

Core Network Compartments: Relative importance of ecosystems players in moving energy through the system

Ursula M. Scharler^a, Brian D. Fath^{b,c}

*a School of Life Sciences, University of KwaZulu Natal, South Africa
email: scharler@ukzn.ac.za*

b Biology Department, Towson University, Towson, USA

c Advanced Systems Analysis Program, IIASA, Laxenburg, Austria

Abstract: Ecosystems that are depicted as nodes (species groups) and links (trophic transfers) encompass well defined roles in terms of their trophic structure. Some are primary producers and furnish the system with newly bound energy or nutrients, whereas others divide themselves over various trophic levels creating a hierarchy of energy use and reuse. All waste and mortality products of nodes comprise the non-living environment of ecosystems, often supporting a considerable part of the system as detritus. All food sources are in general used, but are so to variable extents. Some links are always among the major links, e.g. flows from detritus or remineralisation from bacteria. Similarly, flows into and from high turnover nodes, which are either small species with high turnover rates, or those with disproportional high standing stock play an important role in shunting energy through the system. Ecosystem indices calculated from weighted ecological networks describing the patterns of energy flow through an ecosystem are often applied to empirical data in order to categorise the system as an efficient or inefficient energy user. We calculated flow diversity (as Shannon's Index) and average mutual information (AMI, as the degree of flow constraint) according to the method of Ulanowicz (1986). Special attention was given to the contribution of each system part to the overall holistic property. A comparison of several, mainly estuarine, ecosystems, shows that it is mostly flows involving the same species groups contributing to the bulk to the index value. These were flows from detritus, bacteria, and primary producers. The relative importance of flows from heterotrophic groups (e.g., species and species groups of macrozoobenthos, meiofauna, zooplankton, fish) compared to that of the "main" groups was comparatively minor.

Keywords: Ecological network analysis; Community Modules, Estuarine ecosystems, Species Identification; Ascendency; Flow Diversity

1 INTRODUCTION

In ecosystem level studies, the ecosystem is characterised either in terms of its behaviour as a unit, or that of species and species groups within the context of the entire system. In this paper, we investigate trophic connectivity between species and the resulting patterns of interactions in the context of the entire system.

To describe patterns of energy flows in ecosystems, indices such as Ascendency and Development Capacity have been used (Ulanowicz 1986; Ulanowicz et al. 2009). These are proposed to describe ecosystem behaviour in terms of flow constraints (Ascendency (A), Average Mutual Information (AMI)) and the diversity of trophic flows (Development Capacity (DC), Flow diversity (H)) from the

probabilities of occurrence of weighted trophic flows. A and DC are equal to AMI and H scaled by the total system throughput, TST ($AMI \times TST = A$; $H \times TST = DC$). The indices, especially Ascendency (A) and Development Capacity (DC) have been used to characterise the developmental state of ecosystems (e.g., Latham and Scully, 2002; Patrício et al., 2006), either in relation to environmental changes, or to track changes in ecosystem status over time.

AMI is usually high if there are few pathways transporting the bulk of material and at its lowest if all nodes are fully connected and links transport an equal amount of material. As such, the ecosystem index of AMI (AMI_{SYS}) importantly gives an impression on the overall flow organisation within an ecosystem in terms of its connectivity and flow distribution. H as an ecosystem index, on the other hand, gives an indication on the complexity of the ecosystem and a high H is associated with high uncertainty, complexity and diversity of flows (Ulanowicz, 1986; Latham and Scully, 2002).

The values of AMI and H depend on the magnitude of flows and connectivity of the system. There are various reasons why energy flows are unequally distributed in ecosystems, and they depend on the turnover rate of species, the unequal energy requirements of species, the various degrees of omnivory or the trophic specialisation between species, and the availability of prey.

In addition to comparing whole ecosystem indices, it may be of interest to investigate the proportional contribution of the individual trophic flows to the ecosystem index and so ascertain the importance of individual links within the context of the ecosystem. If the resolution of the network is high enough, then the importance of links from individual species can be calculated (e.g., commercially important fish, crabs, migrating species, etc.), or otherwise those from groups of species (e.g., functional groups).

