

Quantifying the trends expected in developing ecosystems

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Abstract

In this paper we describe an assessment of ecosystem health that is both comprehensive in that it is based on a series of common trends associated with the process of ecological succession, and operational in that the indices capable of quantifying these trends can be easily calculated given appropriate simulation model output or estimates of material exchange. We developed a simulation model which generated output characteristic of an ecosystem advancing through the various stages of succession to test the ability of a suite of systems-level information indices to quantify these trends. Our regression analyses suggest that these indices may be able to capture the trends associated with ecological succession, hence the reversal of many of these trends characteristic of ecosystem response to anthropogenic stress. We further argue that indice performance could be enhanced with the use of more dynamic modelling techniques. In addition, we introduce a methodology for the valuation of non-marketed ecosystem components which could be easily included with our assessment of ecosystem health. We conclude that this measure of ecosystem health in combination with the valuation technique may provide an informative compliment to many past and future regional modelling projects aimed at better understanding and managing the impacts of anthropogenic stress on our regional ecosystems. © 1998 Elsevier Science B.V. All rights reserved.

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1. Introduction

We need to arrive at a healthy balance between our stocks of human-made (HMC) and natural

capital (NC) if we are to continue to survive on this planet. In the past, we have been largely unable to quantify the effects of anthropogenic stress on our natural ecosystems with the degree of certainty required to influence policy decisions. Popper (1990) argues that the natural world is causally open at all scales of observation including those occupied by ecosystems, and suggests

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our inability to predict ecosystem behaviour (Abrams, 1994) is due not to lack of information regarding system dynamics, but to the fact that these systems are intrinsically indeterminate. Therefore, rather than continue to pursue the unattainable goal of predicting ecosystem behaviour, we must begin to use our best current information to reach consensus on predictions of what factors would likely lead to the sustainability of ecosystem structure and function, and develop policy in a flexible, adaptive framework capable of incorporating rather than obviating this uncertainty (Costanza and Ruth, 1998). Crucial to this task is the development of a systems-level measure of ecosystem health which is comprehensive, operational and capable of encompassing the uncertainty associated with ecosystem dynamics.

1.1. Definitions and measures of ecosystem health

Many researchers have attempted to define and develop operational and meaningful definitions and indicators of ecosystem health. Leopold (1941) contributed to the practice of 'land health' by identifying indicators of 'land sickness'. Rapport et al. (1985) expanded on Leopold's original indicators arriving at what he called ecosystem distress syndrome (EDS). Costanza (1992) summarized the wide variety of proposed concept definitions of ecosystem health based on EDS: Health as homeostasis; as absence of disease; as diversity or complexity; as stability or resilience; as vigor or scope for growth; and as balance between system components. Karr et al. (1986) stated that a biological system can be considered healthy when its inherent potential is realized, its condition is stable, its capacity for self repair when perturbed is preserved, and minimal external support for management is needed. Kerr and Dickey (1984) suggested evaluating ecosystem health using the size distribution of biota. Schaefer and Cox (1992) stated that health is achieved when functional ecosystem thresholds are not exceeded. Schindler (1990) provided a detailed account of whole lake acidification experimentation demonstrating a sequence of abnormal signs of ecosystem structure and function. Smol (1992) defined a healthy ecosystem as one that existed

prior to human cultural impact. Odum (1985) and Ulanowicz (1986) suggested that stressed ecosystems are characterized by an inhibition or even reversal of the trends associated with ecosystem development. Costanza (1992) suggested that an ecosystem is healthy if it is stable and sustainable that is if it is active, maintains its organization and autonomy over time and is resilient to stress. Finally, there is a related body of literature that uses the term 'integrity' in place of 'health' when referring to ecosystem transformations under stress, and they generally consider a healthy ecosystem to be pristine (Karr, 1993; Kay, 1993; Woodley et al., 1993; Westra, 1994).

Unfortunately, for each of the above definitions of ecosystem health and integrity there are many methods of measuring or quantifying the particular symptoms of distress resulting in an inordinate number of ecosystem health indicators. These range from single species indicators (Kerr and Dickey, 1984) to a composite of species (Karr, 1991) to measures of biodiversity to system level measures of ecosystem structure, function and organization (Ulanowicz, 1986; Schindler, 1990; Costanza, 1992) to very broad measures which go beyond the biophysical realm and include human and socio-economic aspects (Rapport, 1992). As one increases the complexity of the indicator its relevance increases, but the associated uncertainty increases as well making it more difficult to measure and operationalize the concept. Costanza (1992) discussed this trade-off between ease of measure and relevance (Fig. 1). Therefore, the challenge is to develop a comprehensive definition of ecosystem health that embodies many of the concepts discussed above, and to identify and quantify large-scale ecosystem phenomena which are sensitive to the effects of anthropogenic stress.

Costanza (1992) suggested a comprehensive, multiscale, dynamic, hierarchical measure of system vigor, organization and resilience would serve as an excellent definition of ecosystem health. These concepts are embodied in the term sustainability which implies the systems ability to maintain its structure (organization) and function (vigor) over time in the face of external stress (resilience). Vigor is a measure of system activity,

metabolism or production. Organization is a measure of the number and diversity of interactions between the components of a system, and resilience refers to the ability of a system to maintain its structure and function in the presence of stress (Mageau et al., 1995). Costanza and Patten (1995) describe the debate surrounding the definition of sustainability, and suggest that much of the discussion is misdirected because sustainability is not a definitional concept, but more one of prediction. For example, you cannot demonstrate the sustainability of any ecosystem until after the fact, much like the fitness of an organism. When applied to complex systems such as ecosystems, predictions regarding sustainable configurations are typically highly suspect, and as such should be subjected to elaboration, discussion and debate. Maintaining the sustainability of a system's vigor, organization and resilience embodies all the definitions of ecosystem health discussed above.

1.2. Trends associated with ecosystem response to stress

Fortunately for our purposes, the literature contains a rich history documenting robust trends or patterns associated with the response of a wide variety of ecosystems to many different perturbations. These trends are specific enough to be quantified with a unique suite of indices, and yet comprehensive enough to serve as meaningful, systems-level indicators of ecosystem response to anthropogenic stress.

Woodwell (1967) described various changes in ecosystem structure and function typically associated with the natural process of ecological succession: (1) diversity tends to increase as new niches are occupied; (2) competition increases efficiency and reduces redundancy within a given niche while decreasing the level of competition between niches; (3) nutrient inventories, storage and cy-

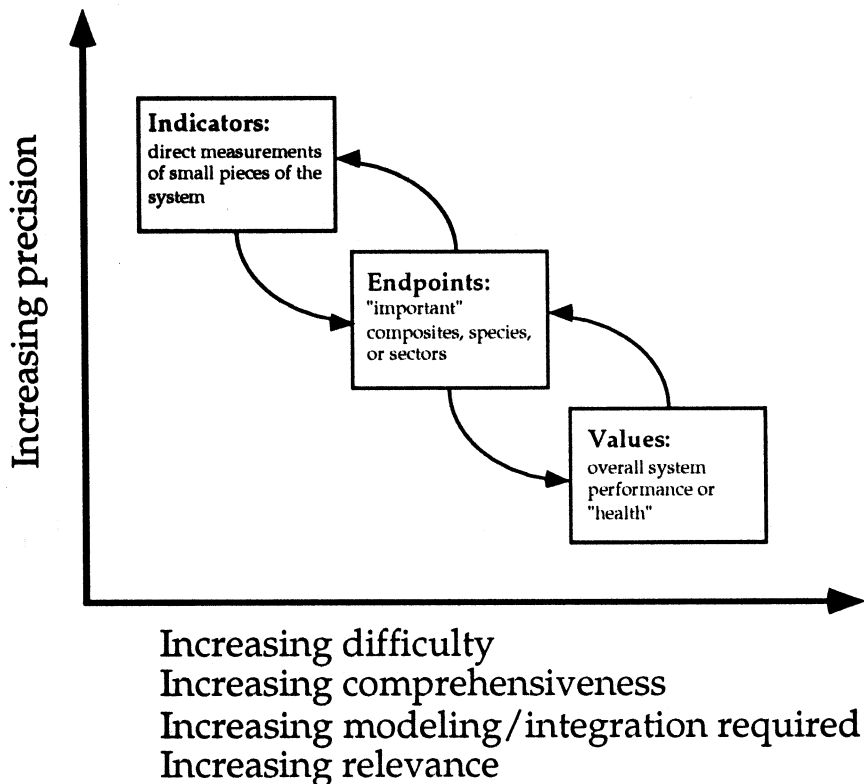


Fig. 1. Diagram depicting the general trade-off between ease of measure and overall relevance of the index (Costanza, 1992).

cling increase; (4) the structural and functional stability of the ecosystem increases, and the ratios of production per unit biomass and respiration tend to decline. If, during this process of successional development, one or more factors essential to the system became exhausted or limited, the process of succession is halted or slowed, respectively. Woodwell (1967) further reasoned that if the system was exposed to an extreme natural or anthropogenic stress, the successional development would not only be halted but reversed. Therefore, the opposite of the trends discussed above would indicate an ecosystem that is stressed. Woodwell (1967) tested these hypotheses by irradiating a section of climax oak/pine forest, and found the pattern from the zone receiving the highest levels of radiation to the lowest was the exact opposite of the pattern of natural succession.

