

**A Review of the Fundamental Measures of  
Information Theory  
and their Application in Ecology.**

**CHAPTER 3  
INFORMATION THEORY MEASURES OF  
STRUCTURAL SELF-ORGANIZATION**

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### 3-1 INTRODUCTION

In this chapter measures of structural self-organization are examined. The focus is on the production-consumption structure<sup>1</sup> of the system. While the measures presented below can, in principle, be applied to any level in the hierarchy of living systems, discussion will be limited to their application in the context of ecosystem food web structures.

The chapter is begun with a review of the fundamental measures of information theory. Previous applications of these measures to the problems of characterizing ecosystem structure and self-organization are then reviewed. This review identifies some of the problems with current use of such measures. Resolutions of these problems will be presented.

This chapter will concentrate on the mathematical formulation of information theoretic descriptions of ecological phenomena and theories. Evaluations of specific theoretical hypotheses which use an information theoretic measure or their application to specific ecosystems is done elsewhere. (See Chapter 4 and 5).

Readers, whose background is in the ecological sciences, will be familiar with information theory from its use to measure species diversity. (Pielou 1975, Grassle, Patil et al, 1979). However the reader is cautioned that the similarity between measures discussed here and measures of species diversity is limited to their mathematical origins. Information theory measures are like any of the more familiar statistical measures, such as variances, correlations etc, in that their ecological or physical meaning is determined strictly by the experiments or events they are used to describe. Connotations attached to an information measure in the context of a specific set of experiments or events are not automatically transferable to another set of experiments or events.

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<sup>1</sup> Function and structure are used, throughout, as they are defined in systems theory. Structure refers to the interconnection of components, the links between the components. Function refers to the role played by a component of the system, or played by some behavior of the whole system in the system's overall operation.

### **3-2 REVIEW OF INFORMATION THEORY**

The origin of information theory is usually associated with the work of Shannon and Weaver (1949) on communication theory. In the context of communication theory applications, the information-theoretic measures are interpreted as the amount of information conveyed by a message. Most of the development and application of information theory has been in the communication theory context. (See Aczel & Daroczy, 1975, and Reza 1961 for reviews.)

A more general interpretation of information theory does exist (Yaglom and Yaglom, 1960, Jaynes 1979). This interpretation focuses on the information gained from performing an experiment rather than the information content of a message. The experiment consists of observing which of  $N$  possible outcomes of the experiment actually occurs. Information theory measures the uncertainty the experimenter has about which experimental outcome will occur. This uncertainty equals the information the experimenter gains from performing the experiment.

Another representation of this interpretation of information theory, is as follows. Consider an observer who ascertains which event, of a set of  $N$  possible events, occurs. Information theory provides a way of measuring the uncertainty this observer has about which event will occur. Alternatively, what is measured by information theory can be interpreted as the amount of information gained, by the observer, when he ascertains which event occurs.

Regardless of whether the experimenter or observer representation is used, both deal with a situation where one of  $N$  possible occurrences is observed to happen. Associated with each of these occurrences is a probability of its taking place, relative to the other possible occurrences. Central to the generalized information theory is the interpretation of these probabilities in accordance with the "probable inference" theory of probability (as versus the more classical "frequency" theory) (Jaynes 1979, Hobson 1971). In this theory the probability of a specific occurrence represents the best estimate of the experimenter (or observer) of the likelihood of the specific occurrence relative to all of the possible occurrences. The observer uses all the knowledge available to him in making this estimate. Jaynes (1957, 1979) has developed a formal mathematical technique, the Maximum Entropy formalism, for deriving the probability

distributions which incorporate all of the observer's knowledge, and only this knowledge. (See Appendix I. <http://www.fes.uwaterloo.ca/u/jjkay/pubs/thesis/a1.pdf>)

Under the probable inference interpretation probabilities reflect the knowledge that a specific observer has about the outcome of a single experiment. Another observer may have different knowledge about the experiment and hence will assign different probabilities to the possible outcomes. Thus the probabilities are observer dependant and have to do with a single experiment.

This is quite different from the classical frequency theory of probability. Under the frequency interpretation, probability is defined as the number of times a specific outcome occurs in a series of experiments divided by the total number of experiments. This definition implies that the probability applies to a series of experiments and is independant of the observer.<sup>2</sup> However Jaynes (1979) has shown that this interpretation is incompatible and in fact nonsensical in the context of discussing the uncertainty about the outcome of a single experiment.

Use of the probable inference theory has several important implications for the interpretation of information theoretic (and in general any statistical) measures. First the measures apply to the outcome of a single experiment. Secondly, we must ask "Whose information?" is represented by the probability distribution. The information theoretic measures can only be discussed in terms of a well defined observer. Thus information theoretic measures are relative measures. Different observers can have radically different information about the outcome of an experiment.

