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Quantifying Constraints upon Trophic and Migratory Transfers in Landscapes

Robert E. Ulanowicz

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Ecosystems are neither machines nor superorganisms, but rather open systems that require a "calculus of conditional probabilities" to quantify. Autocatalysis, or indirect mutualism, as it occurs in causally open systems, may act as a nonmechanical, formal agency (sensu Aristotle) that imparts organization to systems of trophic exchanges. The constraints that autocatalysis exerts upon trophic flows can be quantified using information theory via a system-level index called the ascendency. This quantity also gauges the organizational status of the ecological community. In addition, the ascendency can be readily adapted to quantify the patterns of physical movements of biota across a landscape. In particular, one can use ascendency to evaluate the effects of constraints to migration, even when the details of such constraints remain unknown.

Introduction

In his recent critique of ecology, Peters (1991) warns ecologists to pursue only those concepts that are fully operational. In a strict sense, a concept is fully operational only when a well-defined protocol exists for making a series of

measurements that culminate in the assignment of a number, or suite of numbers, that quantifies the major elements of the idea. Can the ascendency description of ecosystem development be applied to spatial heterogeneities in ecosystems in a way that will yield fruitful insights and/or predictions?

In a recent book (Ulanowicz 1997) I attempted to articulate the full meaning, import, and application of "ecosystem ascendency" as a quantitative description of development in ecosystems. But the section in that volume that dealt with spatial heterogeneities is notable for its brevity and dearth of specific examples. Whence the attempt through what follows to elaborate more fully the potential for employing information theory in landscape ecology. Before proceeding with quantitative definitions, however, it would be helpful to review briefly the conceptual background into which any theory of ecosystems must fit.

Conceptual Background for Ecosystems

According to Hagen (1992), three metaphors have dominated the description of ecosystems (Figure 8.1): (1) the ecosystem as machine (Clarke 1954; Connell and Slatyer 1977; Odum 1971); (2) as organism (Clements 1916; Shelford 1939; Hutchinson, 1948; Odum 1969); and (3) as stochastic assembly (Gleason 1917; Engelberg and Boyarsky 1979; Simberloff 1980). Hagen portrays the debates among the schools that champion each analogy in terms of a three-way dialectic—an antagonistic win/lose situation. He sees, for example, the
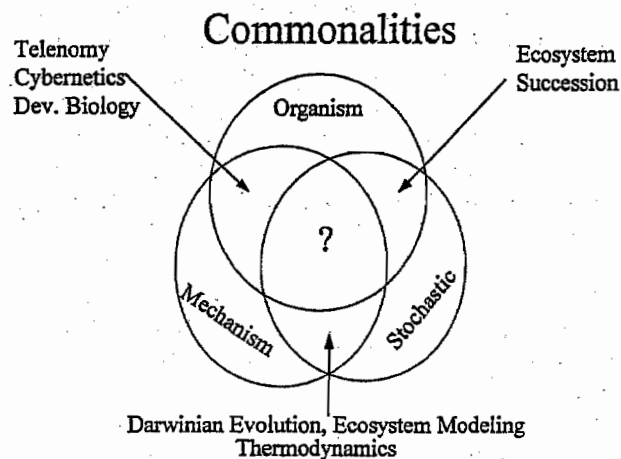
FIGURE 8.1
A Venn diagram depicting overlaps among the three major metaphors for ecosystems. (After Hagen 1992. With permission.)

holistic vision of Hutchinson and E.P. Odum as having been gradually displaced during the 1950s and 1960s by the disciples of the neo-Darwinian/nominalist synthesis.

By way of contrast, Golley (1993) believes that holism in ecology is alive and well. According to Depew and Weber (1994), for example, Clements inadvertently provided the nominalists with lethal ammunition by casting the ecosystem as a "superorganism." Apparently, Clements conflicted physical size and extent with organizational complexity in drawing his unfortunate analogy. If, however, one reverses Clements' phraseology and instead characterizes "organisms as superecosystems," then much of the criticism against holism in ecology is circumvented.

It is pressing the ecosystem metaphors beyond their intended limits that causes many to regard these images as mutually exclusive, and to conclude that truth can lie in only one corner of the triangle, none of which is to suggest that reality (insofar as we are capable of perceiving it) occupies the middle ground. Rather it is to perceive nature as being somewhat more complicated than has heretofore been assumed, and to propose that any adequate description of development in living systems must be *overarching* with respect to simplistic analogs.

As a first step towards amalgamating these analogies, it is useful to consider the commonalities and differences among the metaphors. Of the three, the one most familiar to readers is bound to be the mechanical, for it is the analogy that has driven most of modern science. Depew and Weber (1994) (see Table 8.1) cite four assumptions that undergird the Newtonian worldview: (1) the domain of causes for natural phenomena is *closed*. More specifically, only material and mechanical causes are legitimate in scientific discourse. (2) Newtonian systems are *atomistic*. That is, they can be separated into parts; the parts can be studied in isolation; and the descriptions of the parts may be recombined to yield the behavior of the ensemble. (3) The laws of nature are *reversible*. Substituting the negative of time for time itself leaves any Newtonian law unchanged. (For example, a motion picture of any Newtonian event, when run backwards, cannot be distinguished from the event itself.) (4) Events in the natural world are inherently deterministic. So long as one is able to describe the state of a system with sufficient precision, the laws of nature allow one to predict the state of the system into the future with arbitrary accuracy. Any failure to predict must result from a lack of knowledge.

To Depew and Weber's four pillars of Newtonianism one must add a fifth assumption, *universality* (Ulanowicz 1997). Newtonian laws are considered valid at all scales of space and time. Whence, physicists have no qualms (as perhaps they should) about mixing quantum phenomena with gravitation (Hawking 1988).

When one regards the nominalists' presuppositions, we find them more simple still. Stochasticists agree with Newtonian that causality is closed (only material and mechanical forms allowed) and that systems are atomistic (virtually by definition). But they regard the remaining three assumptions as

TABLE 8.1

Comparisions of Outlooks

Mechanism (Newtonianism)	Organism (Holism)	Stochasticism (Nominalism)
Material, Mechanical	Material, Mechanical Formal, Final	Material, Mechanical
Atomistic	Integral	Atomistic
Reversible	Irreversible	Irreversible
Deterministic	Plastic	Indeterminate
Universal	Hierachial	Local

unnecessarily restrictive and so consider events to be irreversible, indeterminate, and local in nature.

The organismal or holistic worldview differs most from the other two and requires elaboration. Critics of holism, of course, will immediately invoke Occam's Razor as they inveigh against what they regard as wholly unnecessary (and, in their own eyes, illegitimate) introductions. One must bear in mind, however, that Occam's Razor is a double-edged blade, and that those too zealous in its application always run the risk of committing a Type-2 error by excising some wholly natural elements from their narratives.

Unlike the second Newtonian axiom, organic systems (again, almost by definition) are not atomistic, but integral. One cannot break organic systems apart and achieve full knowledge of the operation of the ensemble operation by observing its parts in isolation. Common experience provides no reason why organic systems should be considered reversible. As regards determinacy, in this instance the organic view does lie midway between the other two. The prevailing holistic attitude would probably describe organic systems as "plastic." One may foretell their form and behavior up to a point, but there exist considerable variations among individual instantiations of any type of system or phenomenon. This degree of "plasticity" may vary according to type of system. For example, the Clementsian description of ecosystems as superorganisms implied a strong degree of mechanistic determinism, whereas Lovelock's (1979) description of how the global biome regulates physical conditions on earth appears quite historical by comparison.

But what of causal closure? If causes other than mechanical or material may be considered, does this not automatically characterize the organic description as vitalistic or transcendental? Certainly, to introduce the transcendental into scientific discourse would be to defy convention, but it will suffice simply to point out that the idea of closure is decidedly a modern one. Aristotle, for example, proposed an image of causality more complicated than the current restricted notions. He taught that a cause could take any of four essential forms: (1) material, (2) efficient or mechanical, (3) formal, and (4) final. Any event in nature could have as its causes one or more of the four types. One example is that of a military battle. The material causes of a battle are the weapons and ordnance that individual soldiers use against their enemies. Those soldiers, in turn, are the efficient causes, as it is they who actually

swing the sword, or pull the trigger to inflict unspeakable harm upon each other. In the end, the armies were set against each other for reasons that were economic, social, and/or political in nature. Together they provide the final cause or ultimate context in which the battle is waged. It is the officers who are directing the battle who concern themselves with the formal elements, such as the juxtaposition of their armies via-a-vis the enemy in the context of the physical landscape. It is these latter forms that impart shape to the battle.