Woodwell (1970) further discussed the implications of his findings in the 'irradiated forest.' He was struck by the fact that changes in vegetation patterns along the gradient of radiation exposure were similar to those found along natural gradients of increasing environmental stress such as those associated with increasing elevation along exposed mountain slopes, salt spray and water stress. He also found that the species surviving intense radiation were very similar to those found in typically stressed areas such as roadside ditches, gravel banks and places with unstable soils. In addition, the changes in his climax forest system paralleled those found in association with the oxides of sulphur radiating from Sudbury's smelters (Gorham and Gordon, 1960) and the replacement of Vietnam's extremely diverse forest canopies with bamboo in the wake of massive herbicide applications (Tschirley, 1969).

Odum (1985) developed a more complete list of certain well defined development trends to be expected in stressed ecosystems, and provided a history of theoretical and empirical evidence documenting their occurrence. Odum (1985) argued that increasing community respiration, unbalanced P/R ratios, increasing P/B and R/B ratios, increasing dependence on external energy, and increased export of unused primary production are energetic trends to be expected in stressed

ecosystems. He also provided evidence of increased nutrient turnover, horizontal transport and loss from stressed ecosystems coupled with decreasing internal nutrient cycling. In addition, Odum (1985) highlighted several changes in community structure and function. The proportion of R -strategists tends to increase while the size and life-span of organisms tends to decrease. Food chains shorten as the result of reduced energy flow to higher trophic levels, and biodiversity tends to decline along with an increase in the redundancy of parallel pathways of material exchange. Finally, Odum (1985) suggested evidence of these trends may serve as an excellent ecosystem-level indicator of stress.

Schindler (1990) tested Odum's hypotheses regarding the trends expected in stressed ecosystems by analyzing the effects of nutrient enrichment and acidification on whole-lake ecosystems. Schindler's analysis supported Odum's hypotheses to a large extent. For example, the acidified lakes were characterized by: increased periphyton community respiration, P/R ratios, nutrient export, R -strategists among zooplankton, and decreased utilization of allochthonous inputs, vertical cycling of nutrients, life-spans of fishes, benthic crustaceans, sizes of zooplankton and chironomids, length of food chain, species diversity and efficiency of resource use, all of which support Odum's hypotheses. Schindler also found no evidence of increasing P/B and R/B ratios, no change in exported primary production, a decrease in the horizontal transport of nutrients, a decrease in R -strategists among the fish, and an increase in the average size of phytoplankton all of which apparently contradict Odum's hypotheses, but the majority of these exceptions were explained within the confines of the paradigm. In the eutrophied lakes Schindler (1990) again found general support for Odum's hypotheses, despite a few apparent, often explainable, exceptions.

The most studied, and arguably the most important trend in Odum's list is loss in biodiversity. This trend has a great deal of support from past studies, and has several serious ramifications regarding ecosystem structure and function. Recent work by Tilman et al. (1996) has cast some light on a long-standing debate regarding biodiversity

and ecosystem stability. Elton (1958) suggested decreased diversity would lead to decreased ecosystem stability. McNaughton (1977) presented data on plant productivity in the Serengeti supporting Elton (1958) and Vitousek and Hooper (1993) found the rates of many ecosystem processes were increasing but saturating functions of species diversity. On the other side of the debate, May (1973) using a simple model of multi-species competition showed population dynamics were progressively less stable as the number of competing species increased. Others (DeAngelis, 1975; Gilpin, 1975; Pimm, 1979) reached similar conclusions resulting in a consensus lasting two decades that decreased population stability would lead to decreased ecosystem stability.

Tilman et al. (1996) provided evidence from 12 years of experimentation with 207 grassland plots exposed to the stress of extreme drought that both sides of the debate were correct, and only the assumption that less species stability would lead to less ecosystem stability was in error. Tilman et al. (1996) found that year to year variability in total community biomass was lower in high diversity plots, and the change in community biomass resulting from the stress of drought was negatively correlated with diversity. Finally, in addition to resistance, they found the plots with a higher species diversity recovered more quickly as well (resilience). He also found year to year variability in species abundance was not stabilized by biodiversity suggesting that biodiversity stabilizes community and ecosystem processes, but not population processes. He concluded the difference between species and community biomass resulted from inter-specific competition when stress negatively impacts some species others are allowed to proliferate maintaining ecosystem function while increasing variability in species abundance.

In addition, the literature documents evidence of a positive relationship between biodiversity and productivity. Naeem (1994) looked at the rivet (Ehrlich and Ehrlich, 1981) versus the redundancy (Walker, 1992) hypotheses which mark the extremes along a continuum of belief regarding the contribution of individual species to ecosystem function. They worked with three different levels of biodiversity and found system production was

highest in the most diverse system, and that production levels varied less than in the less diverse systems. Tilman and Downing (1994) found the stress of drought resulted in less production decline in more diverse plots, and that the more diverse stands recovered quicker. Tilman et al. (1996) presented evidence supporting both the diversity-productivity and the diversity-sustainability hypotheses. They found more diverse plots were able to achieve higher productivity, and argued this was because more variety in the strategy of nutrient use by more diverse plant communities allows for more efficient use of nutrients leading to more production. They also reported evidence supporting the diversity-sustainability hypothesis by finding less nutrient leaching in the more diverse plots, and arguing that biodiversity tightens nutrient cycles leading to more sustainable soil fertility.

Finally, there are more specific aspects of diversity that contribute unequally to ecosystem function. Walker (1995) argues that species diversity and functional diversity are important, but the diversity of species within each functional guild is most crucial to maintaining ecosystem function. Therefore, he suggests that when protecting biodiversity one should ensure functional diversity by protecting those species associated with functional guilds containing relatively few species. As Schindler (1990) and Tilman et al. (1996) noticed ecosystem function can be maintained despite loss of species diversity until the final species representing functional guilds begin to disappear. Often it is not enough to maintain high species diversity, but we must be careful to ensure high diversity within each particular guild to maintain overall system function in the face of external stress.

1.3. Quantifying the trends expected in stressed ecosystems

Ulanowicz (1986, 1997) describes six network analysis, systems-level information indices which may be capable of quantifying the changes in ecosystem structure and function associated with the process of succession. They include: (1) total system throughput (TST); (2) average mutual in-

formation (I); (3) system uncertainty (H); (4) system ascendancy (A); (5) development capacity (C) and (6) system overhead (L). These indices stem from a unique and controversial background involving causality in natural phenomenon (Ulanowicz, 1997). For example, Popper (1990) argued that we live in a world of ‘propensities’ which characterize the probability of the occurrence of any event given the situation in which the event occurred. According to Popper, the vast majority of events can be characterized by conditional probabilities with intermediate values (between 0 and 1). It is extremely rare to find an event characterized by a conditional probability of 1 (pure deterministic force) or of 0 (purely random chance of occurring). Ulanowicz (1997) argues the universe is causally open at all scales including ecosystems, and although many events may tend to happen with high probabilities there is no fundamental determinism underlying ecosystem behaviour. He stresses that any setback in scientific progress due to acknowledging chance at the ecosystem scale could be more than offset by new discoveries emanating from a new perspective, and offers quantum physics as an example. In short, chance is part of any ecosystem transaction, and the conditional probability of any event in an ecosystem can be calculated as well as the changes in these probability assignments concurrent with changes in ecosystem structure and function, and it is these changes in probability assignments that drive the behaviour of Ulanowicz’s (1986) indices.

Ulanowicz (1986) identifies mutualism or autocatalysis between system components, connected by cyclic flow, as the underlying phenomenon influencing the changes in ecosystem structure and function measured by the 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 it’s activity it absorbs 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 exchange 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. Therefore, Ulanowicz argues that autocatalysis streamlines the topology of interconnections in a manner that favours 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 interconnecting flows.

TST is the most straight forward of the six indices. It is simply a measure of the sum total of all the inputs, outputs and materials being transferred between components within the system at any given point in time. AMI is a measure of the information we have regarding the network of material exchange within the system. If material from any particular component in the system had an equal chance of flowing to any of the potential recipients then we would have no information regarding the flow network, however, if all material from a particular component was transferred to only one of the potential recipients, we would have complete information regarding the flow structure. These extreme information values never occur in ecosystems, but, Ulanowicz (1986) hypothesizes that AMI increases with ecosystem succession as autocatalytic competition streamlines the network of material exchange. A is simply the product of AMI and TST. Ulanowicz (1980) hypothesized that A increases with successional ecosystem development as autocatalysis increases both TST and AMI.

