



## What is a healthy ecosystem?

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### Abstract

Rapid deterioration of the world's major ecosystems has intensified the need for effective environmental monitoring and the development of operational indicators of ecosystem health. Ecosystem health represents a desired endpoint of environmental management, but it requires adaptive, ongoing definition and assessment. We propose that a healthy ecosystem is one that is sustainable – that is, it has the ability to maintain its structure (organization) and function (vigor) over time in the face of external stress (resilience). Various methods to quantify these three ecosystem attributes (vigor, organization, and resilience) are discussed. These attributes are then folded into a comprehensive assessment of ecosystem health. A network analysis based ecosystem health assessment is developed and tested using trophic exchange networks representing several different aquatic ecosystems. Results indicate the potential of such an ecosystem health assessment for evaluating the relative health of similar ecosystems, and quantifying the effects of natural or anthropogenic stress on the health of a particular ecosystem over time.

### Introduction

To understand and manage complex systems (like ecological and economic systems), we need some way of assessing the system's overall performance – its relative 'health'. The US EPA has begun to shift the stated goals of its monitoring and enforcement activities from protecting only 'human health' to protecting overall 'ecological health'. Indeed, EPA's Science Advisory Board (SAB, 1990) stated: *EPA should attach as much importance to reducing ecological risk as it does to reducing human health risk. These very close linkages between human health and ecological health should be reflected in national environmental policy. When EPA compares the risks posed by different environmental problems in order to set priorities for Agency action, the risks posed to ecological systems must be an important part of the equation.*

Although this statement gives the concept of ecological health importance as a primary EPA goal, it begs the question of what ecosystem health is, while tacitly defining it as analogous to human health. The dictionary definitions of health are: '1. the condition

of being sound in mind, body, and spirit; and 2. flourishing condition or well-being'. These definitions are obviously rather vague. In order to meet the mandate for effectively managing the environment a more rigorous and operational definition of health must be constructed – one that is applicable to all complex systems at all levels of scale, including organisms, ecosystems, and economic systems.

### Defining ecosystem health and sustainability

All complex systems are, by definition, made up of a number of interacting parts. In general, these components vary in their type, structure, and function within the whole system. Thus a system's behavior cannot be summarized simply by adding up the behavior of the individual parts. Contrast a simple physical system (say, an ideal gas) with a complex biological system (say, an organism). The temperature of the gas is a simple aggregation of the kinetic energy of all the individual molecules in the gas. The temperature, pressure, and volume of the gas are related by

simple relationships with little or no uncertainty. An organism, however, is composed of complex cells and organ systems. The state of an organism cannot be surmised simply by adding up the states of the individual components, since these components are themselves complex and have different, noncommensurable functions within the overall system. Indicators that might be useful for understanding heart function – pumping rate and blood pressure, for instance – are meaningless for skin or teeth.

Past explicit or implicit definitions of ecosystem health have included:

- Health as homeostasis.
- Health as the absence of disease.
- Health as diversity or complexity.
- Health as stability or resilience.
- Health as vigor or scope for growth.
- Health as balance between system components.

All of these concepts represent pieces of the puzzle, but none is comprehensive enough to serve our purposes here. In this paper, we develop the concept of *ecosystem health as a comprehensive, multiscale, dynamic, hierarchical measure of system resilience, organization, and vigor*. These concepts are embodied in the term ‘sustainability’ which implies the system’s ability to maintain its structure (organization) and function (vigor) over time in the face of external stress (resilience). A healthy system must also be defined in light of both its context (the larger system of which it is part) and its components (the smaller systems that make it up).

In its simplest terms, then, health is a measure of the overall performance of a complex system that is built up from the behavior of its parts. Such measures of system health imply a *weighted* summation or a more complex operation over the component parts, where the weighting factors incorporate an assessment of the relative importance of each component to the functioning of the whole. This assessment of relative importance incorporates ‘values’, which can range from subjective and qualitative to objective and quantitative as we gain more knowledge about the system under study. In the practice of human medicine, these weighting factors or values are contained in the body of knowledge and experience embodied in the medical practitioner.