The example of a battle also serves to highlight the hierarchical nature of Aristotelean causality. All considerations of political or military rank aside, soldiers, officer, and heads of state all participate in the battle at different scales. It is the officer whose scale of involvement is most commensurate with those of the battle itself. In comparison, the individual soldier usually affects only a subfield of the overall action, whereas the head of state influences events that extend well beyond the time and place of battle. It is the formal cause that acts most frequently at the "focal" level of observation. Efficient causes tend to exert their influence over only a small subfield, although their effects can be propagated up the scale of action, while the entire scenario transpires under constraints set by the final agents. Thus, three contiguous levels of observation constitute a fundamental triad of causality, all three elements of which should be apparent to the observer of any physical event (Salthe 1993). It is normally (but not universally, e.g., Allen and Starr 1982) assumed that events at any hierarchical level are contingent upon (but not necessarily determined by) material elements at lower levels.

One casualty of a hierarchical view on nature is the notion of universality. The belief that models are to be applicable at all scales seems peculiar to physics. If a physicist's model should exhibit a singularity whereby a phenomenon of cosmological proportions, such as a black hole, might exist at an infinitesimal point in space, then everyone soberly entertains such a possibility. Ecology teaches its practitioners a bit more humility. Any ecological model that contains a singular point is assumed to break down as that particular value of the independent variable is approached. It is patently assumed that some unspecified phenomenon more characteristic of the scale of events in the neighborhood of the singularity will come to dominate affairs there. Under the lens of the hierarchical view, the world appears not uniformly continuous, but rather "granular." The effects of events occurring at any one level are assumed to have diminishingly less impact at levels further removed.

Not Quite a Mechanism

Abandoning universality seems at first like a formula for disaster. What with different principles operant at different scales, the picture appears to grow intractable. But upon further reflection it should become clear that the hier-

archical perspective actually offers the possibility to contain the consequences of anomalies or novel, creative events within the hierarchical sphere in which they arise. By contrast, the Newtonian viewpoint, with its universal determinism, left no room whatsoever for anything truly novel to occur. The changes it dealt with, such as those of position or momenta, appear superficial in comparison to the ontic changes one sees among living systems. That is, in the hierarchical world something truly new can happen at a particular level without causing events at distant scales to run amok.

Darwin hewed closely to the Newtonian sanctions of his time. It was therefore a looming catastrophe for evolutionary theory when Mendel purported that variation and heritability were discrete, not continuous in nature. For with discontinuity comes unpredictability and history. The much reputed "grand synthesis" by Ronald Fisher et al. sought to stem the hemorrhaging of belief in Darwinian notions by assuming that all discontinuities were confined to the netherworld of genomic events, where they occurred in complete isolation from each other. Fisher's synthesis was an exact parallel to the earlier attempt by Boltzman and Gibbs to reconcile chance with newtonian dynamics in what came to be called "statistical mechanics" (Depew and Weber 1994).

It appears to be belief and not evidence that confines chance and stochastic behavior to minuscule scales. For, if all events above the physical scale of genomes are deterministic, then one should be able to map unambiguously from any changes in genomes to corresponding manifestations at the macroscale of the phenomes. It was to test exactly this hypothesis that Sidney Brenner and numerous colleagues expended millions of dollars and years of labor (Lewin 1984). Perhaps the most remarkable thing to emerge from this grand endeavor was the courage of the project leader, who ultimately declared,

> An understanding of how the information encoded in the genes relates to the means by which cells assemble themselves into an organism...still remains elusive...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 try to discover the principles of organization, how lots of things are put together in the same place.* [Italics added.]

In a vague way Brenner is urging that we reconsider the nature of causality. In fact, some very influential thinkers, such as Charles S. Peirce, long ago have advocated the need to abandon causal closure. In doing so they were not merely suggesting that the ancient notions of formal and final causes be rehabilitated (as has been recommended by Rosen [1985]). None other than Karl R. Popper, whom many regard as a conservative figure in the philosophy of science, has stated unequivocally that we need to forge a totally new perspective on causality, if we are to achieve an "evolutionary theory of knowledge."

To be more specific, Popper (1959) claims we inhabit an "open" uni-verse—that chance is not just a matter of our inability to see things in suffi-cient detail. Rather, indeterminacy is a basic feature of the very nature of our universe. It exists at *all* scales—not just the submolecular. For this reason, Popper says we need to generalize our notion of "force" to account for such indeterminacy. Forces deal with determinacy: if A, then B—no exceptions! What we are more likely to see under real-world conditions, away from the laboratory or the vacuum of space, Popper (1990) suggests, are the "propen-sities" for events to follow one another: If A, then probably B. But the way remains open for C, D, or E at times to follow A. Popper hints that his pro-pensities are related to (but not necessarily identical to) conditional probabil-ities. Thus, if A and B are related to each other in Newtonian fashion, then $p(B \mid A) = 1$. But under more general conditions, $p(B \mid A) < 1$. Furthermore, $p(C \mid A)$, $p(D \mid A)$, etc. > 0.

Popper highlights two other features of propensities: (1) They may change with time. (2) Only forces exist in isolation; propensities do not. In particular, propensities exist in proximity to and interact with other propensities. The end result is what we call development or evolution. Changes of this nature are beyond the capabilities of Newtonian description.

What Popper does not provide is a concrete way to quantify, and therefore make operational, his notion of propensity. He states only, "We need to develop a calculus of conditional probabilities." So we are left to ask what can happen when lots of propensities "are put together in the same place", to use Brenner's words? How does one quantify the result? In what way do condi-tional probabilities enter the calculus? How does the idea of propensity relate to the Aristotelian concepts of formal and final causes?

We begin our investigation into these issues first by concentrating on what might happen when lots of processes occur in proximity. To do this we take a lead from Odum (1959) and consider all qualitative combinations of how any two processes may affect each other. Thus, process A might affect B by enhanc-ing the latter (+), decrementing it (-), or it could have no effect whatsoever on B (0). Conversely, B could affect A in the same three ways. Hence, there are nine possibilities for how A and B can interact: (+,+), (+,-), (+,0), (-,-), (-,+), (-,0), (0,0), (0,+), and (0,-). We wish to argue that, in an open universe, the first com-bination, mutualism (+,+), contributes toward the organization of an ensemble of life processes in ways quite different from the other possibilities; and, fur-thermore, that it induces the ensemble to exhibit properties that are decidedly nonmechanical in nature. Mutualism is the glue that binds the answers to our list of questions into a unitary description of development.

When mutualisms exist among more than two processes, the resulting con-stellation of interactions has been characterized as "autocatalysis." A three-component example of autocatalysis is illustrated schematically (Figure 8.2). The plus sign near the box labeled B indicates that process A has a propensity to enhance process B. B, for its part, exerts a propensity for C to grow, and C, in its turn, for A to increase in magnitude. Indirectly, the action of A has a pro-pensity to increase its own rate and extent—whence "autocatalysis."
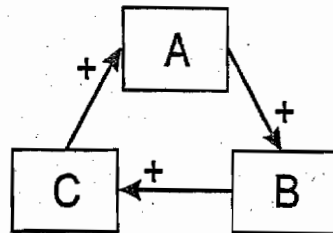
FIGURE 8.2
Schematic of a three-component autocatalytic cycle.

A convenient example of autocatalysis in ecology is the community of processes connected with the growth of macrophytes of the genus *Utricularia*, or the bladderwort family (Bosserman 1979). Species of this genus inhabit freshwater lakes over much of the world, and are abundant especially in subtropical, nutrient-poor lakes and wetlands. A schematic of the species *U. floridana*, common to karst lakes in central Florida, is depicted (Figure 8.3). Although *Utricularia* plants sometimes are anchored to lake bottoms, they do not possess feeder roots that draw nutrients from the sediments. Rather, they absorb their sustenance directly from the surrounding water. One may identify the growth of the filamentous stems and leaves of *Utricularia* into the water column with process A mentioned above.
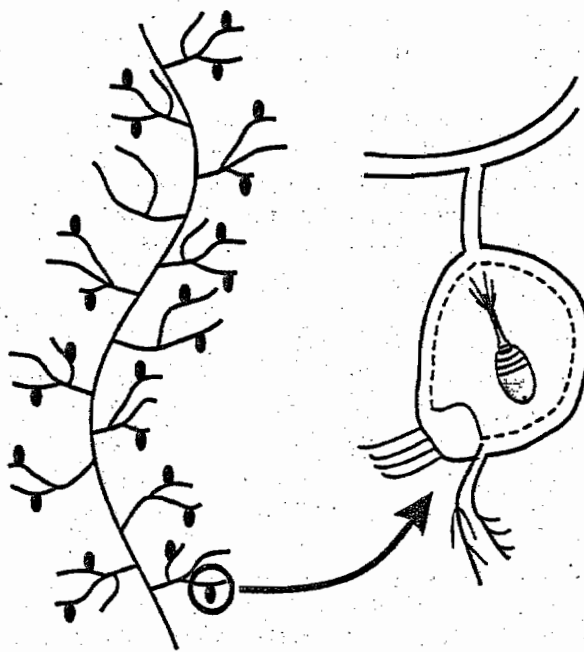
FIGURE 8.3
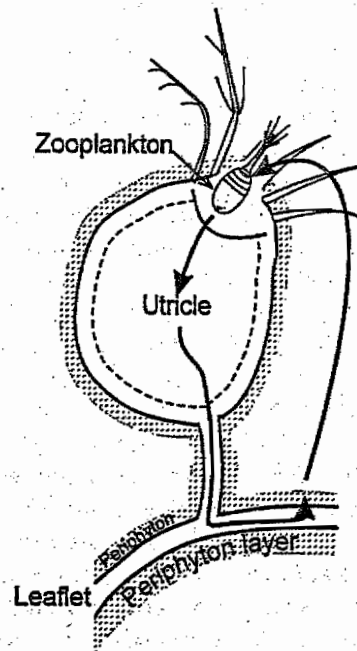Rough sketch of a "leaf" of the species *Utricularia floridana*.