System uncertainty (H), or Shannon’s diversity of individual flows, represents the total number and diversity of flows in a system given some amount of TST. It is a measure of the total uncertainty embodied in any given configuration of flows. C is simply the product of TST and H . C increases as the number and diversity of flows H in a system increases due to the increases in system diversity and TST associated with succes-

sion. TST is limited by the amount of input in combination with the second law of thermodynamics. H increases as a given amount of TST is partitioned among a greater number of exchange pathways associated with an increase in diversity. But, as the diversity increases, the smallest units are more likely to succumb to chance perturbation, hence the flow diversity H cannot increase forever. Therefore, C is limited by the limits on TST and H .

Overhead (L) is the difference between capacity and ascendancy ($C - A$). Ulanowicz (1980) hypothesized that as ecosystems undergo the process of developmental succession, A approaches C at the expense of L . At first, both A and C will increase with succession, but ultimately C will be limited. However, A can continue to increase at the expense of L . A certain level of L is crucial to the maintenance of ecosystem structure and function, hence there are limits to this trade-off of A for L . Ulanowicz (1997) partitions L into four categories: inputs, exports, dissipations and pathway redundancy, and describes the factors which constrain their magnitude.

The contribution of input overhead to total overhead decreases as a given magnitude of input is partitioned into ever fewer recipient categories. A trade-off develops between the benefits of concentrating input in the most efficient input pathways, and the vulnerability of relying extensively on too few input pathways. A decrease in the fraction of input to TST also leads to a decrease in the contribution of input overhead to total overhead. Dissipation overhead decreases with the fraction of respiration to TST, and as the distribution of respiration among system components becomes more equitable. Overhead on useable exports decreases with the utilized proportion of these exports, and the contribution they make to further increases in TST. Finally, overhead resulting from pathway redundancy decreases as the network of material exchanges becomes streamlined by the process of autocatalysis. A trade-off develops between the increasing efficiency resulting from a network of exchanges dominated by only the most efficient transfers, and the vulnerability resulting from the rigidity of such a flow configuration.

In summary, Ulanowicz (1986) offers the following description of ecological succession relative to his indices. In the early stages of ecological succession C , A and L increase due to the dramatic increase in TST associated with the pulse of growth provided by abundant resources. In the later stages of succession, resource limitation initiates the replacement of r -selected species by the more specialized and efficient k -selected species. This shift in species composition leads to higher levels of species and functional diversity increasing TST by allowing the system to better utilize limiting resources, and more efficiently transfer biomass to higher trophic levels. In addition, this shift in species composition triggers an increase in H as new flow pathways continue to evolve while new niches are exploited. AMI also increases as the flow network is streamlined to favour only the most efficient material transfers within each niche or functional guild. This competition within each niche leads to a decrease in overhead as redundant flow pathways are eliminated and mortality, export and respiration rates decrease. At some point the species occupying the most fragile of niches are eliminated by chance perturbation depending on the frequency and severity of natural or anthropogenic stress. This phenomenon provides an upper bound to the potential for increases in H , and the laws of thermodynamics provide an upper bound on TST resulting in an upper bound on C . At these later stages of ecological succession TST, H and C essentially level off, but AMI can continue to increase relative to H , hence, A relative to C at the expense of L . A will continue to increase at the expense of L with C remaining essentially constant until the network of exchanges becomes too brittle or vulnerable to any change in external conditions. Each system develops an optimal balance between A and L depending on the variability of its external environment. Therefore, the indices taken in combination may be capable of quantifying the trends associated with the process of ecological succession, and the reversal of these trends apparent in ecosystems subjected to anthropogenic stress.

In this paper we test the ability of Ulanowicz (1986) indices to quantify trends expected in stressed ecosystems using output from a general

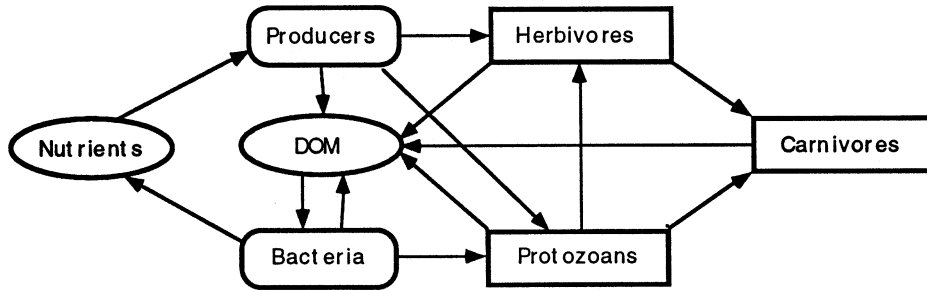


Fig. 2. A general diagram depicting the interactions between the major trophic levels in the general ecosystem model.

ecosystem model capable of depicting a range of behaviour typical of various stages of ecological succession. The resulting correlations support our hypotheses regarding indice response to successional trends suggesting the indices may be used to measure the response of any particular ecosystem to stress provided it is characterized by an appropriate, well-calibrated simulation model, or data directly characterizing material exchanges between system components.

2. Materials and methods

2.1. Model development

We constructed a simple pelagic ecosystem model in STELLA to test the ability of Ulanowicz (1986) system-level, information indices to quantify the trends described above. There were five major living components in the model representing four trophic levels, and two nonliving storages of nutrients and organic matter (DOM) (Fig. 2). Each trophic level contained several different species with differing degrees of functional specialization (Fig. 3). The 'A' species in each trophic level represented generalists (also the 'B' species in the protozoan and carnivore trophic levels), and the 'B, C, D and E' species in each trophic level represented specialists. In addition, the various model coefficients were adjusted to assign the generalist species growth kinetics typical of *R*-strategists (high growth rates, high nutrient K_s values, high respiration rates etc...), and the same was done with the specialists to make their growth kinetics

typical of *k*-selected species (low growth rates, low nutrient K_s values etc...). Therefore, when the system was dominated by the 'A' species it exhibited behaviour typical of an early succession ecosystem, and when the system was dominated by the 'B/C/D/E' species it exhibited behaviour typical of a late successional ecosystem.

The relative dominance of any particular producer or bacterial species depended largely on their growth rates, respiration rates and their abilities to utilize available supplies of nutrient and DOM, respectively (Fig. 4). The relative dominance of species in higher trophic levels depended largely on their feeding efficiencies, respiration rates, mortality rates and the species distribution at the producer and bacterial trophic levels (Fig. 4). However, there were also important 'top down' feedbacks which depended on the feeding rates and efficiencies of the species present in the higher trophic levels. The net result of this dynamic tension between 'bottom up' and 'top down' feedback mechanisms was model output characteristic of an ecosystem advancing through the various stages of ecological succession.

Finally, nutrients entered the system via external input and internal recycling which was directly proportional to DOM regeneration, and exited the system via export and producer uptake (Fig. 5). DOM entered the system via external input, excretion and mortality from the living components within the system, and exited the system via export and regeneration depending on bacterial ingestion in combination with species specific regeneration efficiencies (Fig. 5). The rate of external input and export of nutrients and DOM was held constant throughout the entire simulation.

2.2. Indice calculation

We calculated Ulanowicz (1986) system level information indices within the STELLA model, so we could track these values over the course of any simulation. Ulanowicz (1986) describes the calculation of the network analysis based, systems level information indices in detail, so we provide only a brief summary in this paper. Of the three network measures TST was the most straight forward to calculate. In our ecosystem model TST was measured as the sum of all material being transferred from donor compartment 'i' to recipient 'j' over all flow pathways in any particular time step (Eq. (1)).

$$TST = \sum T_{ij} \tag{1}$$

$$AMI = \sum T_{ij} * \log(T_{ij} * TST / T_j * T_i) \tag{2}$$

$$H = \sum T_{ij} / TST * \log(T_{ij} / TST) \tag{3}$$

$$A = TST * AMI \tag{4}$$

$$C = TST * H \tag{5}$$

$$L = C - A \text{ or } = TST * (H - AMI) \tag{6}$$

AMI and *H* represented the sum of each unique individual compartment's information and uncertainty values, and were calculated within the simulation model using Eqs. (2) and (3), respectively. Where T_i is the sum of all material leaving the *i*th component, and T_j is the sum of all material entering the *j*th component. Ascendancy is simply the product of TST and AMI, and capacity is the product of TST and *H* (Eqs. (4) and (5)). We have chosen this particular form of ascendancy in place of the more comprehensive biomass-inclusive version because it has a definitive upper bound which allows the calculation of corresponding overhead values (Ulanowicz, 1997). Finally, overhead is the difference between *C* and *A*, or the difference between *H* and AMI scaled by TST, and was calculated using Eq. (6).