The whole system indices (H_{SYS} , AMI_{SYS}) represent the sum of the index calculated for each individual flow in the system (AMI_{IND} , H_{IND}). AMI_{IND} and H_{IND} therefore describe the extent to which the individual index contributes to AMI_{SYS} and H_{SYS} . A high AMI_{IND} value denotes a single link between predator and prey for energy transfer, or the dominant link of multiple flows from a predator to various prey, whereas a low value denotes multiple outgoing links transporting a similar amount of material (i.e., there is no dominant link). AMI_{IND} thus denotes how specialised and important the trophic link is in transporting energy between two nodes. AMI_{IND} in relation to AMI_{SYS} shows how important the particular trophic flow is within the context of all flows in the ecosystem in terms of the quantity of energy transported in relation to other flows leaving the same prey.

H_{IND} , on the other hand, describes the contribution of a particular flow to the complexity of the ecosystem (H_{SYS}). Single flow H_{IND} is calculated from a combination of its contribution to complexity due to its occurrence (small or large transport along link in relation to total systems throughput, expressed as p), and the frequency of its occurrence.

In order to ascertain the roles individual species, species groups and abiotic components play in the energy transfer in ecosystems, we use the AMI and H values of individual trophic flows to firstly characterise major pathways in terms of AMI and H originating from prey. Secondly these pathways are compared for several estuarine ecosystems. This we hope to achieve by identifying those flows that contribute most to the potential for development (H_{SYS}) as well as to the realised developmental status (AMI_{SYS}) in terms of energy transfer efficiency in empirical networks.

2.0 MATERIAL AND METHODS

The indices for flow diversity (H_{IND}) and average mutual information (AMI_{IND}) are calculated from trophic flows between prey and predator, or abiotic source and

grazer or detritus feeder. In the calculations below, flows from and to the outside of the system, as well as respiration flows are not considered.

2.1 Flow Diversity (H):

The calculation of flow diversity is achieved through applying Shannon's formula to individual trophic flows. A trophic flow that is rare has a high potential to contribute to complexity, but due to its rare occurrence its actual contribution to the system is comparatively low. The actual contribution of each trophic flow, calculated by Shannon's formula as $H = -K \cdot p_i \log p_i$, can be expressed as (Ulanowicz 1986):

$$H_{IND} = -k \cdot \left(\frac{T_{ij}}{T_{..}} \right) \log \left(\frac{T_{ij}}{T_{..}} \right) \quad (1)$$

Where T_{ij} denotes a flow from compartment i to compartment j , and $T_{..}$ the sum of all flows, over all i and j compartments. The Flow Diversity index for the entire ecosystem, H_{SYS} , is taken as the sum of H_{IND} over all flows.

2.2 Average Mutual Information (AMI):

The Average Mutual Information (AMI) index is used to calculate whether the trophic flow patterns in the ecosystem contribute to ordered or random behaviour of flows between sources and sinks (Ulanowicz 1986). For example, if a node is a source to many other nodes, and energy is distributed equally along all outgoing pathways, there is highest uncertainty about which ones of the outgoing pathways will transport the quantum of energy from the originating node. However, if there is a dominant pathway, there is a higher probability that the quantum of energy will use the dominant pathway.