FIGURE 8.4
An autocatalytic cycle in *Utricularia* systems.

Upon the leaves of the bladderworts invariably grows a film of bacteria, diatoms, and blue-green algae that collectively are known as periphyton. Bladderworts are never found in the wild without their accoutrement of periphyton. Apparently, the only way to raise *Utricularia* without its film of algae is to grow its seeds in a sterile medium (Bosserman 1979). Suppose we identify process B with the growth of the periphyton community. It is clear, then, that bladderworts provide an areal substrate which the periphyton species (not being well adapted to growing in the pelagic, or free-floating mode) need to grow.

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

absorbed by the surrounding bladder walls. The cycle (Figure 8.2) is now complete (Figure 8.4).

Because the example of indirect mutualism provided by *Utricularia* is so colorful, it becomes all too easy to become distracted by the mechanical-like details of how it, or any other example of mutualism, operates. The temptation naturally arises to identify such autocatalysis as a "mechanism," as it is referred to in the field of chemistry. In the closed world of mechanical-like reactions and fixed chemical forms, such characterization of autocatalysis is legitimate. It becomes highly inappropriate, however, in an open universe, such as a karst lake, where connections are probabilistic and forms can exhibit variation. There autocatalysis can exhibit behaviors that are decidedly nonmechanical. In fact, autocatalysis under open conditions can exhibit any or all of eight characteristics, which, taken together, separate the process from conventional mechanical phenomena (Ulanowicz 1997).

To begin with, autocatalytic loops are (1) *growth enhancing*. An increment in the activity of any member engenders greater activities in all other elements. The feedback configuration results in an increase in the aggregate activity of all members engaged in autocatalysis over what it would be if the compartments were decoupled. In addition, there is the (2) *selection pressure* which the overall autocatalytic form exerts upon its components. For example, if a random change should occur in the behavior of one member that either makes it more sensitive to catalysis by the preceding element or accelerates its catalytic influence upon the next compartment, then the effects of such alteration will return to the starting compartment as a reinforcement of the new behavior. The opposite is also true. Should a change in the behavior of an element either make it less sensitive to catalysis by its instigator or diminish the effect it has upon the next in line, then even less stimulus will be returned via the loop.

Unlike Newtonian forces, which always act in equal and opposite directions, the selection pressure associated with autocatalysis has the effect of (3) *breaking symmetry*. Autocatalytic configurations impart a definite sense (direction) to the behaviors of systems in which they appear. They tend to ratchet all participants toward ever greater levels of performance.

Perhaps the most intriguing of all attributes of autocatalytic systems is the way they affect transfers of material and energy between their components and the rest of the world. Figure 8.2 does not portray such exchanges, which generally include the import of substances with higher exergy (available energy) and the export of degraded compounds and heat. What is not immediately obvious is that the autocatalytic configuration actively recruits more material and energy into itself. Suppose, for example, that some arbitrary change happens to increase the rate at which materials and exergy are brought into a particular compartment. This event would enhance the ability of that compartment to catalyze the downstream component, and the change eventually would be rewarded. Conversely, any change decreasing the intake of exergy by a participant would ratchet down activity throughout the loop.

The same argument applies to every member of the loop, so that the overall effect is one of (4) *centripetality*, to use a term coined by Sir Isaac Newton.

By its very nature autocatalysis is prone to (5) *induce competition*, not merely among different properties of components (as discussed above under selection pressure), but its very material and (where applicable) mechanical constituents are themselves prone to replacement by the active agency of the larger system. For example, suppose A, B, and C are three sequential elements comprising an autocatalytic loop (Figure 8.2), and that some new element D: (a) appears by happenstance, (b) is more sensitive to catalysis by A, and (c) provides greater enhancement to the activity of C than does B. Then D either will grow to overshadow the role of B in the loop, or will displace it altogether. In like manner one can argue that C could be replaced by some other component E, and A by F, so that the final configuration D-E-F would contain none of the original elements. It is important to notice in this case that the characteristic time (duration) of the larger autocatalytic form is longer than that of its constituents.

The appearance of centripetality and the persistence of form beyond constituents make it difficult to maintain hope for a strictly reductionist, analytical approach to describing organic systems. Although the system requires material and mechanical elements, it is evident that some behaviors, especially those on a longer time scale, are, to a degree, (6) *autonomous* of lower level events (Allen and Starr 1982). Attempts to predict the course of an autocatalytic configuration by ontological reduction to material constituents and mechanical operation are, accordingly, doomed over the long run to failure.

It is important to note that the autonomy of a system may not be apparent at all scales. If one's field of view does not include all the members of an autocatalytic loop, the system will appear linear in nature. One can, in this case, seem to identify an initial cause and a final result. The subsystem can appear wholly mechanical in its behavior. For example the phycologist who concentrates on identifying the genera of periphyton found on *Utricularia* leaves would be unlikely to discover the unusual feedback dynamics inherent in this community. Once the observer expands the scale of observation enough to encompass all members of the loop, however, then autocatalytic behavior with its attendant centripetality, persistence, and autonomy (7) *emerges* as a consequence of this wider vision.

Finally, it should be noted that an autocatalytic loop is itself a kinetic form, so that any agency it may exert will appear as a (8) *formal* cause in the sense of Aristotle.

One may summarize these various effects of autocatalysis in thermodynamic terms as either extensive or intensive in nature. Extensive system properties pertain to the size of a system, whereas intensive attributes refer to those qualities that are structural and independent of system size. Thus, growth enhancement is decidedly extensive. The remaining properties are intensive and serve to prune from the kinetic structure of the system those pathways that less effectively participate in autocatalysis. The augmented flow activity is progressively constrained to flow along the (autocatalytically)
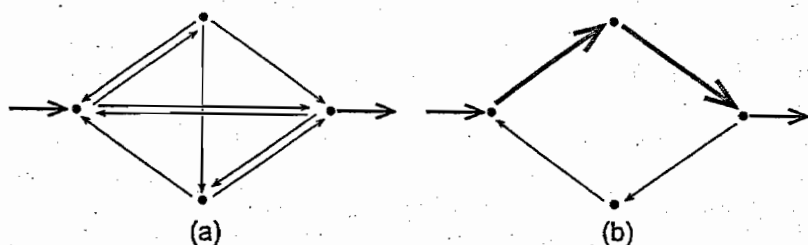
FIGURE 8.5
Schematic depiction of the effects that autocatalysis exerts upon networks. (a) Before;
(b) After.

more efficient routes as the system "develops." The combination of extensive
increase in system activity and intensive system development is depicted
schematically (Figure 8.5).

Quantifying Kinetic Constraints

Properties of systems do not truly enter scientific dialog until they have been
made fully operational. That is, until it becomes possible to quantify and
measure the effects of autocatalysis upon a system, all talk about organiza-
tion and development in living systems remains purely speculative. In order
to ensure that at least some identifiable cause (material causality) will always
remain explicit in our system description, we choose to quantify only those
relationships between compartments that can be measured in terms of a pal-
pable exchange of some material constituent, such as carbon, energy, nitro-
gen, or phosphorus. No one is assuming that these exchanges are the only
ones, nor even the most important ones, that transpire in the system and give
it its form. Whatever the actual natures of the causal events, however, their
effects will be manifested as changes in the material transactions among the
members of the community.

Accordingly, we define T_{ij} as the amount of the chosen medium that is
donated by prey i to predator j per unit space per unit time. As explained
above, not all exchanges are among the n system components. Exogenous
transfers also must be accounted. Thus, we will assume that imports from
outside the system originate in taxon 0 (zero). Furthermore, we will distin-
guish two types of outputs from the system: material that is exported in a
form still usable to some other system of comparable size will be assumed to
flow to component $n + 1$, whereas material that has been reduced to some
marginally useful "ground state" (e.g., carbon dioxide) will be accounted as
flowing to compartment $n + 2$.