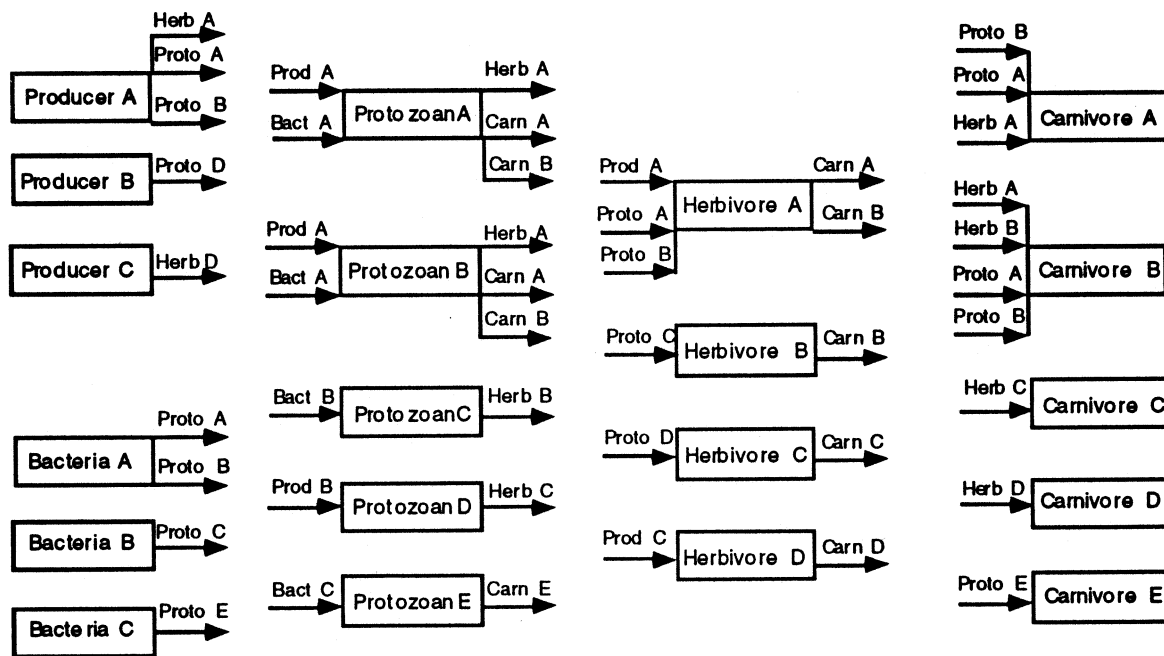
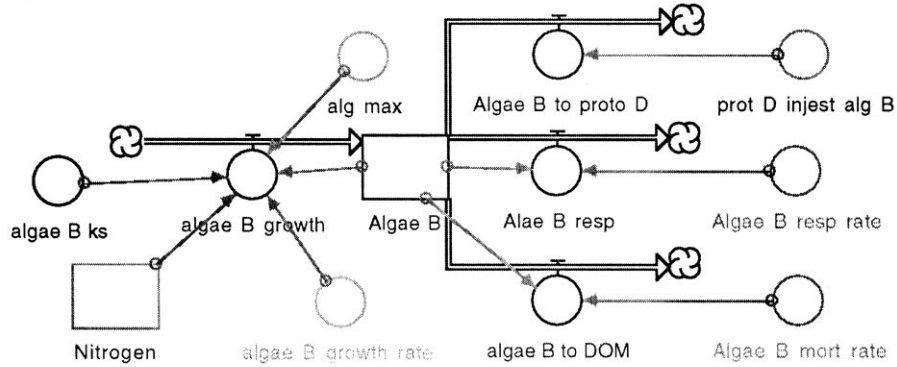


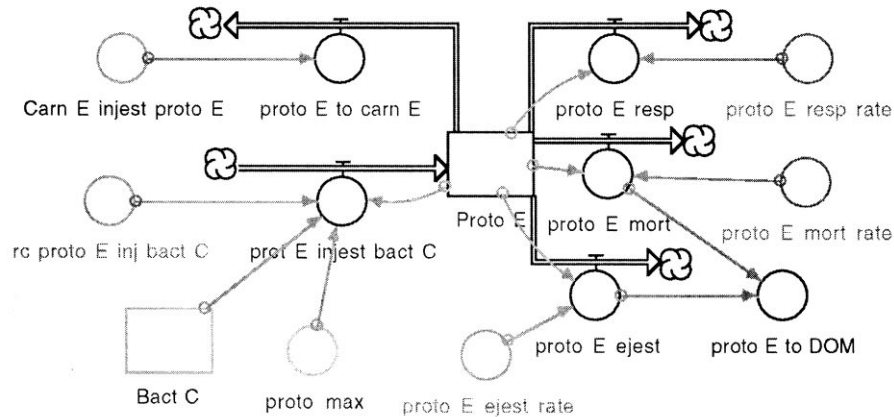
Fig. 3. The complete network of living components in the general ecosystem model. The various levels of specialization are depicted as well.

Producer B



Growth Equation = Producer A * growth rate * (Nutrient / Nutrient + ks) * (1 - Producer A / Producer max).

Protozoan E



Proto E inject Bact C = rc proto E inject Bact C * Bact C * Proto E * (1 - Proto E / proto max).

Fig. 4. The conceptual diagram and growth equation for a primary producer which is representative of the bacterial species as well, and a protozoan which is representative of all species in higher trophic levels.

2.3. Hypotheses and regression analyses

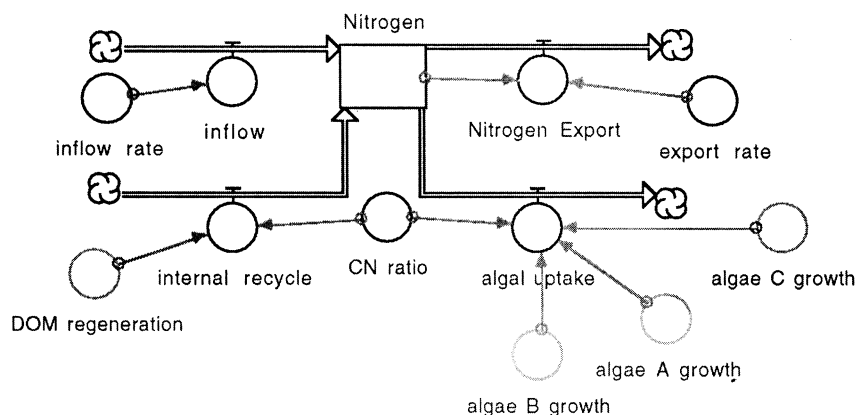
We formulated several hypotheses regarding the response of the indices to the trends discussed above, and tested them by regressing the ratio of the biomass representing the sum of species 'A' biomasses (and the 'B' species in the protozoan and carnivore trophic levels) to the total system biomass with TST, AMI, H , A , C and L . Our hypotheses were divided into those regarding en-

ergetics, nutrient dynamics and community structure. With regards to energetic trends, dominance by species 'A' in each trophic level, given their growth kinetics, should have led to increased respiration rates, export rates, P/B and R/B ratios. These energetic trends should have led to a relative increase in overhead at the expense of ascendancy for any given value of TST. Therefore, we hypothesized a positive correlation between overhead and dominance by species 'A',

and a negative correlation between ascendancy and dominance by species 'A'. From a nutrient perspective, the 'A' species were characterized by low K_s values, and were ingested less efficiently by higher trophic levels. In addition, a percentage of each were lost from the system. These characteristics should have led to a decrease in the efficiency by which nutrients are cycled within the system, and a loss of nutrients from the system. Therefore, we hypothesized a negative correlation between

ascendancy and species 'A' resulting from a decrease in TST and a relative increase in overhead. Finally, from a community structure perspective, dominance by the 'A' species should have led to a relative increase in r -selected species dynamics, and a decrease in the diversity of functional guilds participating in the system. We hypothesized that these trends would lead to a decrease in capacity, ascendancy and overhead, and to a relative increase in overhead at the expense of ascendancy.

Nutrients



Dissolved/Particulate Organic Matter

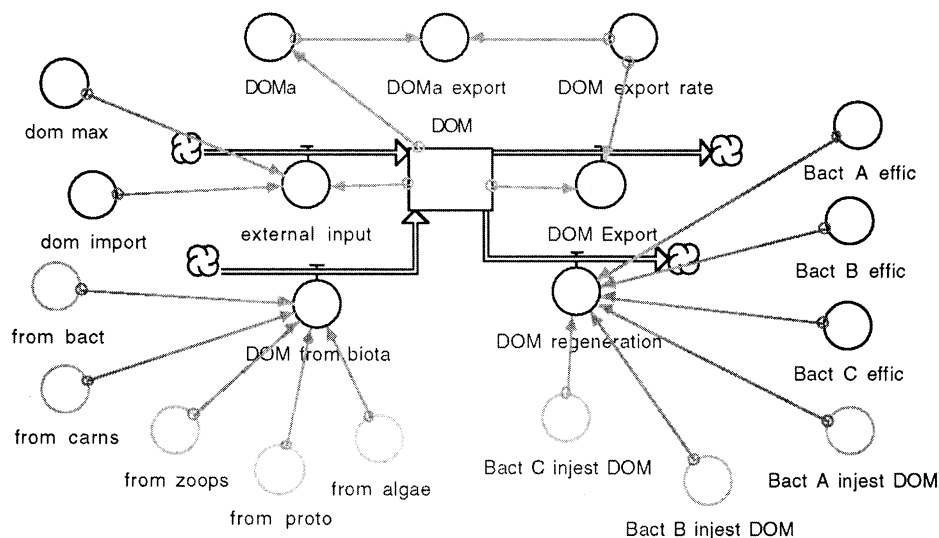


Fig. 5. The conceptual diagram of the nutrient and dissolved/particulate organic matter components indicating the major inputs and outputs to and from these components.