Figure 1 shows the progression from directly measured ‘indicators’ of a component’s status, through ‘endpoints’ that are composites of these indicators, to health with the help of ‘values’. Measures of health are inherently more difficult, more comprehensive, re-

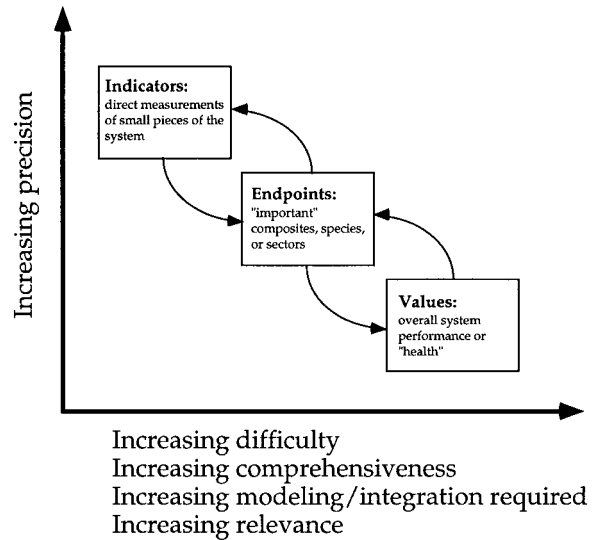


Figure 1. Relationship between indicators, endpoints and values (after Costanza, 1992).

quire more modeling and synthesis, and involve less precision, but are more relevant than the endpoints and indicators from which they are built. It remains to determine which general approaches to developing these measures of health for ecosystems are most effective.

Health is also a scale-dependent characteristic. Figure 2 indicates this relationship by plotting a hypothetical curve of system life expectancy on the y axis vs. time and space scale on the x axis (Costanza & Patten, 1995). We expect a cell in an organism to have a relatively short life span, the organism to have a longer life span, the species to have an even longer life span, and the planet to have a longer life span. But no system (even the universe itself in the extreme case) is expected to have an infinite life span. A healthy and sustainable system in this context is one that attains its full expected life span. For individual humans, this is also an often used cumulative indicator of health (at least in retrospect).

Since ecosystems experience succession as a result of changing climatic conditions and internal developmental changes, they too have a limited (albeit fairly long) life span. The key is differentiating between changes due to normal life span limits and changes that cut short the life span of the system. Things that cut short the life span of humans are obviously contributors to poor health. Smoking, AIDS, etc., and a host of other ailments do just this. Human induced eutrophication in aquatic ecosystems causes a radical change in the nature of the system (ending the life span of

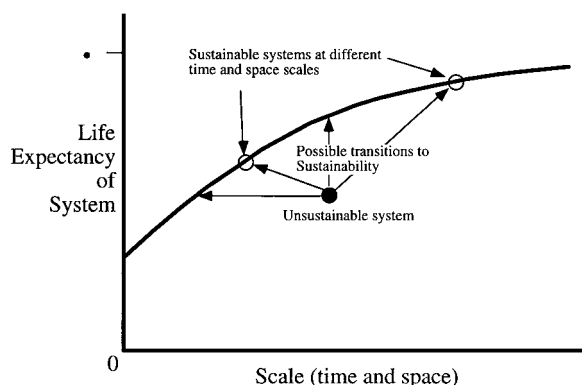


Figure 2. Health and sustainability as scale (time and space) dependent concepts (after Costanza & Patten, 1995).

the more oligotrophic system while beginning the life span of a more eutrophic system). We would have to call this process 'unhealthy' using the above definition since the life span of the first system was cut 'unnaturally' short. It may have gone eutrophic eventually, but the anthropogenic stress caused this transition to occur 'too soon'.

How can we create a practical definition of system health that is applicable with equal facility to complex systems at all scales? Let us first lay out the minimum characteristics of such a definition. First, an adequate definition of ecosystem health should integrate the concepts of health mentioned above. Specifically it should be a combined measure of system resilience, life expectancy, balance, organization (diversity), and vigor (metabolism). Second, the definition should be a comprehensive description of the system. Looking at only one part of the system implicitly gives the remaining parts zero weight. Third, the definition will require the use of weighting factors to compare and aggregate different components in the system. It should use weights for components that are linked to the functional dependence of the system's sustainability on the components, and the weights should be able to vary as the system changes to account for 'balance'. And fourth, the definition should be hierarchical to account for the interdependence of various time and space scales.

Costanza et al. (1992) develop the following definition of ecosystem health: An ecological system is healthy and free from 'distress syndrome' if it is stable and sustainable – that is, if it is active and maintains its organization and autonomy over time and is resilient to stress.