The material assumption and the exhaustive accounting scheme just described make possible the quantification of both the extensive and intensive effects of autocatalysis. To quantify the extensive changes is almost trivial. By a change in system activity is meant any fluctuation in the aggregate of all transactions currently underway. In economic theory this sum is called the "total system throughput" and will appear as

$$T_. = \sum_{i,j} T_{ij} \tag{1}$$

where a dot in place of a subscript indicates that particular subscript has been summed over all components from 0 to n + 2. It follows that any increase in the level of system activity will be reflected as a rise in $T_.$.

Changes in the intensive character of a system are somewhat more difficult to quantify, but the effort is crucial, because in doing so we are addressing the crux of this essay—the quantification of system constraints. We begin this task by first turning our attention to the lack of constraint, or the *indeterminacy* of event i. Such indeterminacy was quantified more than a century ago by Ludwig von Boltzmann

$$S_i = -k \log p(A_i), \tag{2}$$

where $p(A_i)$ is the probability of event A_i happening, k is a scalar constant, and S_i is the *(a priori)* indeterminacy associated with i. Sometimes S_i is called the surprisal of A_i, because, if the probability of A_i is very small (near zero), we become very surprised when it does occur (S_i is large.)

We now try to follow Brenner's advice and quantify what happens when lots of things are put together. Specifically, we ask "How is the indeterminacy of A_i changed whenever event B_j has just occurred?" Or, in terms that pertain more to this essay, "By how much does the presence of B_j *constrain* event A_i?" By "constrain" we mean "decrease the indeterminacy" of A_i. When B_j precedes A_i, any constraint that it exerts upon the latter will be reflected by a change in probability that A_i will occur. This altered probability is nothing other than the conditional probability of A_i, given B_j. Thus, indeterminacy has been diminished to

$$S_{ij} = -k \log p\left(A_i \middle| B_j\right), \tag{3}$$

where S_{ij} is now the *a posteriori* indeterminacy of A_i given B_j. Accordingly, the reduction in indeterminacy that is calculated by subtracting S_{ij} from S_i becomes a measure of the constraint that B_j exerts on A_i. Remembering that the negative of a logarithm is equal to the logarithm of the reciprocal of its argument, and that the difference between two logarithms is the same as the logarithm of the quotient of the two arguments, we find that S_i - S_{ij} becomes

$$S_i = S_{ij} = k \log\left[p\left(A_i \middle| B_j\right) \middle/ p\left(A_i\right)\right]. \tag{4}$$

Here we note that Bayes' Theorem allows one to calculate $p(A_i \mid B_j)$ as the quotient of $p(A_i, B_j)$ by $p(B_j)$, where $p(A_i, B_j)$ is the joint probability that Ai and B_j occur in combination. Whence, (4) may be rewritten in the more symmetrical form,

$$S_i - S_{ij} = k \log\left[p\left(A_i, B_j\right) \middle/ p\left(A_i\right)p\left(B_j\right)\right] \tag{5}$$

Because A_i and B_j are any arbitrary pair of events, it becomes an easy matter to calculate the average amount of constraint that all system elements exert upon each other. One simply multiplies Equation 5 for each combination i and j by the probability that A_i and B_j co-occur and sums over all combinations of i and j. The resulting "average mutual constraint" looks like

$$k \sum_{i,j} p\left(A_i, B_j\right) \log\left[p\left(A_i, B_j\right) \middle/ p\left(A_i\right)p\left(B_j\right)\right] \tag{6}$$

To make Equation 6 operational it remains only to estimate the three probabilities in terms of measured quantities. If one regards the trophic exchanges as entries in an events matrix, then it would follow immediately that:

$$p\left(A_i, B_j\right) \sim T_{ij}/T_{..}$$

$$p\left(A_i\right) \sim T_i/T_{..} \tag{7}$$

$$p\left(B_j\right) \sim T_j/T_{..}$$

Substituting Equation 7 into Equation 6 yields

$$AMI = k \sum_{i,j} \left(T_{ij}/T_{..}\right) \log\left[T_{ij}T_{..}/T_iT_j\right], \tag{8}$$

where AMI is the "average mutual information" of information theory. ("Information" and "constraint" are interchangeable in information theory.) Two familiar results from information theory are that AMI is intrinsically non-negative and that it is bounded from above by the index

$$H = -k \sum_{i,j} \left(T_{ij}/T_{..}\right) \log\left(T_{ij}/T_{..}\right) \tag{9}$$

where H is the overall indeterminacy of the flow structure (Ulanowicz and Norden 1990).

The reader is encouraged to apply Equation 8 to any variety of flow network configurations to convince oneself that the AMI accurately measures the intensive change in kinetic structure from that in Figure 8.5a to the one in Figure 8.5b. A hypothetical example is given (Figure 8.6).
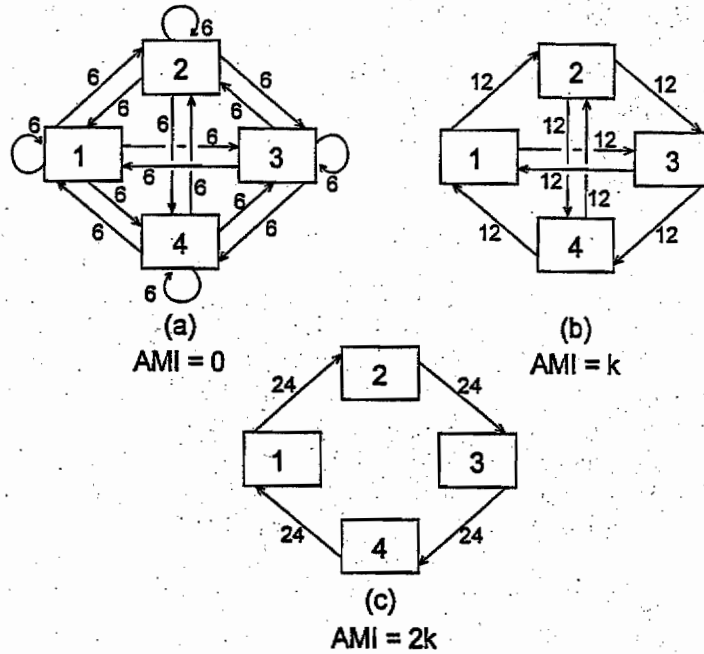

FIGURE 8.6

Three hypothetical networks illustrating how average mutual information (AMI) increases with the degree of network pruning.

The results of the calculations (Figure 8.6) are presented in terms of units of k, which have yet to be specified. The usual convention in information theory is to choose a base for the logarithms (either 2, e, or 10), set k = 1, and call the resulting units "bits," "napiers," or "hartleys," respectively. Doing thusly would leave us with two separate measures for the extensive and intensive attributes of flow networks. Both properties are strongly influenced, however, by a single process—the autocatalysis. We therefore emphasize the unitary origin of changes in both aspects by following the advice of Tribus and McIrvine (1971); we use the scalar factor k to impart physical dimensions to our measure of constraint. Setting k = $T_{..}$ in Equation 8 gives

$$A = \sum_{i,j} T_{ij} \log\left(T_{ij} T_{..} / T_{i.} T_{.j}\right) \tag{10}$$

where the scaled index, A, is renamed the system "ascendency." It is an amalgamated measure of the tendency for a system to increase in both activity and structure (constraint) via internal autocatalysis.

We note that the ascendency is fully operational, as the formula for A consists entirely of measurable quantities. That is, for each and every fully quantified network of trophic exchanges, one may calculate a unique value of A. After one evaluates a number of networks in this fashion, it becomes apparent that certain network attributes are associated with increases in A. These include: (1) specialization, (2) speciation, (3) internalization, and (4) cycling. These same properties, however, are recognized as the broad categories that group the 24 attributes identified by Odum (1969) to characterize the late successional stages of a developing ecosystem. One is prompted, then, to suggest as a phenomenological principle:

> In the absence of major perturbations, ecosystems naturally tend towards configurations of ever-greater ascendency.

Before applying ascendency to spatially heterogeneous ecosystems, it is important to stress two points. The first is that increasing ascendency is only one half of the development story. Ascendency encompasses all that is efficient and productive about the network configuration. Although we have cited the inclination for a system to progress in this direction, it cannot be overemphasized that this tendency is often desultory and at times could culminate in the destruction of the system. For increasing ascendency tells only what happens in the absence of relatively heavy perturbations. Should the system progress too far in the direction of increasing efficiency, it will become "brittle" (Holling 1986) and lack the flexibility to adapt whenever the system is impacted by novel disturbances.

Fortunately, one can readily construct a complement to ascendency using quantities already defined. One recalls that the average mutual information was bounded by the Quantity 9 (which, effectively, quantifies the diversity of system flows). This indeterminacy may be scaled by T in exactly the same manner as was done to the AMI. The result, called the system capacity, becomes an upper bound on the ascendency. The amount by which this capacity exceeds the ascendency is called the system "overhead", and it quantifies all the inefficient, indeterminate, and diffuse processes that remain in the system. The capacity also includes the degrees of freedom inherent that the system can use to reconfigure in the aftermath of a significant perturbation. Without sufficient overhead, a system is doomed to death or major collapse.