To calculate the degree of constraint on a flow is achieved by quantifying the information gain from probabilities of flows occurring. Firstly, the uncertainty that an event (flow) occurs is calculated by

$$H = -K \log p(a_i) \quad (2)$$

Thereafter, the uncertainty that the same event occurs is calculated from the conditional probability by knowing, in addition to what enters j , what leaves i a timestep earlier:

$$H = -K \log p(a_i|b_j), \quad (3)$$

where

$$p(a_i|b_j) = p(a_i, b_j) / p(a_i), \quad (4)$$

and $p(a_i, b_j)$ is the joint probability of the flow from species i to species j and is denoted as $T_{ij}/T_{..}$, whereas $p(a_i)$ as $T_{i.}/T_{..}$. Then, the conditional probability is subtracted from the initial probability:

$$I = -K \log p(a_i) - [-k \log p(a_i|b_j)], \text{ or} \\ I = K \log [p(a_i|b_j) / p(a_i)] \quad (5)$$

Translated into flows, the formula for gain of information is as follows:

$$I = K \log \left(\frac{T_{ij} T_{..}}{T_{i.} T_{.j}} \right) \quad (6)$$

where $T_{i.}$ Denotes all flows leaving compartment i and $T_{.j}$ denotes all flows entering compartment j . The information gain for each individual flow is weighted by the frequency of the flow in order to become AMI_{IND} :

$$AMI_{IND} = K \left(\frac{T_{ij}}{T_{..}} \right) \log \left(\frac{T_{ij} T_{..}}{T_{i.} T_{.j}} \right) \quad (7)$$

AMI_{IND} is highest, if the flow T_{ij} is the only flow leaving i and the only flow entering j . Summing all AMI_{IND} values over all trophic flows renders AMI_{SYS} .

H_{IND} and AMI_{IND} were calculated for three South African and three North American estuarine ecosystems. The indices were depicted for all flows in the system, and flows were grouped according to the identity of the outgoing node, i.e. of the source. These included Primary Producers (PP), Bacteria (B), Zooplankton (ZP), Meiofauna (MF), Macrozoobenthos (MZB), Fish (F), and Detritus (D). The groups responsible for high H_{IND} values contribute most to the actual complexity of the system. Those responsible for high AMI_{IND} values are constrained links between energy sources and sinks.

3.0 RESULTS

The distribution of Flow diversity (H_{IND}) and Average Mutual Information (AMI_{IND}) are presented for trophic flows between all sources and sinks in several estuarine ecosystems, and trophic groups contributing the bulk to H_{SYS} and AMI_{SYS} were identified.

3.1 Flow diversity (H):

The H_{SYS} indices calculated for the ecosystems were, in general, very similar (Figure 1). The largest energy flows, T_{ij} , when converted to H_{IND} , contributed most to the whole systems index of H_{SYS} . This same pattern was apparent for all ecosystems investigated, denoting the rising H_{IND} values with increasing link weight. The same compartment types were responsible for forming the bulk of the H_{SYS} value. These always included detritus, primary producers and bacteria, where detritus provides large amounts of energy to the ecosystems, and both primary producers and bacteria are characterised by high turnover rates relative to the remainder of the system and are thus able to maintain relatively high energy flows.

