Ecosystem Health

*New Goals for
Environmental Management*

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Ecosystem Health
and Trophic Flow Networks

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Ecosystem "health" may best be understood in the context of a
hypothesized natural tendency for systems to grow and develop.
These processes have been quantified using an information-theory
measure called the network ascendency. Ascendency by itself is
not a proper surrogate for system health, but it does form one in-
dex that may be useful in constructing such a description. A
healthy system is hypothesized to require both a high diversity of
intercompartmental transfers and a high mutual information
among them. A newly derived "scope for ascendency" also seems
to afford a sensitive assessment of system performance. These
measures have been applied to comparative data on undisturbed
and impacted tidal marsh creek ecosystems in Crystal River,
Florida. The scope index is particularly sensitive to the effects of
stresses in the disturbed system. The network data also can serve
as input to other analyses that assess the degradation in trophic
functioning and energy processing by the disturbed system.

Health is one of those concepts, like information, that is difficult
to define in direct terms. Instead, both are delimited by what they
are not—that is, by their antonyms, which are more apparent.
Uncertainty, for example, is both central to the human condition

and easily quantified in probabilistic terms, as Claude Shannon (1948) capably demonstrated. Information, however, can be measured only as a decrease in uncertainty. Similarly, health is most obvious to us by what it is not—the occurrence of disease, trauma, or dysfunction. Webster's New Collegiate Dictionary cites as the most common meaning "freedom from physical disease or pain." Compounding matters for ecologists is the analogy of ecosystem health to the health of the human body or the bodies of organisms. Is the extension of the notion of health to other entities simply a rough metaphor, or is there an ontological basis for speaking of the "health of an ecosystem"? Webster provides a trail of clues beginning with the secondary definition of health as a "flourishing condition" or well-being, as might pertain to the economy of a country. The same dictionary describes "to flourish" as "to reach a height of development or influence." This brings us closer to the realm of ecology, for in that discipline there is a strong tradition of studying a phenomenon known as succession. It appears that pioneer ecosystems colonizing a newly opened area progress through a roughly predictable series of states, culminating in what approximates a climax community, whereafter changes at the level of the entire community become insignificant.

If one can somehow quantify the progress of an ecosystem along its pathway of succession (development), then the avenue toward the measurement of ecosystem health is opened: A healthy ecosystem is one whose trajectory toward the climax is relatively unimpeded and whose configuration is homeostatic to influences that would displace it back to earlier successional stages. I intend to use this definition of ecosystem health as the starting point for quantitative assessment.

Before starting the discussion I should note that the postulate of "disease" as impeded development hardly vanquishes all ambiguities. For example, there is widespread confusion over the relationship between development and evolution. To Eugene Odum (1969) evolution is succession (development) writ large. Eric Schneider (1988) tends to agree with Odum and provides the analogy that succession (development) is to evolution as stud poker is to draw poker. The game remains pretty much the same, but the former version is subject to more constraints. Stanley Salthe (pers. comm.) limits the term "development" to those progressions that unfold toward an endpoint that is knowable in advance. Thus development is unlike the less-certain process of evo-

lution, for which the endpoint remains unclear. The question of endpoint becomes crucial to Crawford Holling (1986), who sees the destruction of the climax community by some surprise agent as one link in the necessary cycle of growth, destruction, and renewal, without which evolution could not occur. Hence the notion of health in the longer evolutionary scheme becomes problematical at best. A healthy ecosystem at one temporal scale would serve to impede evolution over the longer duration.

Such controversies notwithstanding, I believe that focusing on health as related to the progress of succession is a good place to begin quantitative narration. It is entirely possible that a metric tailored to the process of development might still pertain to the process of evolution in the absence of an identifiable endpoint. The betting here is that development and evolution are, as Schneider suggests, manifestations of the same game under different constraints.