Ecosystem health is thus closely linked to the idea of sustainability which is seen to be a comprehensive, multiscale, dynamic measure of system resilience, organization, and vigor. This definition is applicable to all complex systems from cells to ecosystems to economic systems (hence it is comprehensive and multiscale) and allows for the fact that systems may be growing and developing as a result of both natural and cultural influences. According to this definition, a diseased or unhealthy system is one that is not sustainable and will not achieve its maximum life span. The time and space frame are obviously important in this definition. Distress syndrome (Rapport et al., 1985, 1992) refers to the irreversible processes of system breakdown leading to the termination of the system before its normal life span. To be healthy and sustainable, a system must maintain its metabolic activity level as well as its internal structure and organization (a diversity of processes effectively linked to one another) and must be resilient to outside stresses over a time and space frame relevant to that system.

What does this mean in practice? Table 1 lays out the three main components of this proposed concept of system health (resilience, organization, and vigor) along with related concepts and measurements in various fields.

What we are looking for is an assessment that combines these three basic aspects of system performance and health – vigor, organization, and resilience. To operationalize these concepts (especially organization and resilience) will require a heavy dose of systems analysis, synthesis, and modeling, combined with broad-based input from the full range of stakeholders involved in the management of ecosystems.

In this paper we propose a systems level assessment of ecosystem health that is reasonably easy to measure, and incorporates values in a general manner allowing for the possibility of reaching a consensus. More specifically, we identify three components of ecosystem health that encompass many of the concepts discussed above, describe the quantification of these components, illustrate how they can be incorporated into a quantitative assessment of ecosystem health, examine some initial testing of the assessment, and discuss opportunities for future testing.

### Three components of ecosystem health

The vigor of a system is simply a measure of its activity, metabolism or primary productivity. Examples

Table 1. Indices of vigor, organization, and resilience in various fields

Component of health	Related concepts	Related measures	Field of origin	Probable method of solution
Vigor	Function Productivity Throughput	GPP, NPP, GEP GNP Metabolism	Ecology Economics Biology	Measurement
Organization	Structure Biodiversity	Diversity index Average mutual information (Ulanowicz, 1986) Predictability (Turner et al., 1989)	Ecology	Network analysis
Resilience		Scope for growth (Bayne, 1987) Population recovery time (Pimm, 1984) Disturbance absorption capacity (Holling, 1987)	Ecology	Simulation modeling
Combinations		Ascendancy (Ulanowicz, 1986) Index of Biotic Integrity (Karr, 1991)	Ecology	

include gross primary productivity in ecological systems, and gross national product in economic systems. It has been hypothesized that a system's ability to recover from stress, or to utilize it, is related to its overall metabolism, energy flow (Odum, 1971), or to its 'scope for growth' (Bayne et al., 1987) which is the difference between the energy required for system maintenance and the energy available to the system for all purposes. Each of these measures is aimed at the system's capability to respond to generalized stress.

The organization of a system refers to the number and diversity of interactions between the components of the system. Measures of organization are affected by the diversity of species, and also by the number of pathways of material exchange between each component. For example, a highly organized system is characterized by a high diversity of specialized components, and their corresponding specialized exchange pathways. Organization decreases as the diversity of species and the specialization of exchange pathways decrease. It is important to realize that for any given level of species diversity organization can vary with the pattern of exchange pathways between them. A system containing species that feed on only one or two specific prey items, and are in turn prey for only one or two other species, will have higher values of organization than a system containing the same number of generalist feeders with multiple pathways of exchange between them. Organization, therefore, extends traditional measures of diversity by also considering the patterns of exchange between system components.

The resilience of a system refers to its ability to maintain its structure and pattern of behavior in the presence of stress (Holling, 1986). In the context of this paper, it may refer to the system's ability to maintain its vigor and organization in the presence of stress. A healthy system is one that possesses adequate resilience to survive various small-scale perturbations. The concept of system resilience has two main components. The most commonly used aspect refers to the length of time it takes a system to recover from stress. A second aspect refers to the magnitude of stress from which the system can recover, or the system's specific thresholds for absorbing various stresses. A related point involves the alternative system states once thresholds are crossed; these may vary from total system collapse to a stable state that may actually be more beneficial. The limits of ecosystem stability or resilience are currently being debated. Holling (1986) argues that the limits range from the assumption of complete global stability, implicit in many of humanity's past efforts to manage, to the idea of ecosystems being extremely fragile.