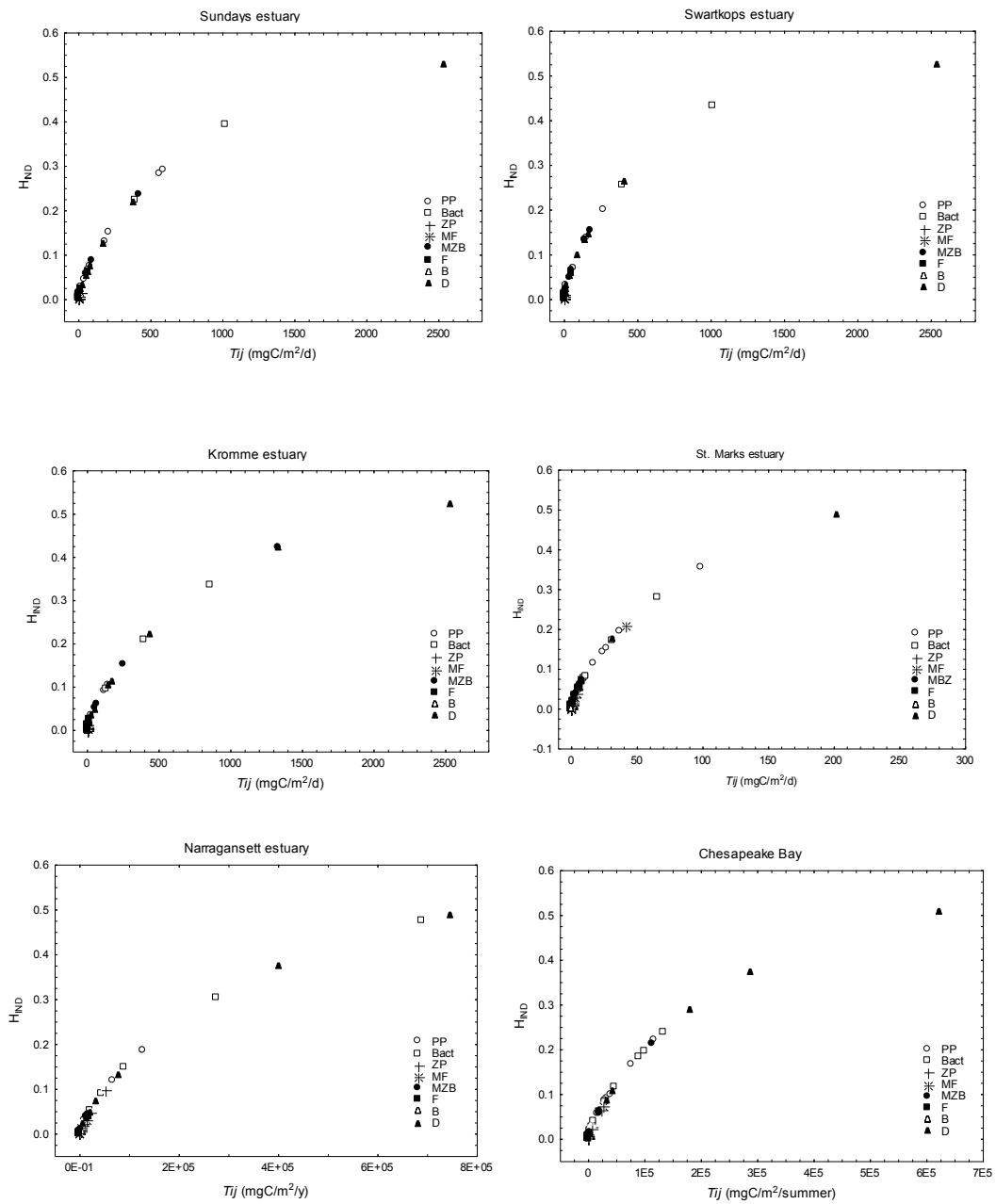


Figure 1: H_{IND} values of South African (Sundays, Swartkops, Kromme) and North American (St. Marks, Narragansett, Chesapeake) estuarine ecosystems

The proportion of trophic flows responsible for 80% of the contribution to H_{SYS} values were between 11 and 16% of all flows. Consequently, 84-89% of the flows contribute only 20% to the H_{SYS} value in all empirical networks.

The nodes the flows were originating from always included various forms of detritus, bacteria and primary producers. In some cases, bulk detritus feeders (e.g., deposit feeding or suspension feeding macrobenthos) or highly aggregated groups (e.g., meiofauna) that may have a large outflow due to the aggregation are included in the top 80%.

The nodes with the lowest contributions always include zooplankton and fish groups, incidental feeding links (e.g., those that feed on detritus and incidentally ingest bacteria) or highly disaggregated groups that consequently have small flows.

3.2 Average Mutual Information (AMI):

Similar to the H_{IND} values, there are only few AMI_{IND} values that constitute the bulk of the AMI_{SYS} values (Figure 2). Of the ca 100 to 270 trophic flows per system, between 4 and 10% contribute 80% to the AMI_{SYS} value. These links are thus contributing the bulk to the energy efficiency of the entire system and are of utmost importance in feeding available energy through the system. In general, the same nodes (mainly detritus, bacteria, primary producers), as for H_{IND} , are part of the 4-10% of flows, and similarly the higher trophic levels contribute very little to the system.