The second issue concerns the role of biomasses or stocks in system development. The ascendency as formulated above contains no explicit mention of taxon bemuses. Yet classical dynamics suggest that stocks cannot be entirely ignored. Fortunately, a way was recently discovered to incorporate stocks of components into the ascendency in a manner that accords with the

requirements of information and probability theories (Ulanowicz and Abarca–Arenas 1997). The new formulation for the ascendency is

$$A = \sum_{i,j} T_{ij} \log\left[T_{ij} B^2 / B_i B_j T_\cdot\right]$$ (11)

where B_i is the biomass of component i. Definition 11 will be employed to calculate the ascendency in the remainder of this paper.

Landscapes of Flows

If ascendency theory as presented here should seem a bit abstract, the reader should find compensation in knowing that abstractness carries with it broad generality. For example, the flow T_{ij} was defined as the trophic exchange from prey i to predator j. It could just as well represent the movement of a given amount of a species from spatial position i to location j. Similarly, B_i could represent the density of the given population at location i. When one substitutes these new variables into Equation 11, the ascendency that results now applies to the migration of the given population over the landscape. The ascendency hypothesis as it pertains to migration translates into:

> In the absence of massive perturbations, the populations of an ecosystem distribute themselves across a landscape in a way that leads progressively to higher system ascendencies.

(It should be noted in passing that it is likewise possible to apply the ascendency measure to several populations migrating across a landscape while simultaneously engaging in trophic interactions at each point in space ([Ulanowicz 1997].)

It is the utility of applying ascendency-like variables to biotic movements across landscapes that we wish to explore in the remainder of this essay. In the interest of simplicity, it will help if we keep the landscape rather simplistic. Toward this end, we will consider a 10 ¥ 10 grid of spatial elements upon which we will run five separate models in the manner of cellular automata (CA). The elements of the two-dimensional spatial array will be numbered sequentially by a single running index (Figure 8.7). To simplify the boundary conditions at the edges of the landscape, we shall assume that the edges "wrap around" in both the horizontal and vertical directions. That is, transport beyond the "eastern" (right-hand) edge of the domain will feed into the western margin, as shown in the figure.

The first model simulates nearest neighbor diffusion. Material or organisms in adjacent cells exchange material across their common boundary at a

	91	92	93	94	95	96	97	98	99	100	
10	1	2	3	4	5	6	7	8	9	10	1
20	11	12	13	14	15	16	17	18	19	20	11
30	21	22	23	24	25	26	27	28	29	30	21
40	31	32	33	34	35	36	37	38	39	40	31
50	41	42	43	44	45	46	47	48	49	50	41
60	51	52	53	54	55	56	57	58	58	60	51
70	61	62	63	64	65	66	67	68	69	70	61
80	71	72	73	74	75	76	77	78	79	80	71
90	81	82	83	84	85	86	87	88	89	90	81
100	91	92	93	94	95	96	97	98	99	100	91
	1	2	3	4	5	6	7	8	9	10	

FIGURE 8.7
The numbering scheme used in a 10 × 10 gridwork of landscape elements. Marginal rows and columns illustrate the "wrap-around" boundary conditions.

rate that is proportional to the difference in population density or biomass across that same boundary. Thus, for any time step we calculate in the horizontal (west–east) direction,

$$T_{i-1,i} = D\left(B_{i-1} - B_i\right)$$
$$T_{i,i+1} = D\left(B_i - B_{i+1}\right) \tag{12a}$$

and in the vertical (north–south) direction,

$$T_{i-10,i} = D\left(B_{i-10} - B_i\right)$$
$$T_{i,i+10} = D\left(B_i - B_{i+10}\right) \tag{12b}$$

(where D is a constant coefficient of exchange). The biomasses at all locations are thereafter incremented in the fashion

$$B_i* = B_i + T_{i-1,i} - T_{i,i+1} + T_{i-10,i} - T_{i,i+10}, \tag{13}$$

where B_i* becomes the biomass at gridpoint i during the next iteration.
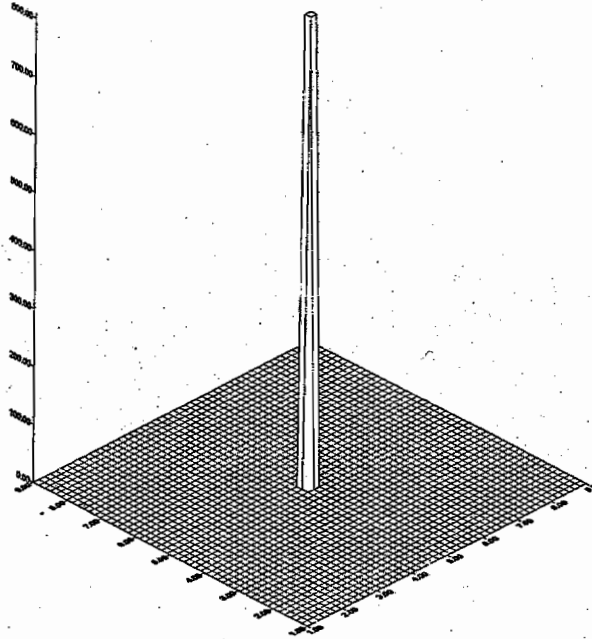
FIGURE 8.8A
Animal density profiles (arbitrary units) for a random-walk dispersion. At the beginning.

This simulation of diffusion also approximates a random-walk migration scenario. We begin the simulation with a given quantity of organisms concentrated in a single cell at the center (Figure 8.8A). For the chosen value of the diffusion parameter ($D = 0.1$), dispersion across the landscape is quite rapid (Figure 8.8B and Figure 8.8C), and a virtually uniform dispersion is reached by timestep 100. As one might expect, the system ascendency for this scenario dies off in approximately exponential fashion (Figures 8.9).

To examine the dynamics in somewhat greater detail, we wish to plot how the full ascendency is distributed across the landscape. The reader will recallthat Formula 11 involves a double summation. To gauge the contribution to the ascendency made by all organisms arriving at a given gridpoint, one simply sums over the first index while leaving the other one free. That is, for each gridpoint j, one may calculate