Mageau et al. (1995) illustrated the three components of system health in a three-dimensional plot (Figure 3). The two-dimensional planes formed when each of the components are zero are labeled. The first plane describes systems characterized by various combinations of organization and resilience, but no vigor. Systems with little or no vigor, such as ice, rocks and minerals, are 'crystallized'. The second plane describes systems characterized by various

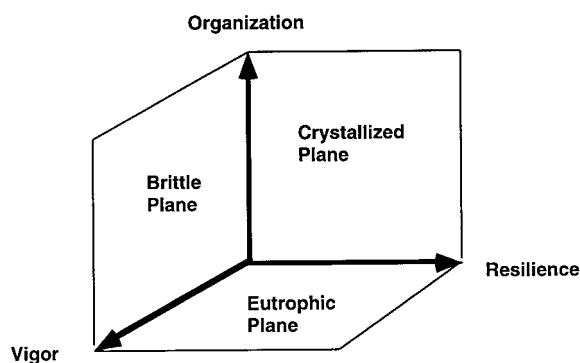


Figure 3. A three-dimensional plot of system vigor, organization, and resilience. Each of the planes formed when one component is zero are also labeled.

combinations of resilience and vigor, but with no organization. Systems with little or no organization, such as nutrient enriched lakes, streams and ponds, or early successional ecosystems dominated exclusively by 'r' selected species, are 'eutrophic'. The third plane indicates systems that are characterized by various combinations of vigor and organization, but no resilience. Natural variation in external environments preserves resilience preventing systems from reaching the extreme of this plane, but certain highly managed systems, such as agriculture, aquaculture, and plantations, approach this plane and are 'brittle'. Crystallized, eutrophic, and brittle systems are not healthy. Instead, a healthy system is characterized by some balance between vigor, organization, and resilience. We propose that a 'healthy' system is one that can develop an efficient diversity of components and exchange pathways (high organization) while maintaining some redundancy or resilience as insurance against stress, and substantial vigor to quickly recover or utilize stress in a positive manner.

### Quantifying system vigor, organization, and resilience

We have begun to develop and test quantitative measures of systems vigor, organization, and resilience using a combination of data from field experimentation, simulation modeling, and network analysis studies. This data will allow various indices of vigor, organization, and resilience to be calculated and compared over a range of scales. If these tests are encouraging, then the indices most capable of measuring vigor, organization, and resilience can be formulated into an integrated assessment of ecosystem health applica-

ble to large scale ecosystems, economic systems, and ecological economic systems.

### Measuring vigor

Vigor is the most straightforward of the three components to measure. Vigor can be measured directly and relatively easily by existing methods in most systems. Examples include Gross Primary Production (GPP) and organism metabolism in ecological systems and Gross Domestic Product (GDP) in economic systems. These empirical measures quantify the magnitude of input (material or energy) available to an ecosystem (GPP), or the overall activity (measured in dollars per unit time) of an economic system. But, as investigators in several fields have long recognized, vigor alone is not an adequate measure of health.

### Measuring organization

It is more difficult to quantify organization than vigor because quantifying organization involves measuring both the diversity and magnitude of system components and the exchange pathways between them. Diversity indices and multispecies indices fail to incorporate exchange pathways connecting system components. Network analysis is a potential approach to the problem of measuring organization. It involves the quantitative analysis of interconnections between components of a system (species) and their connections with the larger system (their abiotic environments). Practical quantitative analysis of interconnections in complex systems began with the economist Leontief (1941) using what has come to be known as Input-Output (I/O) analysis. Recently these concepts have been applied to the study of interconnections in ecosystems (Hannon, 1973, 1976, 1979, 1985a-c; Costanza & Neill, 1984). Related ideas, under the heading of compartmental analysis, were also developed (Barber et al., 1979; Finn, 1976; Funderlic & Heath, 1971). Isard (1972) was the first to take advantage of the similar methodology by attempting a combined ecological/economic system I/O analysis, and several others have proposed ecological/economic mass-balance models (Daly, 1968; Cumberland, 1987). Ulanowicz (1986) has used information theory to develop a specialized suite of systems-level, network analysis indices. One particular index (Average Mutual Information) may be used as a comprehensive measure of organization. Average Mutual Information (AMI) transcends the traditional diversity indices used in ecology by estimating not

only the number of different species in a system, but, more importantly, how they are organized.

