicitly quantitative that which had been only intuitive. Beyond regretting death and taxes, one may now aspire to measure the entropy productions that thereby ensue.

Similarly, ascendancy provides the ecologist with a gauge of ecosystem status. In the event of perturbation, the size and trophic organization of the ecosystem can now be measured before and after the fact. The ascendancy and its related variables give the economist tools that are more powerful than the gross community product for judging the vitality of an economic system. The propensities of individual economic exchanges can be calculated to indicate how well that activity accords with the economic community at large.

Perhaps even more importantly, the theories of ascendancy and propensity could impart significant momentum to a new and more dynamic worldview. For science today is truly schizophrenic in its view of nature. At one extreme is the model of the world as a universal clockwork – the Cartesian and Newtonian attitude that everything is connected in rigid and deterministic sense to other elements of the universal machine. At the

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other extreme is the disconcerting inference from quantum physics that, at its core, nature is chaotic and without form.

Like Lucretius, who saw only atoms and the void, prevailing dogma provides no middle ground between the motion of the planets and the vagaries of quarks. When contemporary science applies its models to living systems, the fit is usually awkward – like the shell game of neo-Darwinism that distracts the observer from the agencies at hand by oscillating between the realms of molecule and machine.

In contrast, Popper, and others such as Peirce and Prigogine, are assuring us that the living world at the level of more immediate experience is amenable to scientific narration and quantification. Furthermore, causes of behavior there do not originate only at the edges of life and propagate inward – they can appear within its very fabric! Living beings are neither automata nor epiphenomena; some degree of autonomy is proper to each organism.

To the strict determinist, this idea of an open universe was too horrible to contemplate, like staring into the yawning abyss. They might concede that probabilities could be useful in describing confusing situations, but would argue that behind an indeterministic appearance, there lies hidden a deterministic reality. This was the motivation behind Einstein's famous quotation, "God does not play dice!" It appears that Popper is now responding to his hero: "God plays dice all right. But not to worry – they're loaded!"

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