$$A_j = \sum_i T_{ij} \log\left(T_{ij} B^2 / B_i B_j T_{..}\right), \tag{14}$$

where A_j is the contribution made by all organisms at point j towards the full landscape ascendency. Figure 8.10 shows the distribution of the landscape ascendency for the diffusion model at timestep 6. The distribution resembles an eroded volcanic crater. (The humps along the rim are artifacts of the small
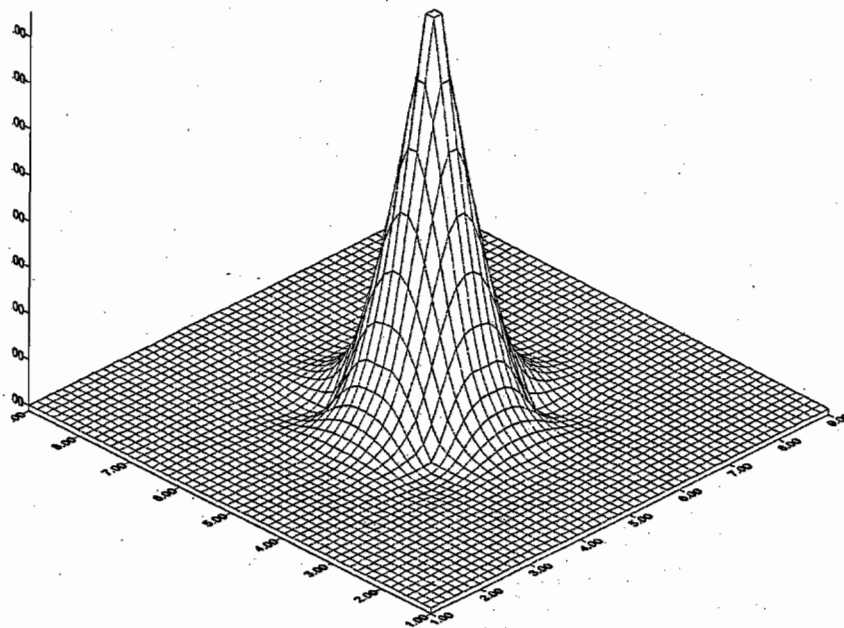
FIGURE 8.8B
Animal density profiles (arbitrary units) for a random- walk dispersion. After the first time step.
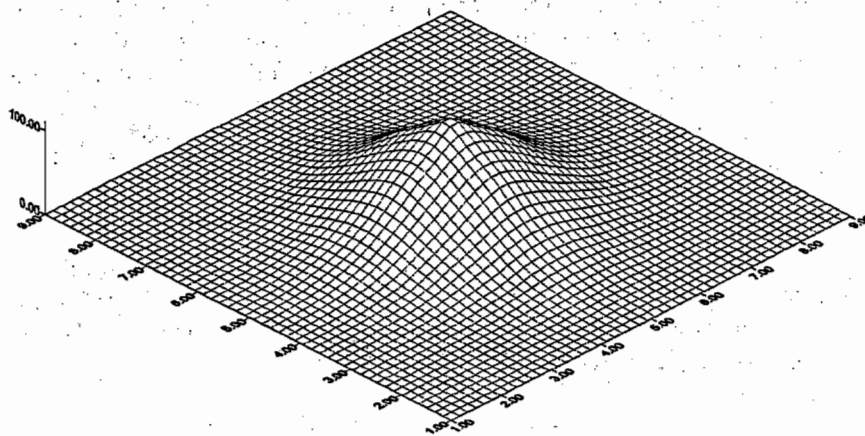
FIGURE 8.8C
Animal density profiles (arbitrary units) for a random- walk dispersion. After 6 time steps.
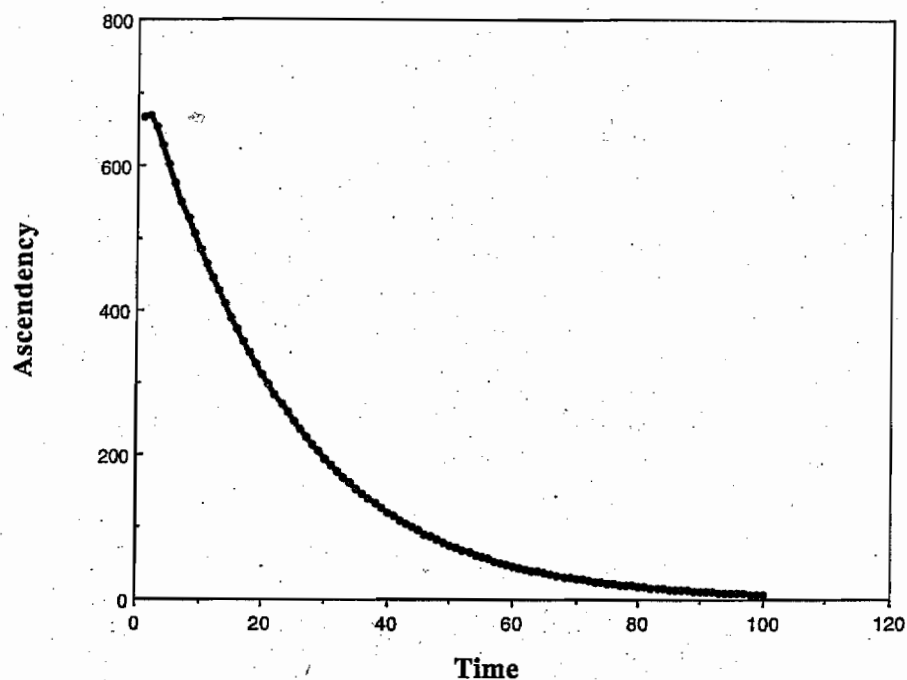
FIGURE 8.9
Change in total landscape ascendency during the random-walk dispersion scenario.
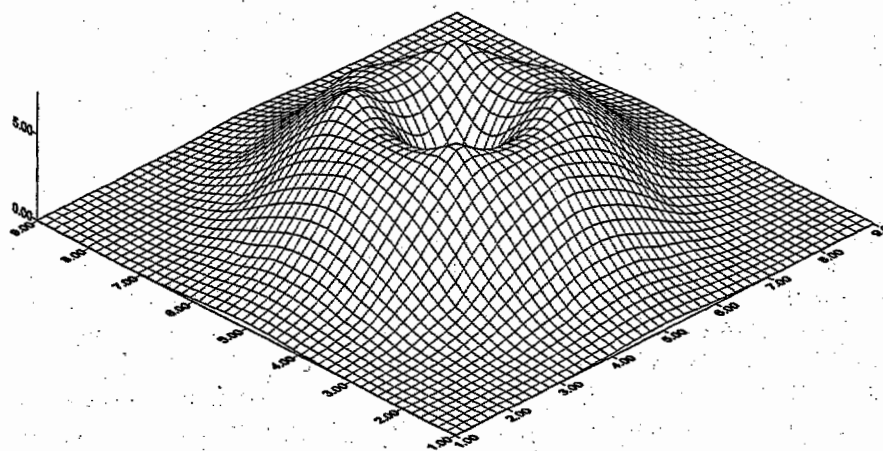
FIGURE 8.10
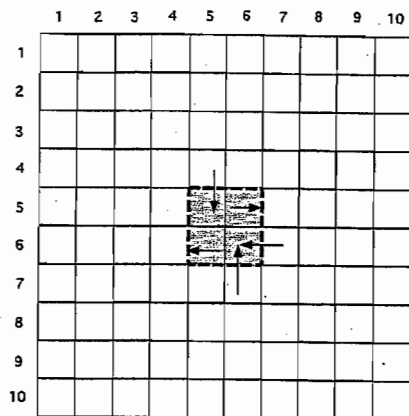Distribution of the spatial components of ascendency after timestep 6 of the random-walk scenario.

FIGURE 8.11
"Maxwell's Box" scenario for animal aggregation.
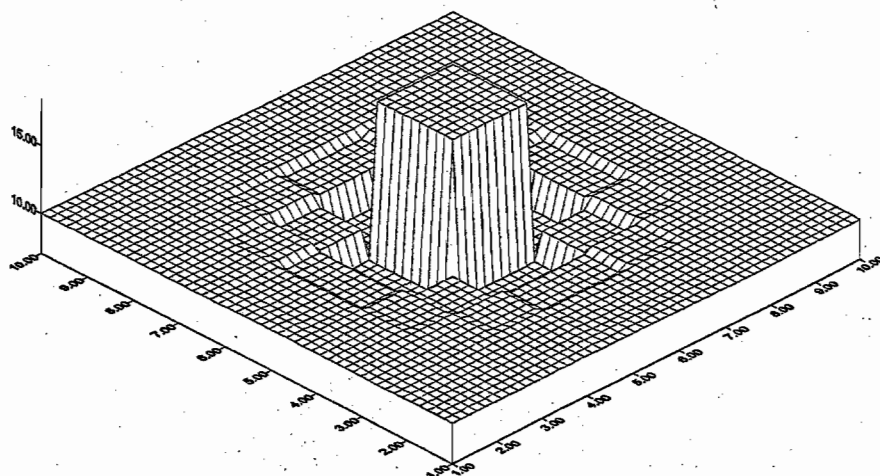
FIGURE 8.12A
Animal density profiles (arbitrary units) for Maxwell's Box aggregation. After 5 timesteps.

number of gridpoints in the landscape.) The key thing to notice is that the important action is not occurring at the center (where there is greatest density, but little diffusion), but at a certain distance from the center, where biomass gradients are steepest and migration strongest.

As old as the myth of Pandora's Box is the notion that some processes are irreversible. It is not surprising, therefore, to find that one cannot readily run the dispersion model in reverse. An approximation to such a reversal we shall call "Maxwell's Box." Maxwell's Box is an area of four grid cells at the center of the landscape (Figure 8.11). It is called Maxwell's Box in analogy to the famous Maxwellian Demon, which was a hypothetical being stationed at a pinhole in a partition that separates two chambers that initially are filled
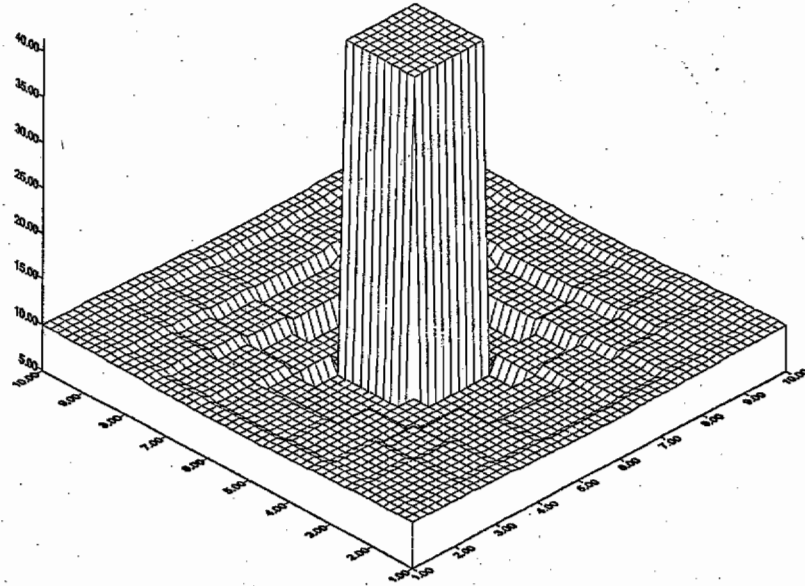
FIGURE 8.12B
Animal density profiles (arbitrary units) for Maxwell's Box aggregatioN. After 25 timesteps.

with a mixture of two gases, say A and B. The demon operated a frictionless, massless trapdoor over the hole, which he would open if a molecule of B approached from the left or if a molecule of A came from the right. Otherwise, he would leave the flap closed. Eventually, the gases would separate—A into the left chamber and B into the right in ostensible contradiction to the Second Law of Thermodynamics. In our analog, if an animal wanders into Maxwell's Box, it does not leave. The situation is analogous to animals doing a random-walk search for suitable habitat (the box). Once they find it, they stay put. Eventually, most of the animals wind up in the box (Figure 8.12A and Figure 8.12B).