The "probable inference" theory of probability and the resulting general information theory is not well known outside the mathematical community. This is particularly true in the ecological community whose main exposure to information theory is in the context of ecological diversity. In the context of ecological diversity, information theory is almost exclusively discussed in terms of the frequency interpretation of probability and communication theory (Pielou 1975, Flores, Barretto, Da Costa, 1979). Thus before going on to the application of information theory to measuring structural self-organization, a tutorial review emphasising the more general interpretation of

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<sup>2</sup> Jaynes (1979) discusses the differences and relationship between the two interpretations in detail .

information theory is presented. This tutorial will also serve to provide a standard nomenclature for reviewing measures proposed by other authors.

## THE MEASURES

Consider an experiment<sup>3</sup> A, which consists of observing which of N possible outcomes occurs. Suppose that the probability of the ith outcome being observed is  $P_i[A]$ . Then the average uncertainty an observer has about which event (i.e. which outcome of the experiment) will occur is given by:

$$H[A] \equiv \sum_{i=1}^n -P_i[A] \log P_i[A] \quad 0 \leq H[A] \leq \log N \quad (1)$$

$H[A]$  also measures the information gained, on average, from observing which event occurs. It increases as the number of possible events (N) increases. It also increases as the likelihoods of the occurrences of the events become more similar, that is as the differences between the  $P_i[A]$  decrease. Maximum uncertainty occurs when each event appears equally likely ( $P_i[A]=1/N$ ). In this case  $H[A]=\log N$ . The uncertainty ( $H[A]$ ) decreases as one or two events become more likely (larger  $P_i[A]$ ) relative to the other events. The function  $H[A]$  is known as the SHANNON ENTROPY. It has certain well known properties such as Symmetry, Normality, Expansibility, Decisivity, Strong Additivity, Recursivity, Maximality, and Sub-Additivity. (See Aczel & Daroczy, 1975.)

Now consider a second experiment B which consists of observing which of M possible outcomes occurs. The probability of the jth outcome is  $P_j[B]$ . The possibility of experiment A influencing experiment B, or B influencing A, can be explored using the conditional probabilities  $P_i[A/B_j]$ ,  $P_j[B/A_i]$ <sup>4</sup>. These indicate the probability of an outcome of one experiment occurring given that the outcome of the other experiment is known. Let us assume that the probability distributions are complete. Then the observer's average uncertainty about experiment B, given that he already knows the outcome of A is:

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<sup>3</sup> Experiment and event are used interchangeably.

<sup>4</sup>  $P_i[A/B_j]$  = probability that outcome  $A_i$  occurs given that  $B_j$  has occurred.

$$H [ B/A ] \equiv \sum_{i=1}^n -P_i [ A ] \sum_{j=1}^m P_j [ B/A_i ] \log P_j [ B/A_i ] \quad 0 \leq H [ B/A ] \leq H [ B ] \quad (2)$$

This is the **CONDITIONAL ENTROPY**. It also measures the average information the observer gains from observing event B given he already knows which event A occurred. The inequality states that the observer's maximum conditional uncertainty about B is the same as the uncertainty (Shannon entropy) he would have if he had no a priori information. The minimum conditional uncertainty ( $H[B/A]=0$ ) occurs when the outcome of A completely predicts the outcome of B.

The composite event  $A \cap B$  has a complete probability distribution associated with it, such that the probability of  $a_i$  and  $b_j$  being the outcome of the two experiments is

$P_{ij} [ A \cap B ] = P_j [ B/A_i ] P_i [ A ] = P_i [ A/B_j ] P_j [ B ]$ . The observer's average **UNCERTAINTY ABOUT THE COMPOSITE EVENT** is given by (1).

$$H [ A,B ] \equiv \sum_{i=1}^n \sum_{j=1}^m -P_i [ A ] P_j [ B/A_i ] \log ( P_i [ A ] P_j [ B/A_i ] )$$

Using (1) and (2) it can be shown that:

$$H [ A,B ] = H [ A ] + H [ B/A ]; \quad 0 \leq H [ A,B ] \leq H [ A ] + H [ B ] \quad (3)$$

The inequality states that the maximum average uncertainty about the composite event occurs when the outcomes of experiment A and B are independent. Note that Bayes Theorem implies that  $H[A,B]$  is symmetric, that is  $H [ A,B ] = H [ B,A ]$ .