ECOSYSTEM DEVELOPMENT

A seminal albeit controversial synopsis of the trends apparent in ecological succession was given by Odum (1969). His list of twenty-four attributes of mature systems is cast at various levels of the hierarchy from the individual to the whole ecosystem and includes such indicators as gross production/community respiration quotient, biochemical diversity, organism size, niche specialization, and "information." Elsewhere (Ulanowicz 1980) I have focused on those attributes that could be identified as properties of quantified networks of trophic interactions. These properties were grouped into four categories: greater species richness; more niche specialization; more developed cycling and feedback; and greater overall activity. On purely phenomenological grounds I then argued that all four of these trends could be encapsulated into a single index: the network ascendency.

Ascendency is the product of two factors, one that gauges the level of system activity and another that captures the degree of trophic organization. The former is taken explicitly from economic input/output theory (see Chapter 12 of this volume). If T_{ij} is the transfer from compartments i to j $(i, j = 1, 2, 3,..., n)$ of some commensurable system product, if exogenous inputs are assumed to

derive from a hypothetical zeroth compartment, and if exogenous outputs flow to an imaginary compartment $n + 1$, then

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

is the calculated value of the total system throughput. As T defines the size of the system, any increase in T will be reckoned as growth in the very same sense that economic growth is considered to be any increase in the gross national product.

The organization of the network is slightly more difficult to quantify. Again, the reason is that "organization," like health and information, is best described by what it is not. In fact, it can be argued that there is a one-to-one correspondence between what is perceived as organization and what is measured as information in mathematical terms. If one has no knowledge about how the flows T_{ij} relate to each other, one's uncertainty about the system structure is measured by the Shannon-Weaver index of uncertainty:

$$H = -\sum_{i=0}^{n} \sum_{j=1}^{n+1} (T_{ij}/T) \log(T_{ij}/T)$$

Once one knows how the flows are connected in the network, one's uncertainty is then reduced by an amount known as the "average mutual information":

$$I = \sum_{i=0}^{n} \sum_{j=1}^{n+1} (T_{ij}/T) \log\left[T_{ij} T \Big/ \left(\sum_{k=1}^{n+1} T_{ik} \right) \left(\sum_{m=0}^{n} T_{mj} \right) \right]$$

One can prove for any network of exchanges T_{ij} that $H \geq I \geq 0$. Any increase in the organization I of a system can be taken as development.

The product of T and I is called the system ascendency (A), so named because of the dual meaning the word imparts. In the absence of major perturbation, succession proceeds in the direction of increasing ascendency (Ulanowicz 1986a). (The system "as-

cends" to more mature configurations.) Looked at differently, a configuration with higher ascendency can dominate over a system with a lower value of A and presumably would displace the latter whenever there is free communication between them.

Although the two factors in the ascendency relate to different concepts, the increase in ascendency can usually be traced to the influence of a unitary agent—autocatalysis, or indirect mutualism. Growth usually does not occur without development and vice versa. I argue that autocatalysis is an agent rather than a mechanism, because it exhibits properties that cannot be traced to the separate behavior of its constituent parts (Ulanowicz 1989).

ASCENDENCY AND SYSTEM HEALTH

If, as has been argued, the natural course of ecological succession is in the direction of increasing ascendency, it would at first seem reasonable to choose ascendency as a surrogate for ecosystem health. While there usually is some correlation between health and ascendency, the correspondence is not exact. Discrepancies between the two can be traced to at least two causes. First, increases in ascendency signify any combination of growth and development. It often occurs that most of the increase in A can be traced to an increase in the scaling factor, T. It also sometimes happens that T can increase at the same time that I decreases, but the increase in T predominates and the resultant product $A = TI$ still increases. This latter situation provides a convenient quantitative definition of the phenomenon of eutrophication (Ulanowicz 1986b). The sudden accessibility to new resources by the producer organisms results in amplified flows among the lower trophic members that overwhelm and often extirpate higher trophic elements. The resultant decrease in species richness and associated transfers causes the mutual information of the flows to drop, but this decrease is more than compensated by the concomitant rise in total system throughput. The system ascendency rises, but the "health" of the system by most standards has definitely suffered.