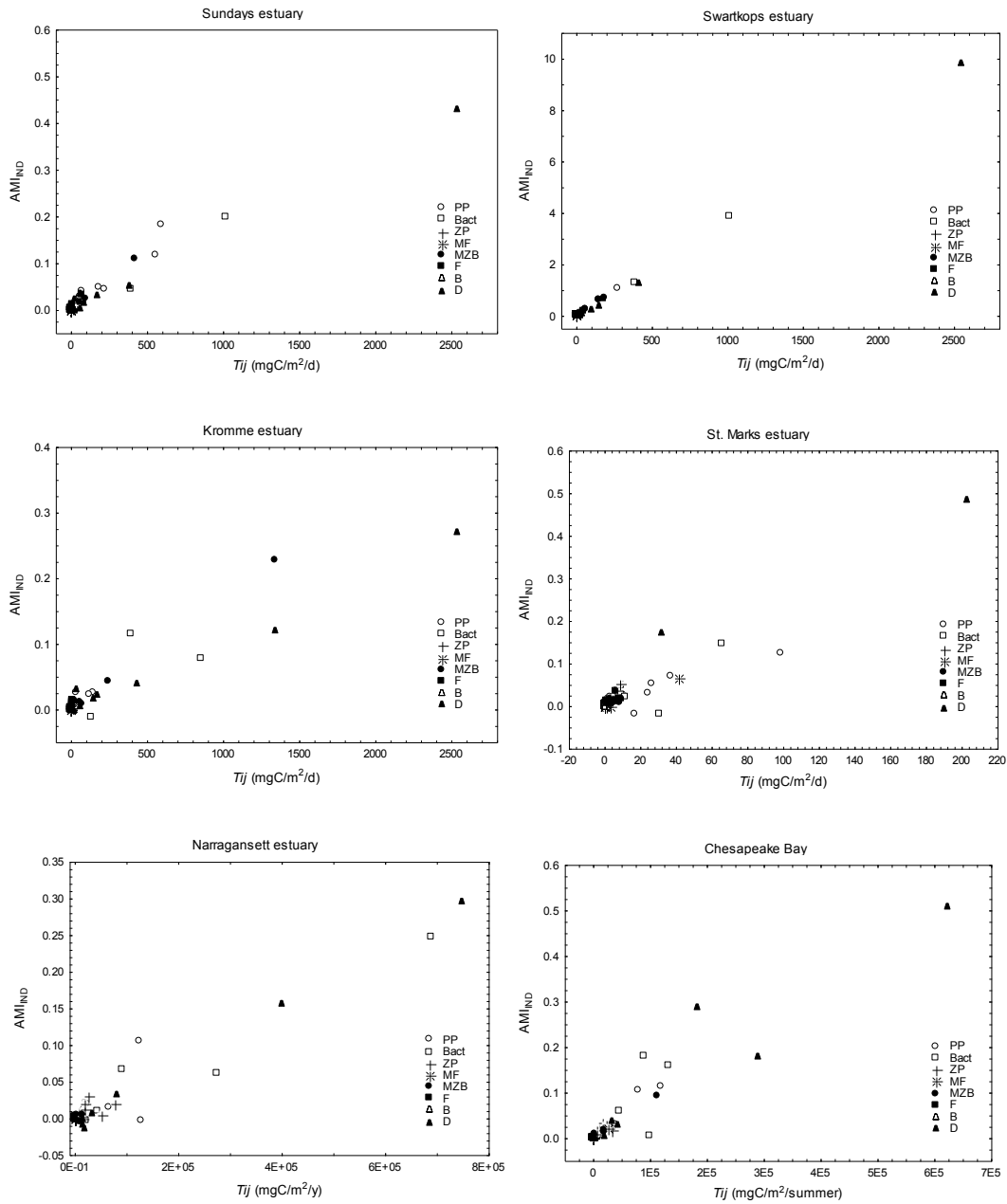


Figure 2: AMI_{IND} values of South African (Sundays, Swartkops, Kromme) and North American (St. Marks, Narragansett, Chesapeake) estuarine ecosystems.