Overall, dominance by members of the ‘A’ species should have produced behaviour characteristic of early successional ecosystems which should have led to increases in overhead at the expense of ascendancy for any given capacity and TST. Whereas, an increase in dominance by members of the B, C, D, and E species should have produced behavior characteristic of late successional ecosystems which should have led to relative increases in ascendancy at the expense of overhead for any given capacity and TST. In addition, dominance by the more efficient species B, C, D and E should lead to an overall increase in TST, AMI and H , and drive corresponding increases in ascendancy, capacity and perhaps overhead depending on the relative influence of TST.

3. Results

3.1. Component biomass values

Fig. 6 depicts the carbon biomass of each system component over the course of the entire simulated successional event. Supplies of available nutrient and DOM declined to limiting levels by the midpoint of the simulation, and remained at those levels for the duration. The primary producer and decomposer components displayed similar behaviour. The total biomass of each component category increased throughout the entire simulation while species B and C essentially replaced species ‘A’ by the midpoint of the simulation. The protozoans and herbivores exhibited the same basic pattern including an increase in total biomass throughout the entire simulation along with a replacement of the generalist species by the specialists around the midpoint of the simulation. Finally, carnivore biomass also increased throughout the entire simulation, however, the C, D and E species were unable to completely replace the A and B species as they did in the other trophic levels.

3.2. Network information indices

Fig. 7 depicts the response of the systems-level, network, information indices to the component

biomass results described above. Capacity (C) and its two components overhead (L) and ascendancy (A) increased throughout the first half of the simulation, and then levelled off in the second half. Average mutual information (AMI) also increased in the first half of the simulation and then levelled off in the second. System uncertainty (H) increased rapidly at the start of the simulation, double-peaked and then declined by the midpoint remaining constant for the latter half. Finally, total systems throughput (TST) increased throughout the entire simulation, but at a slower rate in the latter half.

Fig. 8 illustrates the response of overhead and its five components per unit TST to the simulated results described above. This total weighted overhead index declined throughout the entire simulation, but at a more rapid rate in the first half. The five components of overhead also declined throughout the entire simulation, but at differing rates. The weighted measures of export and input overhead declined at the fastest rate, DOM and respiration overhead components declined at an intermediate rate, and the overhead attributed to internal transfers declined at the slowest rate.

3.3. Regressions: biomass ratios versus indices

Fig. 9 illustrates the relationship between the various network indices and the ratio of r -selected species biomass to total system biomass (BR). There was a strong negative correlation between C , A , AMI and TST ($R^2 = 0.94, 0.97, 0.96, 0.96$, respectively) and the BR. L was also negatively correlated with the BR, but the correlation was not as strong ($R^2 = 0.88$). However, the overall L/TST measure was positively correlated with the BR ($R^2 = 0.91$). Finally, there was no correlation between the BR and H ($R^2 = 0.02$).

4. Discussion

4.1. Simulated successional changes in species composition

We attempted to create an ecosystem model capable of simulating the general process of eco-

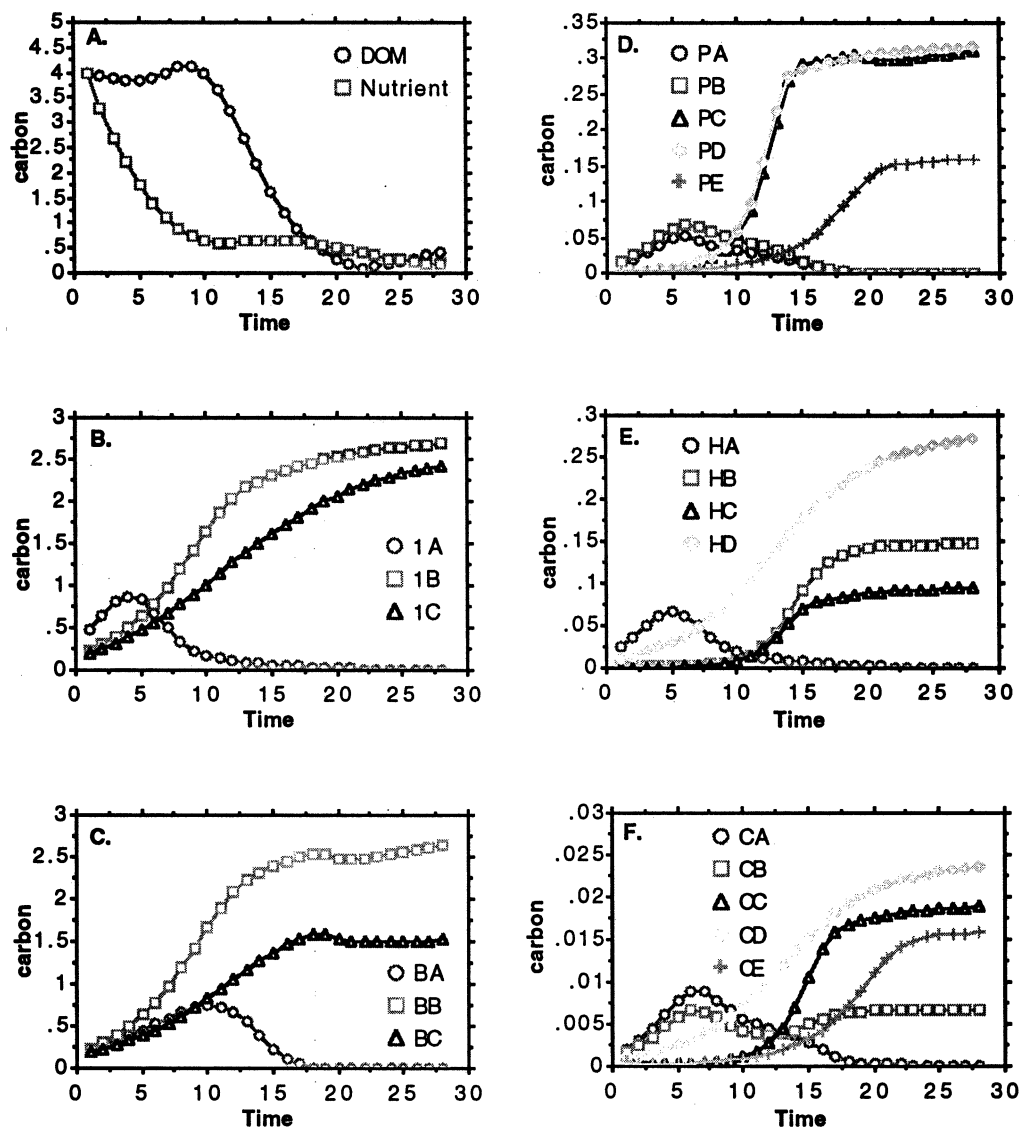


Fig. 6. The biomass value in carbon of each of the main system components throughout the entire simulated ecological succession event. Each graph depicts all the species within a given trophic level. (A) Nutrients and DOM; (B) primary producers; (C) bacteria; (D) protozoans; (E) herbivores; (F) carnivores.

logical succession discussed above (Woodwell, 1967; Odum, 1985; Rapport et al., 1985; Tilman et al., 1996). In our model the relative supply of Nutrient and DOM influenced the species composition and relative biomass of the primary producer and decomposer trophic levels respectively (Fig. 6A,B,C). The *r*-selected species in

these trophic levels had much higher growth rate and half-saturation parameters than their *k*-selected counterparts. Therefore, their initial rapid growth caused the decline in nutrient and DOM which ultimately led to a shift in species composition in favour of the more efficient (lower half-saturation parameters) *k*-selected species. This in

turn influenced the species composition and relative biomass of species representing the higher trophic levels. In general, as the levels of DOM and nutrient

declined throughout our simulated version of ecological succession the k -selected species replaced the r -selected ones at the lowest trophic levels