The size of a system is seen to be only marginally connected with its health. Although size may allow a larger system to displace a smaller configuration, it does not immediately follow that the former is necessarily healthier than the latter. Here an analogy with the human situation is helpful. A 2.3-meter leviathan should

have little trouble beating up a 1.2-meter dwarf in a hand-to-hand confrontation (unless, perhaps, the latter's name happens to be David). It does not necessarily follow, however, that the giant is healthier than the smaller person. Thus a descaled version of the ascendency—such as $I = A/T$ (Ulanowicz and Mann 1981) or I/H (Field et al. 1989)—should be more tightly correlated to the developmental stage and thus to ecosystem health.

Even a scale-independent ascendency is not an unerring index of system health. A high value of the mutual information of flows, I, usually indicates narrow trophic specialization. With such "stenotrophy" comes a decline in the number of alternative pathways that could grow to compensate for a disturbance in a major route of nutrient or energy flows. The parallel but secondary routes function as a "strength-in-reserve" with which the system can adapt to unexpected and novel disturbances. Systems that "overdevelop" lose such homeostatic capability and appear "brittle" (Holling 1986) to even slight impacts.

It is not sufficient that I/H be a large fraction in order to conclude that a system is healthy. It is necessary also that both numerator and denominator possess magnitudes as large as possible (Ulanowicz 1986b). The denominator is the diversity of flows, which in turn requires a diversity of compartments for its sustenance. Thus we are led to a heuristic justification for preserving species diversity, an ethic that some suggest needs no rational justification (Sagoff 1988).

Finally, it should be noted that ascendencies are usually calculated from data on static, balanced networks. On the average inputs are balanced against outputs. It may be, however, that either inputs or outputs predominate in a system—that is, the system is growing or shrinking—and the ascendency as formulated is relatively insensitive to which condition might be prevailing at the time of measurement. For this reason one might wish to use an index possessing some antisymmetry that distinguishes inputs from outputs. Winberg (1956), for example, defines the "scope for growth" of a population as the rate by which the inputs to the species exceed its outputs, and Genoni and Pahl-Wostl (1991) have suggested extending this notion to the entire community. Such a straightforward extension, however, fails to incorporate system structure and would likely be too rough a measure to capture even the major factors comprising ecosystem health. In its place I have suggested using the "scope for ascendency," a measure that

bears a formal resemblance to the ascendency but distinguishes between inputs and outputs in the system. The equation for the scope is

$$S = \sum_{i=0}^{n} \sum_{j=1}^{n} (T_{ij}/2) \log\left[T_{ij} T \Big/ \left(\sum_{k=0}^{n} T_{kj}\right)^2\right] - \sum_{i=1}^{n} \sum_{j=1}^{n+1} (T_{ij}/2) \log\left[T_{ij} T \Big/ \left(\sum_{k=1}^{n+1} T_{ik}\right)^2\right]$$

As with the conventional scope, S is usually positive when inflows dominate and can become negative when losses prevail. It is not generally zero at steady state, but more often positive, owing to the limited number of exogenous inputs in relation to the more dispersed nature of the outputs. When the scope is applied to a simplistic mechanical system like the steady-state Atwood's machine,[1] it gives results similar to the power generation function (Odum and Pinkerton 1955; Smith 1976). S is zero for steady-state extremes of component efficiency (0 and 1) but reaches a maximum at some intermediate first-law efficiency. Thus S appears (at this stage of research) to quantify the effectiveness with which the system utilizes the given resources.

APPLICATION TO CURRENT DATA

As the ascendency and associated indices pertain to the state of the entire ecosystem, they therefore require data on all transfers occurring in the community. The collection of such data is usually a laborious task. For this reason, fully quantified networks of ecosystems remain scarce, although recently there has been a spurt of attempts to elaborate flow networks (Pauly, pers. comm.). Despite this encouraging trend, I know of only one set of data (taken over fifteen years ago) systematically assembled to compare the networks of an impacted ecosystem with those of a control counterpart (Homer and Kemp 1975; see also Ulanowicz 1986a). These data were taken from a tidal marsh tributary creek off Crystal River, Florida, and from a similar creek that was subjected to an average 6°C rise in ambient temperature because of exposure to the effluent from an adjacent nuclear power generating station.