Ulanowicz (1986) described the quantification of AMI along with several other systems-level, network analysis indices in detail, so we provide only a brief summary. The first step in quantifying these indices is to estimate a matrix of material and energy exchanges between system components. Each cell in the matrix carries the label  $T_{ij}$  designating a specific transfer from a particular component in row  $i$  to a particular component in column  $j$ . Estimating matrices of this type for ecosystems is difficult, but with field experiments directed at estimating trophic transfers (such as various tracer experiments and feeding patterns), improvements in simulation modelling, and the development of modelling software such as ECOPATH (Christensen & Pualy, 1992) our abilities are increasing. The systems-level information indices can then be quantified using the conditional probabilities calculated from these matrices. One can gain valuable insight into ecosystem structure and function by studying the changes in these indices which accompany ecosystem perturbations.

Ulanowicz (1986) identified mutualism or autocatalysis between system components, connected by cyclic flow, as a nonmechanistic, ecosystem phenomenon which provides evolution and ecological succession with a sense of direction. This natural process dictates the behavior of the system-level information indices. In autocatalysis an increase in the activity of any component increases the activity of all other members in the cycle and ultimately itself, resulting in configurations that are growth enhancing via positive feedback. These autocatalytic configurations also exert selection pressure on their members. If a more efficient species enters the cycle, its influence on the cycle will be positively reinforced, or if the species is less efficient, negative reinforcement will decrease its role. In addition, as the autocatalytic cycle increases its activity it adsorbs resources from its surroundings. Therefore, as ecosystems undergo the process of succession in the absence of stress autocatalysis increases the amount of material being transported throughout the system and the efficiency by which its members transfer material and energy. Finally, different members may come and go, but the fundamental structure of the autocatalytic cycle remains, making the loop independent of its constituents.

Ulanowicz (1986) argued that autocatalysis streamlines the topology of interconnections in a manner that favors those transfers that more effectively engage in

autocatalysis at the expense of those that do not, resulting in networks that tend to become dominated by a few intense flows. For example, as specialists replace generalists in the process of ecological succession each species or system component exchanges material along fewer pathways. Ulanowicz (1995) then described how these effects can be quantified using a modified average mutual information equation. The statement  $p(a_i, b_j)$  refers to the probability that a unit of medium leaves component  $i$  and enters component  $j$  ( $T_{ij}$ ). 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  $\sum T_j/T$ . Finally, the conditional probability  $p(b_j|a_i)$ , that a quantum enters  $j$  after leaving  $i$  is approximated by  $T_{ij}/(\sum T_i)$ . Substituting these estimators into the equation for average mutual information yields an equation which quantifies the degree to which autocatalysis has organized or streamlined the system's flow structure.

$$AMI = \sum T_{ij}/T \log(T_{ij}T/T_jT_i)$$

Ulanowicz (1986) also developed two related concepts. First, he scales the average mutual information equation by the total system throughput (since autocatalysis tends to increase  $T$ ) to yield a network property called system ascendancy ( $A$ ).

$$A = TI = \sum T_{ij} \log(T_{ij}T/T_jT_i)$$

Ulanowicz (1980) hypothesized that in the absence of major perturbations autonomous systems tend to evolve in a direction of increasing network ascendancy – first via an increase in total system throughput, and then via increasing average mutual information as competition for limiting resources begins to streamline the network of system exchanges. The autocatalytic process tends to increase overall system throughput, efficiency, and organization, all of which result in increased system ascendancy values. Odum (1969) reached similar conclusions arguing that more developed systems usually contain a larger number of elements which exchange more material and energy among themselves over less equivocal routes. In addition, Odum (1969) found more developed systems tended to internalize or recycle waste products more efficiently, decreasing their losses to the external world and their dependence on imported resources. Finally, Mageau et al. (in press) demonstrated the

positive relationship between ascendancy and ecosystem development using a general model of ecological succession.

Ulanowicz (1986) identified a third information index: 'system uncertainty' ( $H$ ). This is the upper bound on the total uncertainty if we had no information regarding material exchange. Uncertainty also reflects the total complexity of the system,

$$H = \sum (T_{ij}/T) \log(T_{ij}/T)$$

or the total number of potential pathways of material exchange between system components. As a natural system develops, and autocatalysis streamlines the exchange network, AMI increases approaching  $H$  as information replaces uncertainty. Ulanowicz multiplies  $H$  by total system throughput ( $T$ ) to yield 'development capacity' ( $C$ ). Therefore, with ecosystem development in the absence of perturbation, as AMI approaches  $H$ ;  $A$  approaches  $C$ .