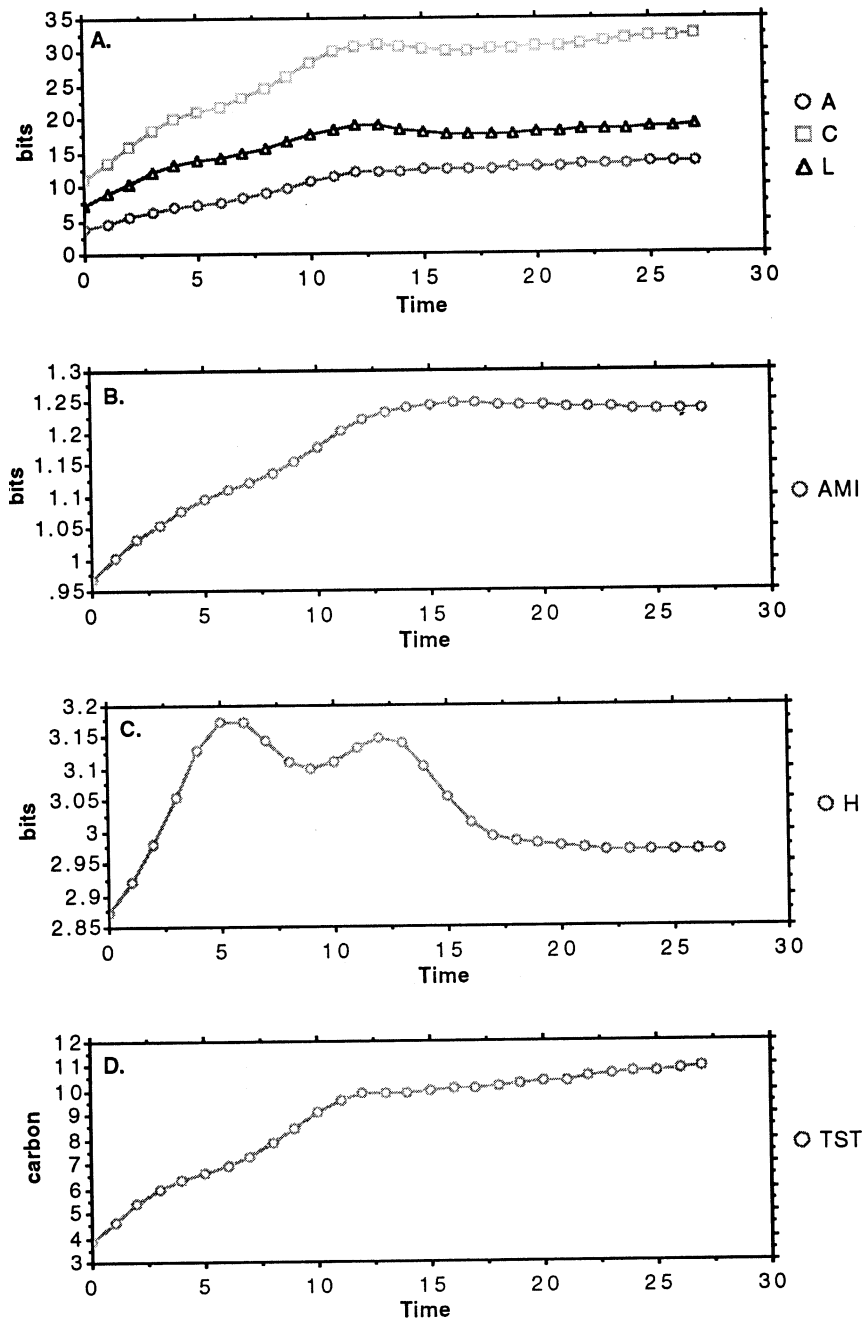


Fig. 7. Index values throughout the entire simulated ecological succession event. Information is measured in units of 'bits', and TST in units of carbon.

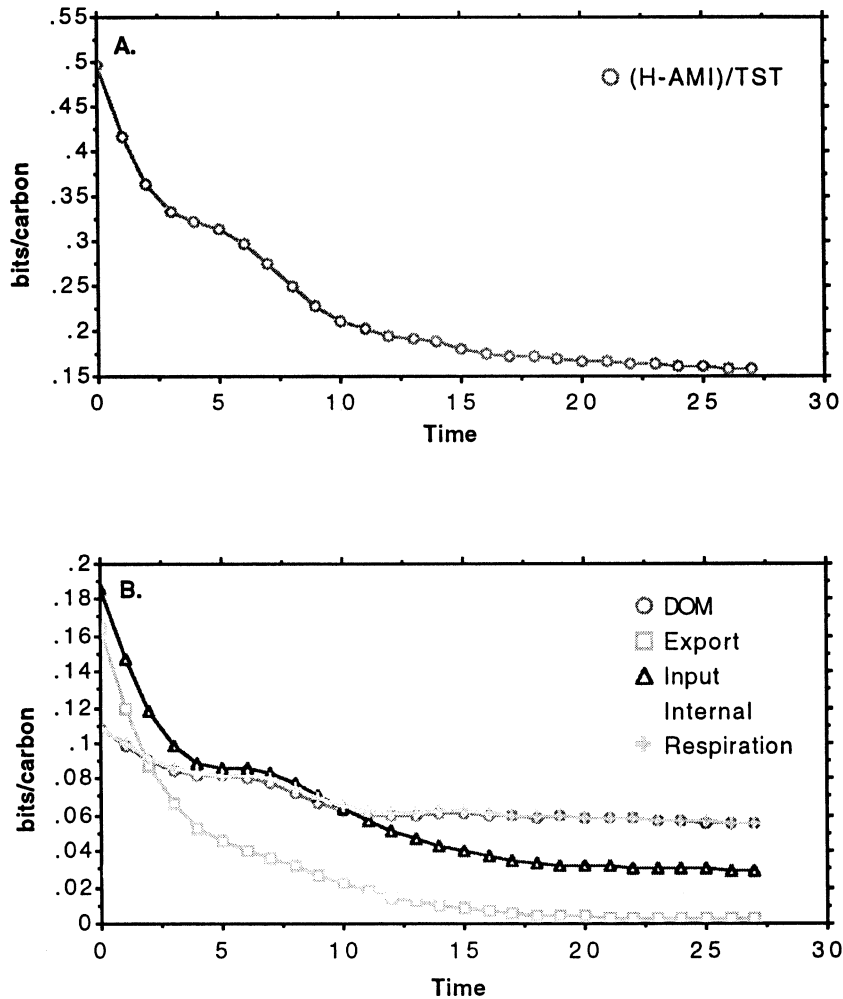


Fig. 8. The value of total system overhead (A) and its five components (B) divided by TST over the entire simulated ecological succession event. Units are in bits/carbon.

leading to similar species compositional shifts at successively higher trophic levels (Fig. 6D, E, F).

Due to the differing characteristics of our simulated r and k -selected species the above compositional shifts led to the following changes in system characteristics: (1) higher biomass values within each trophic level as species with more efficient growth kinetics better incorporated limiting resources, and more efficiently transferred their biomass to successively higher trophic levels; (2) increased TST as higher biomass values led to more material transfer between components; (3) a more streamlined flow network as

increasing dominance by specialist species decreased the redundancy of pathways of internal material transfer; (4) decreased community respiration and export of unused primary production per unit biomass; (5) increased diversity of both species and pathways of material transfer between them as specialists occupied more niches than their generalist counterparts. Each of these system characteristics are, of course, representative of the trends associated with ecological succession. The remaining question is how do the network indices respond to these system dynamics?

4.2. Indice response to simulated successional trends

In general the system-level, information indices responded to our simulated ecological succession event as hypothesized indicating that they may serve as a useful measure of the trends associated with ecological succession, hence, the arrestment or reversal of these trends associated with anthropogenic stress. Ascendancy (*A*) increased

throughout the simulation due to increases in its two components AMI and TST (Fig. 7A, B, D). The rate of increase in *A*, AMI and TST was greatest in the first half of the simulation corresponding to the gradual replacement of *r*-selected species by the more efficient and specialized *k*-selected species within each trophic level. The greater efficiency of the *k*-selected species led to higher levels of TST, and their specialization (fewer pathways of material exchange per species)