The mix of species inhabiting the control and impacted ecosystems closely resembled each other; however, the food web of the disturbed system appeared less connected than that of the control (see Figures 1 and 2). The question here is: Do the ascendency and related variables reflect any degradation in the health of the impacted system? The answer is a qualified yes.

The level of trophic activity in the impacted system was almost 20 percent less than in the control creek. The heated system was obviously operating beyond its optimal temperature. As T scales the ascendency, it showed an almost proportionate decline in magnitude. The unscaled indices all fell in the impacted system, but the decrements were hardly significant. I fell by 1.7 percent, H by 1.1 percent, and I/H by a scant 0.7 percent. The conclusion one draws is that the activity level is sensitive to temperature changes but, at least within this range of temperature shift, the basic structure of the ecosystem remains virtually unchanged. The same response was noted for seasonal changes in the Chesapeake Bay mesohaline ecosystem by Baird and Ulanowicz (1989).

The scope for ascendency fell by over 7 percent in the Crystal River, probably reflecting the impaired ability of the heated system to utilize effectively what resources it does capture. The greater sensitivity of S to structural changes recommends it as a preferred index for gauging system performance.
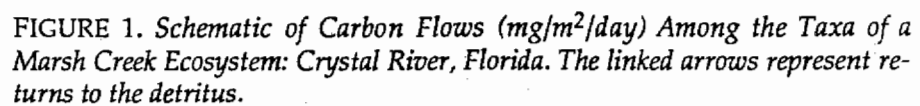
OTHER INDICATORS OF SYSTEM HEALTH

Ascendency involves an information-theory view of trophic dynamics. There are other ways of looking at the whole system that help to indicate the system's performance, although the relationship of these other portrayals to ecosystem health remains less direct than those of the more fundamental index, the ascendency.

Odum (1969) notes as one of his twenty-four criteria that mineral cycles tend to be more closed in mature ecosystems.

FIGURE 2. *Schematic of Carbon Flows in a Nearby Heated Marsh Creek Ecosystem. This ecosystem is similar to the one depicted in Figure 1, except that it was perturbed by a 6 °C average elevation in temperature due to thermal efflu-ent from a nearby nuclear power generating station.*

FIGURE 1. *Schematic of Carbon Flows (mg/m²/day) Among the Taxa of a Marsh Creek Ecosystem: Crystal River, Florida. The linked arrows represent returns to the detritus.*

with the stingray at a value of 3.68. The situation is further clouded by the fact that six species seemed to flourish in the warmer environs. The trophic status of the needlefish, for example, increased from 3.46 in the control community to 3.68 in the impacted one. Likewise, the bay anchovy improved significantly from 2.02 in the undisturbed to 2.67 in the stressed network.

The individual trophic ranks appear to indicate that the heated system is doing better at moving material to higher trophic levels—a conclusion that is avoided once one aggregates both webs into their straight-chain configurations. This mapping involves apportioning the activity of each species to integral, sequential members of a chain according to the fractions that arrive at that compartment over pathways of corresponding integer length (Ulanowicz and Kemp 1979; Ulanowicz in press). The aggregation is done in such a way as to preserve material balance. The results of trophic aggregations are shown in Figure 3.

One notices immediately that the trophic chain representation of the control creek (Figure 3a) is one step longer than that of the impacted system (Figure 3b) and that almost five times as much medium reaches the fourth trophic level in the undisturbed community. The arrow from box I to box II represents pure herbivory (grazing), while that from the box marked D (for detritus) to box II signifies detritivory. Herbivory falls only slightly in the impacted system, whereas the drop in detritivory is more significant. The detritivory/herbivory ratio falls (as Odum predicted) from forty-one in the control system to thirty-six in the stressed, even though a greater proportion of activity in the stressed system is being devoted to recycling. The aggregated trophic chains show unambiguously that the control creek is performing better than the heated ecosystem.