4.0 CONCLUSION AND DISCUSSION

From the results above it is apparent that some nodes are more important than others in contributing to the energy efficiency and the potential to develop within the framework of the given amount of energy of a given ecosystem. These included mainly the lower trophic levels, both abiotic components as well as those converting abiotic energy into biomass (primary producers, bacteria). The higher trophic levels (zooplankton, fish) in general contributed very little to the overall system organisation in terms of energy flows.

The bulk of the indices that describe the potential for development are thus those that provide high energy flows relative to the other nodes of the system, either due to their high biomass or high turnover rate. In addition, the way networks are initially built plays a strong role in the magnitude of the indices. This has previously been demonstrated for Ascendency (Ulanowicz and Abarca-Arenas, 1997; Allesina et al., 2005). In this study, highly aggregated nodes which had an increased energy flow due to aggregation, also contributed more to the H_{SYS} and AMI_{SYS} values compared to if they had been disaggregated into species or smaller species groups.

The consequence from this finding is that the ongoing discussion on trends and comparability of Ascendency and Development Capacity (Ulanowicz, 1986) between ecosystems is thus also applicable to the AMI_{SYS} and H_{SYS} values, as well as H_{IND} and AMI_{IND} . A higher degree of aggregation will increase the contribution of the flow values to the system value, whereas the resolution in the assignment of feeding links will have an effect on the number of links making a small or large contribution.

This effect is apparent from the networks analysed for this study, and it is typical of many ecological networks, in that individual fish species are assigned a node, whereas primary producers, detritus, zooplankton and benthic invertebrates are mostly grouped into functional or species groups with few exceptions.

Consequently, it is of importance that in addition to the comparison of A and DC, as well as AMI_{SYS} and H_{SYS} values, the contribution of individual links is investigated. Ecosystems may thrive purely on primary producers binding energy, on detritus and their main consumers (e.g., bacteria). Other trophic groups, although important for humankind, may, purely in terms of energy flow, not be of great importance to an ecosystem. However, if H is interpreted as providing room for development, this may be the room created for higher trophic levels which, after all, are of higher importance in terms of sustainability of ecosystems for humankind.

Future studies based on this initial investigation can investigate further the trophic groups and their ranking in the H_{IND} and AMI_{IND} values, to establish clear preferences of certain nodes in certain positions. Secondly, this method is useful when comparing time series of networks of the same system. Time series are perhaps better study objects since they are in general built in the same way and missing nodes or links reflect real changes rather than the method of the researcher. Consequently, the change in the AMI_{SYS} and H_{IND} values can be tracked and the change in position of individual nodes over time in the importance of the system ascertained.

REFERENCES

- Allesina, S., C. Bondavalli, and U. Scharler, The consequences of the aggregation of detritus pools in ecological networks. *Ecological Modelling* 189, 221–232, 2005.

- Latham, L.G., and E.P. Scully, Quantifying constraint to assess development in ecological networks. *Ecological Modelling* 154, 25–44, 2002.
- Patrício, J., R.E. Ulanowicz, M.A. Pardal, and J.C. Marques, Ascendency as Ecological Indicator for Environmental Quality Assessment at the Ecosystem Level: A Case Study. *Hydrobiologia* 555, 19–30, 2006.
- Ulanowicz, R.E. *Growth and Development*. Springer Verlag, New York, 1986
- Ulanowicz, R.E., and L.G. Abarca-Arenas, An informational synthesis of ecosystem structure and function. *Ecological Modelling* 95, 1–10, 1997.
- Ulanowicz, R.E., S. Goerner, B. Lietaer, and R. Gomez, Quantifying sustainability: Resilience, efficiency and the return of information theory. *Ecological Complexity* 6, 27–36, 2009.