#### Measuring resilience

Measuring the resilience of a system is difficult because it implies the ability to predict the dynamics of that system under stress. Predicting ecosystem impacts over time generally requires dynamic simulation models (Costanza et al., 1990). There are two different definitions on resilience in the literature. Pimm (1984) defines resilience as the time it takes for a system to recover from stress. Holling (1986) defines resilience as the magnitude of stress beyond which the system never recovers its former state. Figure 4 illustrates these two components of resilience (Mageau et al., in press).

We combine these two ideas into a single measure of resilience. The Recovery Time ( $R_T$ ) can be estimated simply by measuring the time it takes for a system to recover from a wide variety of stresses to some previous steady state. Mageau et al. (in press) demonstrated how the maximum magnitude of stress ( $MS$ ) from which a system can recover can be measured by progressively increasing simulated stress until the system reverts to some new steady state, and documenting the magnitude of the stress that caused the shift. We then propose that an overall measure of resilience can be obtained from the ratio of  $MS/R_T$ .

When calculating this measure of system resilience the choice of indicators to be tracked over time is very important. The ordinate axis in Figure 4 indicates the candidates for this function. The population of a single species would be easiest to track, but would tell us

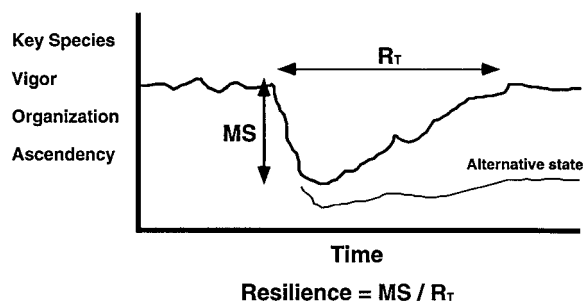


Figure 4. The two components of resilience, and how they are integrated into a single quantitative measure. Candidates for tracking system performance through time are listed on the vertical axis. The lower line indicates the alternative state of a system which was unable to completely recover from stress.

the least about the entire system's response to stress. As discussed earlier, increasingly complicated measures such as those suggested for vigor, organization and their combination (ascendancy) will tell us more about the system's response, but at the expense of ease of measure and reliability. Mageau et al. (in press) concluded that AMI may serve as the most sensitive indicator for this purpose.

This comprehensive empirical measure of resilience can be used to test the ability of other indicators to serve as proxies or quantitative measures of resilience. The first potential proxy is the ratio of gross primary production per unit respiration (GPP/R). This ratio is a measure of the excess vigor or energy available to the system. Our hypothesis is that as this ratio increases a system has more energy in reserve which will allow it to recover from stress more easily and quickly. To test this hypothesis we plan to study the correlation between the empirically measured value of resilience and the GPP/R ratio.

The second potential proxy, Weighted Systems Overhead (L/TST) or (H-AMI), is another information index developed by Ulanowicz (1986). Overhead quantifies the number of redundant or alternate pathways of material exchange, and may be thought of as a system's ability to absorb stress without dramatic loss of function. Ulanowicz (1986) suggested that higher values of system overhead tend to be associated with systems in earlier stages of development before autocatalysis has eliminated alternative, redundant, less efficient pathways of material and energy transfer (low AMI value). Overhead values can also be high in systems containing large seed populations which have the potential to maintain system vigor and efficiency under different conditions (an example of high H value). As with the GPP/R ratio the correlation

between weighted systems overhead and our empirical measure of resilience will be determined.

In conclusion, field experiments, network analysis, and simulation modelling studies can be used to generate trophic exchange networks. These networks can then be used to calculate Ulanowicz's (1986) system level information indices (TST, AMI, H), the field measures (GPP, Biodiversity, and GPP/R) and the empirical measure of resilience (MS/Rt) to test their ability to serve as proxies for measuring our three main components (vigor, organization, and resilience) of system health.