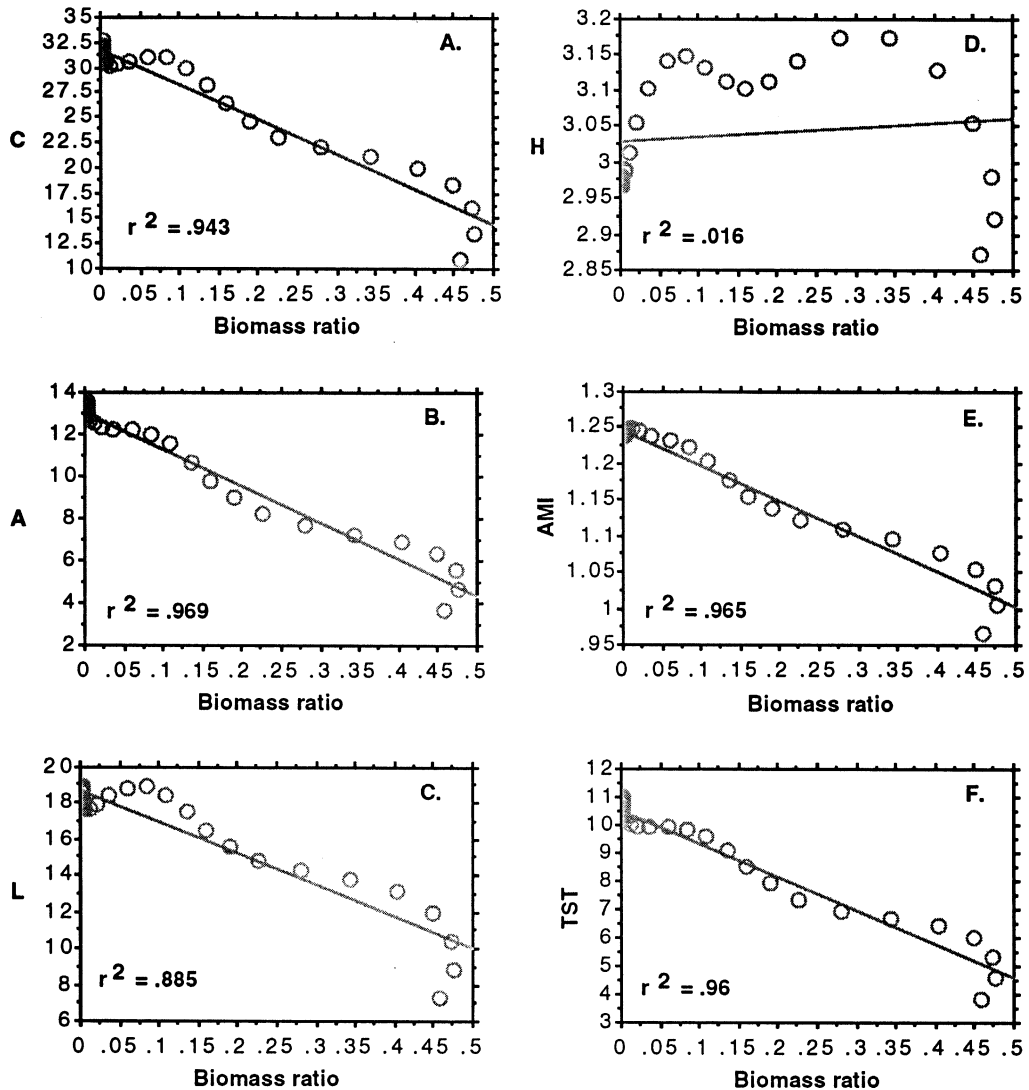


Fig. 9. A phase-plane plot of the relationship between the Biomass Ulanowicz (1986) network, information indices. (A) Capacity; (B) ascendancy; (C) overhead; (D) uncertainty (E) average mutual information; (F) total system throughput.

led to higher values of AMI. After the midpoint of the simulation the rate of increase in AMI was near zero, whereas TST and A continued to increase, but at a much slower rate. Steady co-dominance by the limited number of k -selected species in the second half of the simulation likely constrained any further rise in AMI, and the gradual increase in TST as the result of slowly increasing biomass fueled the slight rise in A .

Capacity (C) increased throughout the simulation in a manner similar to that of TST. However, at the midpoint of the simulation there was a slight decline in capacity which corresponded with the noticeable decline in uncertainty (H) following its double peak (Fig. 7A, C, D). Uncertainty is a measure of the diversity of material exchange pathways, and increases as a given amount of TST is more equally partitioned into ever more pathways (Ulanowicz, 1986). The double peaks in uncertainty corresponded to the period in the simulation when all species existed as the specialists were slowly replacing the generalists. It was at this unique point in the simulation when the number of pathways of material exchange per unit system throughput was at its peak. H then levelled off after a steep decline corresponding to the point when the generalist k -selected species completely out competed their r -selected counterparts and dominated for the remainder of the simulation. Therefore, the behaviour of capacity was largely the result of TST, but the slight decline at the midpoint of the simulation, and the decreased slope in the second half of the simulation was attributed to declines in H .

Overhead (L) also increased throughout the simulation in a manner similar to TST. However, L showed a slight peak at the midpoint of the simulation followed by a gradual decline in the third quarter, and then a gradual increase in the fourth. L is measured as the difference between C and A , or as $TST(H - AMI)$ (Ulanowicz, 1986). Because AMI was nearly constant for the entire second half of the simulation the behaviour of L was largely determined by the rate of increase in TST and decline in H . In the third quarter of the simulation the rapid decline in H overcame the slight increase in TST resulting in the slight decline in L . In the fourth quarter of the simulation

H levelled off and the slight increase in L was attributable to the slight increase in TST.

This behaviour in L was inconsistent with our hypotheses. According to theory (Ulanowicz, 1986) overhead should decrease with ecological succession as A approaches C , or AMI approaches H . These phenomena occur as the more efficient specialists tend to dominate the food web resulting in a greater diversity of flow pathways, but fewer connections per node, less mortality, less respiration and export per unit biomass, and inputs which are partitioned into fewer components. L increased throughout the simulation because of the dominant influence of TST. However, L/TST declined throughout the simulation in a manner more consistent with our hypotheses (Fig. 8A). In addition, each of the five components of overhead also declined throughout the simulation when corrected for the dominant influence of TST (Fig. 8B). Further evidence supporting our hypotheses comes from the fact that AMI approaches H in the second half of the simulation as AMI remains constant while H declines, and this leads to a slight convergence in the A and L curves as A makes up a larger proportion of C (Fig. 7A, B, C).

Finally, as a more empirical measure of the ability of the network indices to quantify the trends associated with ecological succession we plotted and quantified the relationship between each indice and the ratio of the biomass of the r -selected species with the total system biomass (BR) (Fig. 9). A low BR indicates dominance by k -selected species and represents a system in the later stages of ecological succession. Whereas a higher BR indicates dominance by r -selected species characteristic of an early successional ecosystem. Therefore, the strong negative correlation between the BR and A , C , AMI, and TST supported our hypotheses based on the theory behind the network indices. We hypothesized that overhead would be positively correlated with the BR, but as explained earlier a negative correlation resulted due to the dominant effects of TST. However, the fact that the correlation was weaker than that of A , C , AMI and TST lends some support to our initial hypotheses. In addition, there was a strong positive correlation between

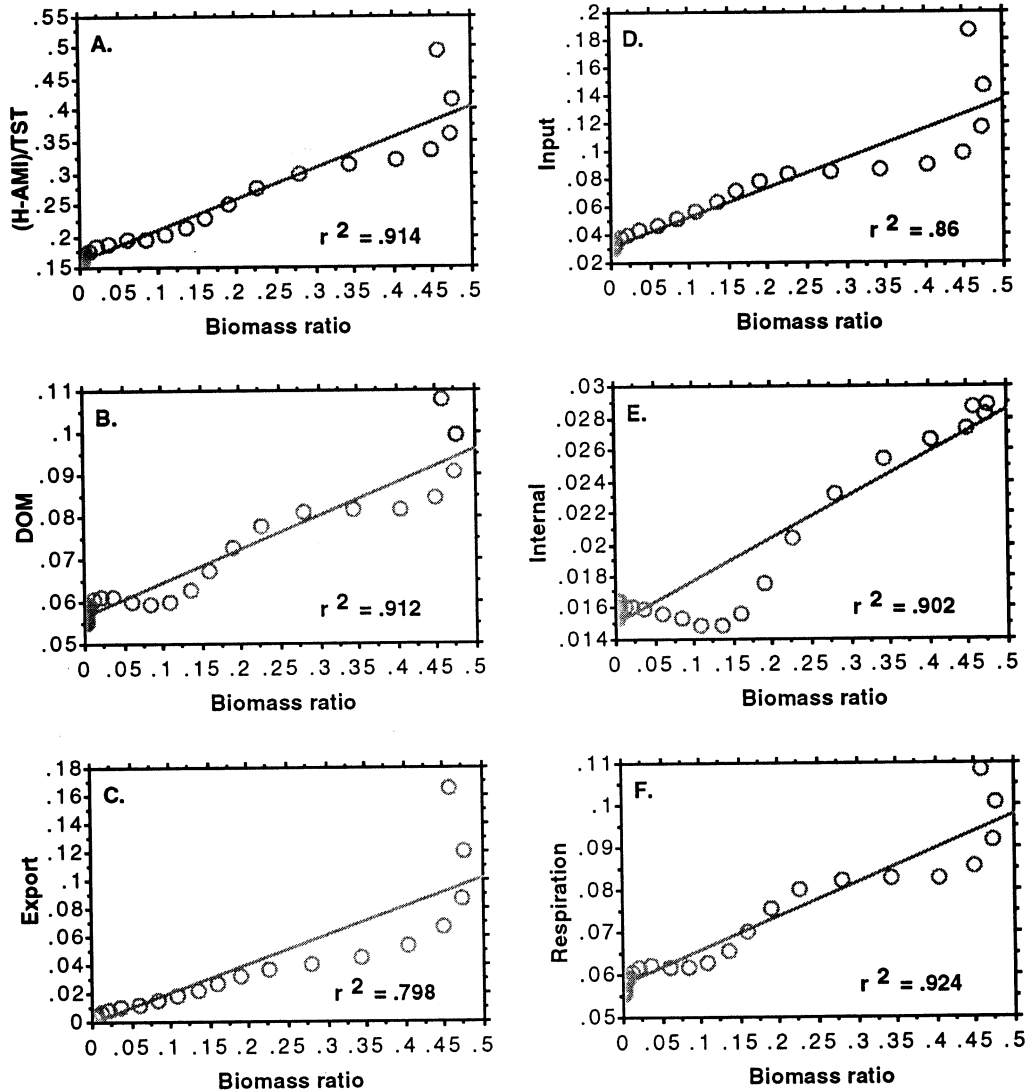


Fig. 10. (A) A phase-plane plot of the relationship between the value of total system overhead per unit TST and the biomass ratio; (B–F) the relationship between each of the five components of overhead per unit TST and the biomass ratio.

the BR and the overhead values per unit TST (Fig. 10A, B).