At first thought, one might anticipate a logistic-like increase in system ascendency over time, i.e., the reverse of Figure 8.9. Instead, the ascendency rises for about 30 timesteps, then goes into a slow decline (Figure 8.13.) The initial rise is due primarily to an increase in mass segregation that is occurring over the landscape. The slow decline results from the gradual decline in activity as most of the animals end up in the box. The distribution of ascendency over the landscape at timestep 25 is rather unremarkable—a hill in the middle of the landscape, similar to the form in Figure 8.8C.

For the third scenario we impose a uniform migration of animals from north to south. This is accomplished by amending Equation 12b to read:

$$T_{i-10,i} = UB_{i-10} + D(B_{i-10} - B_i)$$

$$T_{i,i+10} = UB_i + D(B_i - B_{i+10})$$

$$(12c)$$
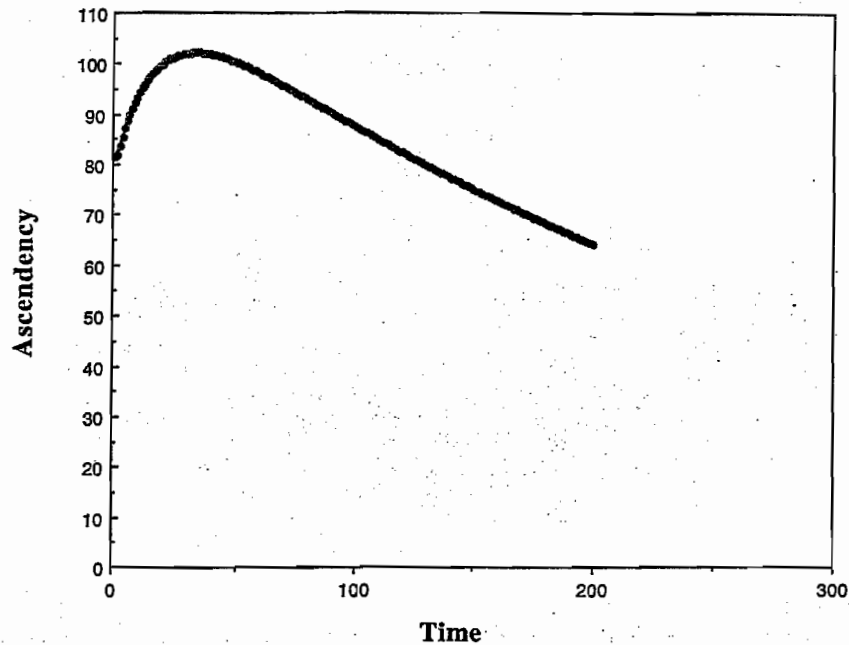
FIGURE 8.13
Change in total landscape ascendency during the course of Maxwell's Box aggregation.
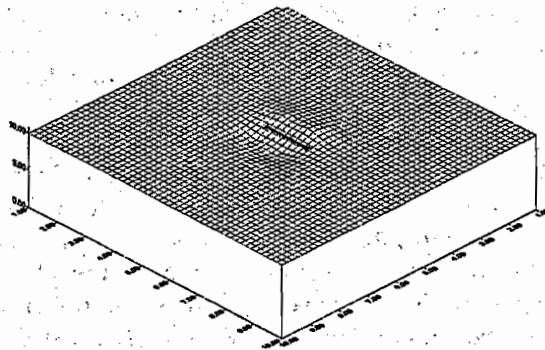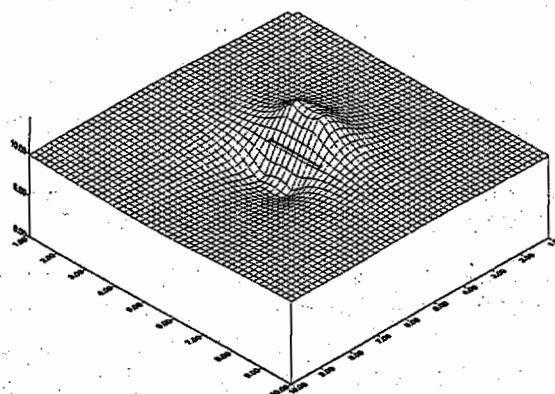

FIGURE 8.14A
Development of animal distributions along a migratory stream that encounters a crosstream barrier. After 2 timesteps.

where U is a constant rate of migration (or advection, as the case may be). In contrast to the endpoint of our first diffusion scenario (a uniform density across the landscape), the uniform flow possesses both a preferred direction and an observable amount of net migration activity. These attributes give rise to a nonzero ascendency (256.8 flow bits) and an appreciable total system
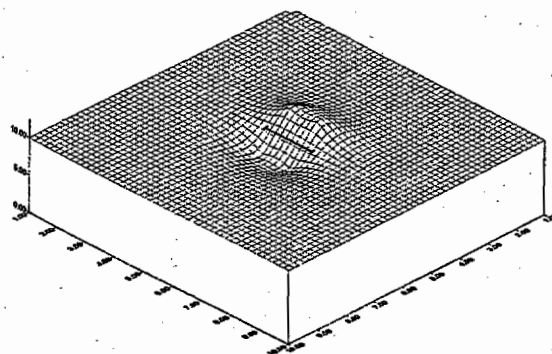
FIGURE 8.14B
Development of animal distributions along a migratory stream that encounters a crosstream barrier. After 10 timesteps.

FIGURE 8.14C
Development of animal distributions along a migratory stream that encounters a crosstream barrier. After 100 timesteps.

throughput (40.5 flow units), respectively. One may say, therefore, that the flow field possesses 256.8 flow bits of organization.

With the fourth scenario we address directly the title of this chapter. In the very middle of the uniform flow field we place an impermeable barrier two gridpoints wide. As might be expected, organisms begin to accumulate upstream and become depleted downstream of the barrier (Figure 8.14A and Figure 8.14B). Diffusion in the east-west directions eventually brings the system to a steady-state after about 100 timesteps (Figure 8.14C). Isopleths of animal density reveal the regions of accumulation and depletion, as well as a faint "bow-wake" forward and aft of the barrier itself (Figure 8.15). The migratory flow field reveals a parting of the migration stream around the barrier (Figure 8.16). The accompanying steady-state distribution of the landscape ascendency (Figure 8.17). It resembles a valley that is perpendicular to the barrier, flanked on both sides by two ridges that parallel the
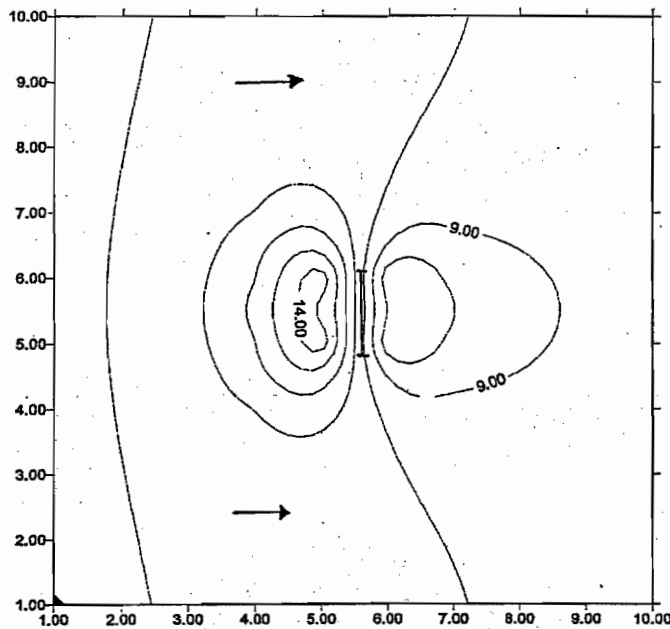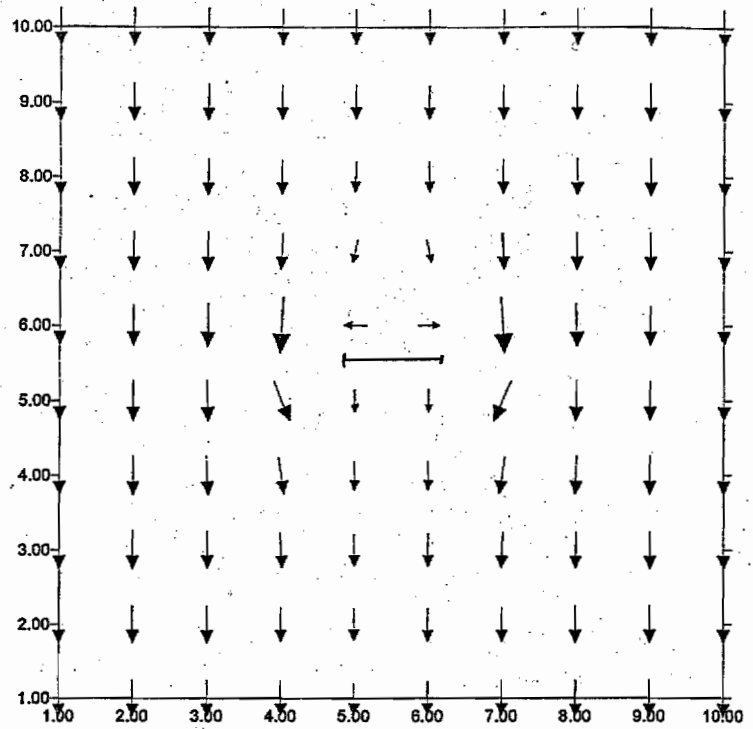
FIGURE 8.15
Isopleths of animal densities (after 100 timesteps) in relation to the barrier imposed upon a uniform migratory stream.