### A network analysis-based quantitative assessment of ecosystem health

In this section we demonstrate how vigor, organization, and resilience can be folded into a single comprehensive assessment of ecosystem health. This comprehensive health assessment could be constructed using any of the various measures of Costanza's (1992) three components of health. For example, Mageau et al. (1995) illustrated an ecosystem health plot based entirely on the network analysis measures of vigor, organization, and resilience. If vigor, organization, and resilience are approximated by TST, AMI and H-AMI, respectively, then the fundamental components of ecosystem health suggested by Costanza (1992) could be quantified given only a system's network of material exchanges. Taken a step further, ascendancy can be calculated by  $(TST * AMI)$ , and overhead can be calculated by  $(TST * (H-AMI))$ . Therefore, a quantitative assessment of ecosystem health which depicts a system's ascendancy versus its overhead can easily be constructed (Figure 5). As the vigor of a system increases the system is driven out away from the origin. The position of the system in regard to the diagonal depends on the relative ratio of ascendancy to overhead. A highly ascendent or organized system will plot above the diagonal, and a system with high overhead or resilience will plot below the diagonal. As a general hypothesis, we believe that systems with a balance between organization and resilience within a given range of system vigor can be characterized as 'healthy'. In other words, an ecosystem must be free to develop in the absence of serious perturbation to realize its full potential while maintaining adequate resilience to insure against stress, and vigor to quickly recover from small-scale perturbations.

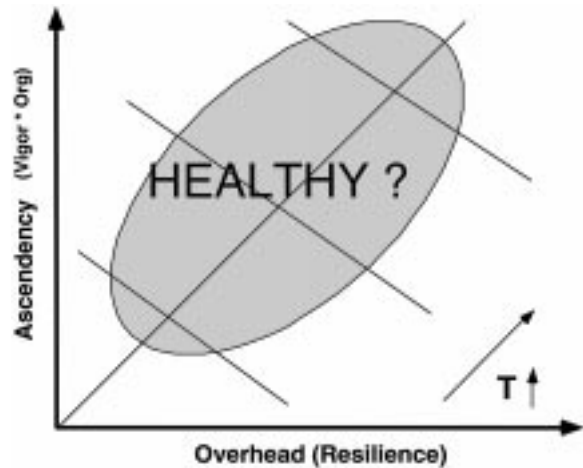


Figure 5. A conceptual diagram of the network analysis-based quantitative index of ecosystem health. The 'healthy' region is indicated by the shaded area, and represents a balance between system vigor, organization, and resilience.

Ulanowicz's (1980) increasing ascendancy hypothesis provides the criteria by which a system's trajectory through development is analyzed. 'Healthy' ecosystems are those characterized by unimpeded natural development trajectories. In general, as ecosystems develop following some large-scale perturbation, their characteristic trajectories move along the plot from an area of low ascendancy and high resilience to an area of higher ascendancy and lower resilience. However, these trajectories differ depending on the predictability of the system's external environment. All natural environments have some degree of unpredictability, and this natural uncertainty will ultimately impede the development trajectory of the system, protecting it from excessive loss of resilience. Due to wide fluctuations in the relative predictability of natural environments the 'healthy' region is system specific. For example, estuaries are very dynamic environments relative to the open ocean. Therefore, the healthy region for estuaries will shift towards the resilient portion of the plot, and that of the open ocean will shift towards the ascendent portion. With a general knowledge of this background natural perturbation, we can quantify the effects of more dramatic anthropogenic perturbations on the development trajectories or 'health' of ecosystems. Thresholds which signal the point at which a system can no longer recover from a perturbation may be determined and used as the outline for a system's 'healthy' region.

Several estimates of ecosystem material and energy exchange networks appear in the literature (Wulff



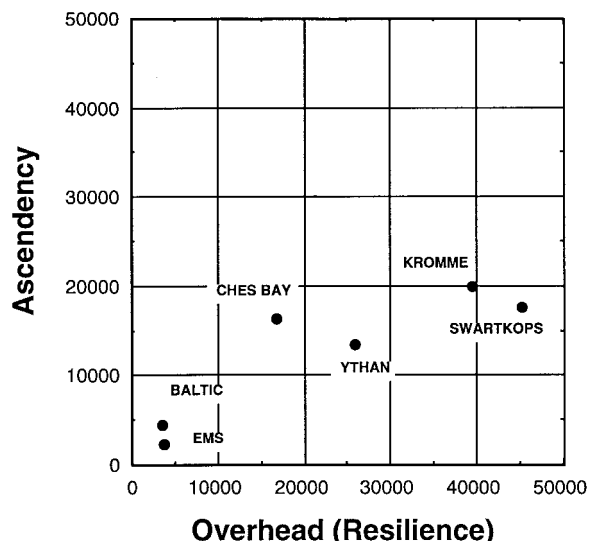


Figure 6. A comparison of the relative positions of six different estuaries using the network analysis-based assessment of ecosystem health.