CONCLUSION

Assessing the health of ecosystems requires a pluralistic approach and a number of indicators of system status (Karr 1991; Schaeffer et al. 1988). Ambiguities remain, however, regarding how to relate these indices to the fundamental notion of system development, which is a critical process in defining ecosystem

John Finn (1976) developed an index that measures the fraction of overall activity devoted to recycling. The implication is that systems with higher values of the Finn index are more mature. While Odum spoke of mineral cycles, Finn and colleagues (Richey et al. 1978) tried to apply the index and the concept to carbon cycling in lakes, only to get very equivocal results. Carbon, however, is tied closely to energy, and the fraction of carbon that is recycled is indicative of the system's inability to utilize fully the energy resources available to it. Hence, a high Finn index for carbon could be a sign of a more stressed community. This appears to be the case with the Crystal River systems, where the Finn index of 7.1 percent in the control creek rises to 9.4 percent in the heated counterpart. Wulff and Ulanowicz (1989) also noted that the Finn index of carbon cycling in the less impacted Baltic ecosystem was 22.8 percent, but rose to 29.7 percent in the more eutrophic Chesapeake community. If anything, the Finn index when applied to carbon flux appears to be a counterindicator of ecosystem health. (Of course, the same index when calculated on the limiting nutrient might yield altogether different results.)

There are other aspects of carbon cycling that bear on the system's performance. If one enumerates the number of cycles in the two creeks (Ulanowicz 1983), for example, one finds a total of 119 simple directed cycles in the control creek, but only forty-six in its impacted counterpart. Furthermore, the cycles in the control creek tend to have more trophic links and involve more of the higher species. There are forty-two cycles of trophic length 4 and twenty-six of length 5 in the control creek, whereas there were only fourteen cycles of length 4 and no cycles of length 5 in the impacted creek.

With respect to food chains, Odum has characterized pioneer systems as resembling linear grazing chains, whereas more mature systems seem more "web like" and involve greater detrital feeding. One can see by inspection of Figures 1 and 2 that the control creek has a higher topological connectivity and thus appears more web like. What Odum fails to mention is that one would also expect more mature or less stressed systems to have longer feeding pathways and more species of higher trophic rank. Stephen Levine (1980) has shown how the average trophic rank of each species may be calculated from a quantified food web. The species with the highest trophic rank in the control creek was the needle-fish (3.46), which tied for the highest rank in the impacted system

health. By contrast, the ascendency measures espoused here require copious data on the workings of the entire system—data that take much effort to assemble. The chief advantage in using these measures, however, lies in their hypothetical connections to what is really meant by healthy system functioning.

As more and more ecosystem networks are elaborated, moreover, the process of estimating flows for entire systems becomes progressively less difficult. Such facilitation stems from a growing pool of expertise, a larger body of published data, and a greater availability of software (such as ECOPATH II by Pauly et al. 1987) that actually assists the investigator in constructing quantified ecosystem networks. Ten years hence, estimating changes in ecosystem flow networks may not appear so formidable a task as it now seems. And with the increasing interest in analyzing flow networks should come the discovery of new relationships between what now appear as ad hoc indices (that is, diversity) and the more fundamental processes of growth and development of ecosystems, which underlie the notion of ecosystem health. Such a justification for the use of population diversity indices in ecosystem management was mentioned earlier, and surely other connections could follow.