migratory stream. The ridges are highest just downstream of the barrier, whereas the greatest flow magnitudes appear just upstream and to the sides of the barrier.

Comparison of the system properties of the undisturbed stream flow with those corresponding to flow around the barrier is likewise revealing. Interestingly, more total flow occurs with the barrier in place (49.88 flow units) than in the unimpeded situation (40.50). This increase is an artifact of both the particular boundary conditions and the lack of any explicit resistance term in the CA scheme. As a consequence of the augmented flow, the ascendency increases from 256.8 flow bits in the uniform migration to 322.3 with the barrier. The mutual information of the flow field $(A/T_{\cdot})$ increases from 6.341 bits without the barrier to 6.462 bits with the constraint. One may conclude, therefore, that the barrier constraint adds 65.5 flow bits of ascendency to the dynamics of the system and 0.121 bits to its organization.

As a final exercise we compare the organization inherent in purely random movements across the whole landscape with that pertaining to the same amount of migration between two specific points in the field. In the former simulation, the origins and destinations for 10,000 "flights" were chosen at random from the entire field of 100 gridpoints. (This is different than the random walk considered earlier, where transitions were confined to nearest neighbors.) The first 40 of these "flights" are graphed in Figure 8.18. In the highly constrained migration, 5000 flights occurred from gridpoint 19 to cell
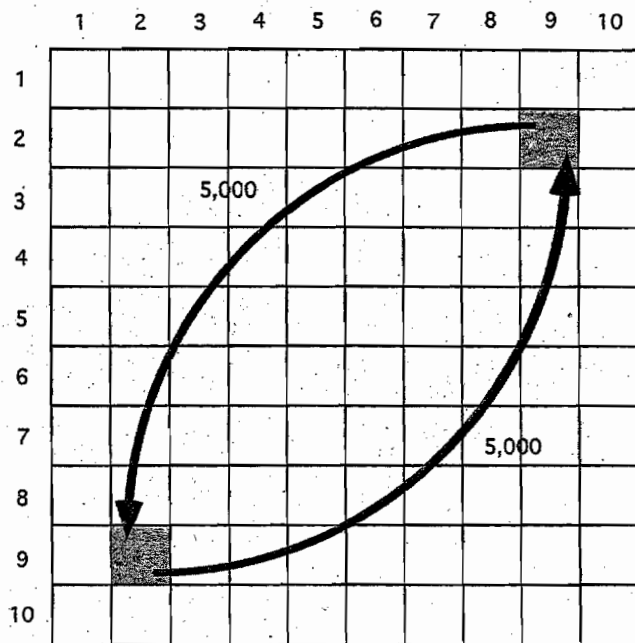
FIGURE 8.16
Vector field of animal movements around a barrier (corresponding to Figure 8.14C).
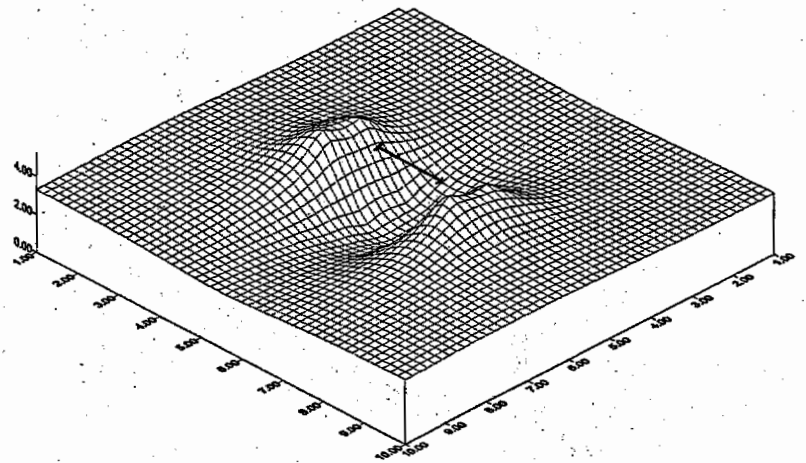
FIGURE 8.17
Distribution of the ascendency components across the landscape after timestep 100 of the "barrier" scenario.
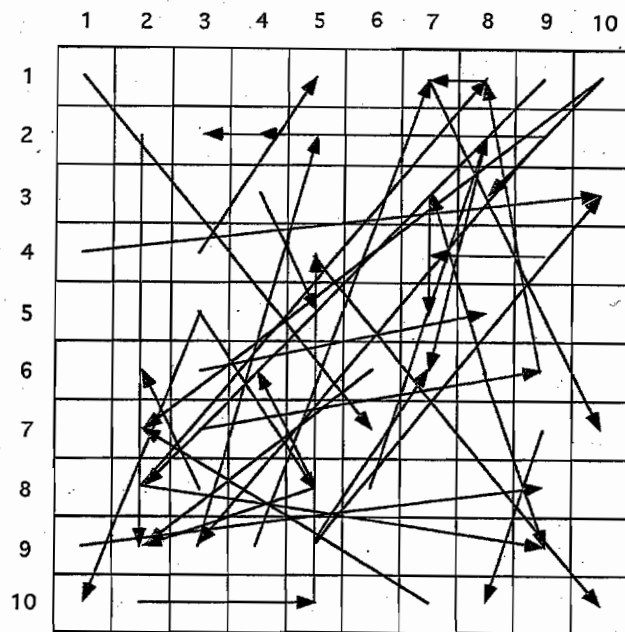
FIGURE 8.18
The initial 40 (of 10,000) random "flights" across a landscape.

FIGURE 8.19
Schematic of 10,000 highly determinate migrations between two specific gridpoints in a landscape.

82 and the same number in the reverse direction (Figure 8.19). The latter scenario resembles the migratory flights of certain bird populations between two areas of suitable habitat situated among a sea of unsuitable locales.

In both cases the total activity was the same—10,000 flow units. In the random flight scenario these transitions resulted in 9,517 flow bits of ascendency distributed more or less evenly over the landscape. In the highly constrained situation the same amount of activity yielded 122,900 flow bits of ascendency, concentrated at the two sites of suitable habitat. The AMI in the first case was 0.9517 bits, whereas that for the latter was 12.29 bits. Although we have no knowledge concerning the details of the constraints operating in the second case, we nonetheless can conclude that they contribute almost 113,400 flow bits to the dynamics of the system. Furthermore, almost 13 times as much information is associated with the very organized process of migration depicted in Figure 8.17.

Conclusions

Coming to terms with an indeterminate world requires that we explore new methods for quantifying natural phenomena. Earlier perspectives, which view phenomena either as determinate and continuous or wholly stochastic, must be supplemented by a "calculus of conditional probabilities." Such a calculus has already been provided by information theory. It is counterproductive to consider that information theory has only narrow application to problems related to communications theory. Rather, it is universally applicable whenever indeterminate phenomena become significant—which encompasses most of the life and social sciences.

In particular, the information indices that have been used to quantify trophic constraints among an ecological community can likewise quantify the organizational constraints operating on populations of animals that move across a landscape. Thus, the hypothesis of increasing ascendency might pertain to landscape ecology as well. Because the hypothesis is cast in terms that can be quantified using data on population distributions and migrations, it can be made operational and thus subject to falsification.

From a more practical point of view, the distribution of ecosystem ascendency over the landscape can be calculated to identify the "hot spots" where the most significant quantitative events are occurring.

Finally, it should be noted that the theory of ascendency treats a spatially distributed ecosystem as a grand process, rather than as a frozen picture of the world. It would seem that such transition is necessary if landscape ecology is to become a viable life science.

Acknowledgments