et al., 1989). We initially tested our ecosystem health assessment using exchange networks representing six different estuaries (Baird & Ulanowicz, 1993). The resulting plot indicates the position of each estuary in regards to its characteristic ascendency, overhead, and total system throughput (Figure 6). The combined effects of natural and anthropogenic stress on the degree of system development are illustrated by the ecosystem health plot. For example, the Swartkops and Kromme estuaries have the highest values of total system throughput. The Swartkops is a warm, productive, well-mixed estuary subject to high levels of agricultural and industrial pollution, and is, therefore, subject to high levels of both natural and anthropogenic stress which have hindered its development. The Kromme estuary is also subject to high levels of natural perturbation due to its extremely unpredictable environment, but it is a relatively pristine estuary, and this may explain its more 'healthy' position on the ecosystem health plot. Similar arguments can be made for the other estuaries. Given data sufficient to construct reasonable estimates of exchange networks, comparative plots are an excellent way to quantify the relative health of various similar ecosystems (Baird & Ulanowicz, 1993).

Several flow networks have also been generated using simulation model output (Wulff et al., 1989). Estimating flow networks using simulation models allows one to study the time series of a system's response to a perturbation, and also to study the effects of many dif-

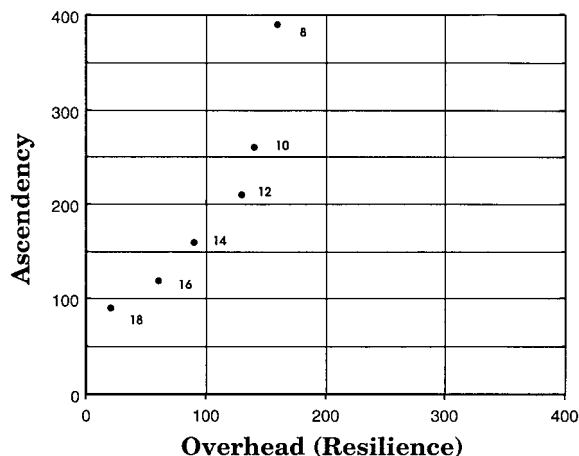


Figure 7. A comparison of the relative position of an open-ocean plankton community various days after an upwelling event using the network analysis-based assessment of ecosystem health.

ferent perturbations. The position of successive days following the simulated effects of an upwelling event using data from the southern Benguela region (Field et al., 1989) is shown in Figure 7. Essentially, this plot illustrates the successional development trajectory of an open ocean plankton community recovering from a natural perturbation. According to Field et al. (1989), the upwelling event provides a pulse of nitrogen, and flushes most members of the plankton community out of the system. In the initial days of the simulation the pulse of phytoplankton growth and associated increase in total system throughput both begin to decline along with an increase in system overhead. But, as time progresses, and nitrogen limitation increases, the relative ascendency begins to increase at the expense of overhead as competition for limiting nitrogen increases system efficiency. By the 18th day following the upwelling event the simulated system has returned to a condition characterized by high ascendency, low overhead, and low total system throughput – exactly what you might expect for a highly efficient, nutrient limited, open ocean, plankton community.

## Conclusions

In this paper we offer a comprehensive definition of ecosystem health based on a system's characteristic levels of vigor, organization, and resilience. We identify several potential measures of these health components ranging from common field measures to network analysis indices to measures derived using simulation models. We explain how these various measures of

vigor, organization, and resilience can be folded into a comprehensive assessment of ecosystem health, and provide an example using the network analysis indices. Finally, the potential of such an assessment was demonstrated using a variety of flow networks obtained from (Wulff et al., 1989). In general, we feel the proposed health assessment has the potential to allow comparison of the relative health of similar ecosystems, and the response of particular systems to natural or anthropogenic stress.

The various indices described in this paper need to be compared, and their potential for serving as useful measures of vigor, organization, and resilience needs to be tested. Trophic exchange networks from a wide variety of aquatic ecosystems (Christensen, 1995) will be required for such an analysis. The various measures of vigor, organization, and resilience can then be combined to form overall ecosystem health plots, and these plots can be compared to hypothetical plots based on existing theory (Ulanowicz, 1986; Odum, 1969) and the results of theoretical modelling studies (Mageau et al., in press).

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