Is ecosystem health nothing but a broad metaphor? Some consider the very notion of an ecosystem to be only a mental construct, but they are clearly in the minority. A recent poll of interest by ecologists in various subdisciplines revealed "ecosystems" to be the most popular topic (Waring 1989). As real (and measurable) as ecosystems themselves is the notion that they grow and develop. Systems exhibiting growth and development almost by definition are subject to disruption of these fundamental processes—whence enters the notion of health. No one is suggesting, as some have imputed to Clements and Shelford (1939), that ecosystems are the ontological equivalents of organisms. But from an operational point of view, it makes great sense to attempt to measure a system's growth, development, and health by using indices that can guide (and often temper) our efforts to manage the ecosystems that sustain humankind.
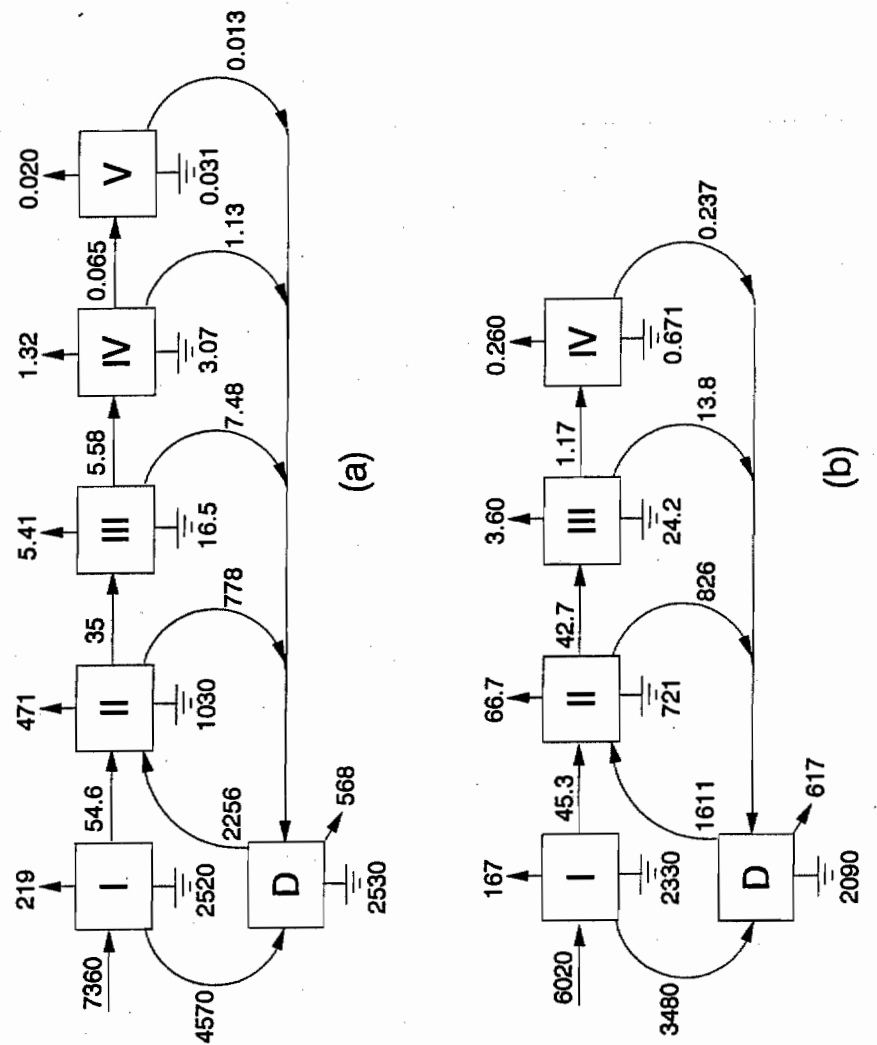
FIGURE 3. *Aggregated Trophic Transfers (mg C/m²/day) Occurring in (a) the Unperturbed Marsh Creek and (b) the Heated Creek.*

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Notes

1. Atwood's machine consists of two unequal weights attached to the ends of a rope that is strung over a pulley. The rope and pulley are usually assumed to be frictionless. When allowed to free-fall, the heavier weight performs work in raising the lighter one. For the most part, you could consider Atwood's machine as a hypothetical artifact useful in clarifying various issues about work and energy.