4.3. Limitations of simulation modelling

Overall, the behaviour of the suite of network indices in relation to our simulated ecological succession event was largely consistent with Ulanowicz (1986) theory of indice response to

ecosystem development. In the first half of our simulated ecological succession event we witnessed a dramatic increase in TST, *A*, *C*, and *L* as available resources were quickly utilized. In addition, the BR declined as the *k*-selected species replaced their *r*-selected counterparts leading to the dramatic increase in AMI. Finally, *H* peaked when all species in the system were equally represented at the midpoint of the *r* to *k*-selected dominance shift.

In the second half of our ecological succession event TST, C , and A continue to increase slightly while AMI, H and L essentially level off. The continued increase in TST, C and A are consistent with our hypotheses, however we also suspected AMI would continue to increase while H remained fairly constant and L declined. In hindsight these apparent contradictions can be attributed to limitations imposed by our simulation model that would likely be absent in natural systems. For example, in our model the maximum number of species in each trophic level was either three, four or five. This resulted in a cap on the value of H , and the peaks in H corresponding to the points in the simulation when all species were co-dominant. Beyond this point as the k -selected species attained clear dominance biodiversity and H actually declined from their co-dominance peaks. In a natural system as diversity increases with succession H would likely continue to increase well beyond the levels representing the relatively early successional co-dominance of r and k -selected species. This suggests that determining the appropriate levels of aggregation may be crucial to the success of using simulation models in combination with the network indices to measure the health of any given ecosystem.

Another problem with our simulated succession event was that TST tended to dominate the more interesting contributions of AMI and H throughout the entire simulation. In the later stages of succession changes in AMI and H should dominate the relatively small changes in TST. The problem is that ecosystem simulation models are typically rigid in structure, and offer only a mechanical description of ecosystem dynamics. Once the original framework of a model is set, the values representing the component biomasses and their interconnecting flows can vary dramatically, but new components or pathways of medium exchange between them (changes in network topology) often cannot arise, nor can previous ones disappear.

Ulanowicz (1986) indices are sensitive to both changes in the relative magnitude of medium transferred within a static network topology, and changes in the actual topology itself. In our simulation model, the network topology was fixed, so

our indices were only responding to the first of these two factors, and TST tended to dominate the more subtle effects of AMI and H . In natural systems, of course, the topology of food webs are not fixed. A simulation model capable of capturing each of these factors would lead to far more variability in the measures of AMI and H , hence A , C and L . Jorgensen (1986, 1988a,b, 1992) describes a new generation of structurally dynamic simulation models based on goal functions which evaluate the unique parameter set that optimizes the function at each particular time step, and which may be capable of depicting the interesting changes in network topology often missed by more traditional modelling approaches. It is crucial to develop these more dynamic simulation models capable of simulating changes in network topology if Ulanowicz (1986) indices are to be used to measure the hindrance or reversal of the trends associated with ecological succession.

Christensen (1995) used Odum (1969) list of successional attributes to develop and index of ecosystem maturity, and examined the correlation between his maturity index and many of Ulanowicz (1986) indices using 41 steady-state models of aquatic ecosystems. Christensen found that overhead was positively correlated with his index of system maturity. This is in agreement with our findings discussed above, although counter to Ulanowicz (1980) hypothesis. As described above, we suggest that the dominating effects of increasing TST along with ecological succession or maturity relative to the more subtle effects of AMI and H typical of topologically rigid simulation model output may explain this apparent positive correlation. In fact, Costanza suggests replacing TST with net system throughput (NST) which would simultaneously avoid the problems associated with the dominant effects of TST over H and AMI, and make the analysis independent of scale or the level of system aggregation.

Christensen also found that relative ascendancy (A/C) was negatively correlated with his maturity index, which is directly opposed to Ulanowicz (1980) hypothesis, and our report of ascendancy increasing along with the process of ecological succession. The measure of A/C can be reduced to AMI/ H . Ulanowicz (1980) hypothesized that at

some point in the later stages of ecological succession the value of H will no longer increase as chance perturbations effectively trim further increases in diversity. However, AMI can continue to increase despite the relatively constant value of H as a greater proportion of material flows along the most efficient transfer pathways. Prior to this point in the later stages of ecological succession both AMI and H are hypothesized to increase, and it is possible that H may increase faster than AMI as organization lags behind increasing flow diversity. Therefore, the negative correlation between A/C and maturity may be attributed to the fact that none of the systems analyzed by Christensen (1995) had advanced beyond this critical point in maturity, or the simulation models representing these systems were simply unable to capture the subtle changes in network topology that would drive the hypothesized relation between maturity and A/C .

4.4. Valuation of non-marketed ecosystem products and services

The ecological economic literature describes many techniques aimed at the valuation of non-market ecosystem products and services. These techniques range from the strictly biophysical approaches such as embodied energy (Costanza, 1980) to a variety of contingent valuation approaches based primarily on the cognitive decisions or preferences of human beings. Each of these methods have their strengths and weaknesses based on their relative abilities to capture the biophysical and preference components of value, and the degree of uncertainty their estimates contain.

Ulanowicz (1997) describes a robust valuation technique based on a modified version of ascendancy which incorporates component biomass values. In this approach, the contribution of each component to the overall system ascendancy represents the value of the stocks stored there in the context of the functioning of the entire ecosystem. Therefore, the ascendancy characterizing a particular component in the system represents the relative value of that component as a member of the functioning ecosystem. The ascendancy for each

component can be easily calculated along with the indices described above, and can be converted to a monetary value given some ratio of dollars/ascendancy. This ratio can be determined from a component in the system with a defined market value (i.e. salmon or lumber). This ascendancy based valuation technique is extremely inclusive and easy to calculate, but it provides only a conservative estimate of value relative to some marketable ecosystem product.

One must obtain a comprehensive estimate of the value of the entire ecosystem in question for use in place of the value of a single species to overcome the problem of overly conservative individual component value estimates (Costanza et al., 1997). A better estimate of overall ecosystem value, hence individual component values, could be obtained by summing the known market values of the many products and services the system provides, and including a conservative estimate of any additional instrumental and intrinsic value. This estimate of overall system, hence individual component value would be no more arbitrary than any other valuation technique currently offered, and would be more comprehensive than one based on only the value of a single species. In regards to overall system valuation, the same trade-off (between precision and comprehensiveness) characterizing the various measures of ecosystem health appears to arise. Perhaps, in addition to developing an ecological economic model, a group of individuals with a vested interest in the particular system could arrive at a consensus regarding the optimal balance between precision and comprehensiveness while estimating the value of their particular ecosystem (Costanza and Ruth, 1998). Finally, given the uncertainty embodied in any estimate of overall ecosystem value, it may be extremely useful to consider the most likely consequences of such an estimate on the health of the ecosystem when making a valuation decision. The valuation procedure suggested here would provide such immediate feedback, and the opportunity to factor the likely consequences of any particular estimate on the health of the ecosystem into the decision making process.

5. Conclusion

We feel the ecosystem health assessment described in this paper is both comprehensive in that it is based on the system-wide trends expected in stressed ecosystems, and operational in that the indices can be calculated given output from appropriate simulation models. Our general simulation model successfully depicted many of the trends characteristic of ecological succession (Odum, 1969), and, in many cases, Ulanowicz (1986) indices responded to these trends as hypothesized. The apparent discrepancies were likely attributed to limitations inherent in typical simulation models such as limited diversity due to aggregation, and the dampening effects of rigid network topology on the variation of H and AMI relative to TST. We suggest these indices may be used to quantify the trends associated with ecological succession, hence the reversal of these trends associated with anthropogenic ecosystem stress. Finally, an ascendancy based valuation methodology can be included as part of the analysis making it possible to not only quantify the health of a particular ecosystem, but to estimate the economic value of its individual components as well. We conclude that this assessment of ecosystem health in combination with the ascendancy based valuation technique may provide an informative compliment to many past and future regional modelling projects concerned with better understanding and managing the impacts of anthropogenic stress on our natural ecosystems.

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