The **MUTUAL INFORMATION** is defined as:

$$I [ A,B ] \equiv H [ A ] + H [ B ] - H [ A,B ]$$

This is symmetric. Using equation (3) and inequality (2) leads to:

$$I [ A,B ] = H [ B ] - H [ B/A ]; \quad 0 \leq I [ A,B ] \leq H [ B ] \quad (4)$$

$I [ A,B ]$  measures the reduction in the observer's average uncertainty about event B due to his knowing which event A occurred (or vice versa). In other words it measures the average information gained about the outcome of experiment B from performing experiment A. It is a maximum when  $H[B/A] = 0$ , that is the outcome of A completely predicts the outcome of B. It is a minimum when  $H[B/A] = H[B]$ , the outcome of A tells

the observer nothing about the outcome of B. It is not an entropy measure in the strict mathematical sense. It increases as the average conditional uncertainty decreases.

The final measure to be discussed is called the redundancy. The redundancy (R) is defined as:

$$R \equiv \frac{\max I[A,B] - I[A,B]}{\max I[A,B]} \quad 0 \leq R \leq 1 \quad (5)$$

( $\max I[A,B]$  = the maximum value  $I[A,B]$  can take on for the given experiments A and B.)

The redundancy is a measure of how useful it is to perform experiment A if the experimenter's objective is to decrease his uncertainty about experiment B. Performing experiment A is said to be redundant if it does not provide any additional information about experiment B. In this case the redundancy is a maximum and  $I[A,B] = 0$ . In the other extreme the redundancy is a minimum when performing experiment A gives maximum information, that is tells the experimenter the outcome, a priori, of experiment B. Performing experiment A is not redundant relative to determining the outcome of B and  $I[A,B] = \max I[A,B] = H[B]$ .

Some confusion has occurred over this measure. This is due to incorrectly interpreting R as a measure of the redundancy of performing experiment B after having performed experiment A. The reason for this interpretation, even though it is incorrect mathematically, is that it seems reasonable given the English language use of the word redundancy. However, the name "redundancy" for R makes English language sense in the context of network structures. For further reading Yaglom and Yaglom is recommended.

### **3-3 EXAMPLES: APPLICATION TO POPULATION DIVERSITY MEASURES**

Two examples of information theory derived diversity<sup>5</sup> measures are now considered. The purpose of this discussion is to point out three mathematical principles which are neglected in traditional ecological applications of information theory measures. These are:

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<sup>5</sup> Diversity is used throughout in its strict mathematical sense, that is the evenness of the distribution amongst alternative choices (e.g. compartments) and the total number of alternatives available.

- if a measure is a valid information measure of an experiment described by a probability distribution then it is a measure of the diversity of outcomes associated with the distribution;
- the Shannon entropy is a valid uncertainty measure for finite collections;
- information measures are valid for a specific observer only. This observer must be clearly defined.

The last two principles follow from the probable inference theory of probability. They are discussed in detail in Jaynes (1979).

#### SHANNON-WEAVER INDEX

The Shannon-Weaver (or Shannon-Wiener, depending on the author) index of species diversity is probably the best known information theoretic measure used in ecology. (Pielou 1975, Grassle, Patil et al, 1979).

The measure is

$$H \equiv \sum_{i=1}^n -p_i \log p_i \quad (6)$$

where  $p_i$  is the proportion of the total number of individuals in the ecosystem or community which are from the  $i$ th species.

As pointed out earlier, when applied in an ecological context the Shannon-Weaver index is interpreted according to the frequency theory of probability and the communication theory approach to information theory. Thus the last two principles stated above have been neglected in applying the Shannon-Weaver index in ecology. To more correctly discuss the Shannon-Weaver index as an information measure, as outlined in Section 3-2, consideration must begin with the definition of the observer.

Consider an experiment in which an observer detects an individual member of an ecosystem or community. If the only information he has is the proportion of the total number of individuals which are from each of the species (i.e. the  $p_i$ ), then according to (1) his average uncertainty, about which species the individual he has detected belongs to, is given by the Shannon-Weaver index (6). It is only in the context of this experiment that the Shannon-Weaver index has any meaning as an information or entropy measure.

Now that the observer whose uncertainty is described by the Shannon-Weaver index has been defined, attention is turned to the first of the three principles stated above. The fact that the Shannon-Weaver index is an entropy measure only in the context of the above described experiment does not constrain its applicability as a measure of diversity. There are a number of valid diversity measures (for example Simpson's index, see Odum 1983, Table 18-1, or Peet, 1974) which are not information theory measures. Often this point is forgotten. Some ecologists have misinterpreted the first principle to mean that if a measure is not a valid information theory measure then it is not a valid diversity measure. This would have been a correct interpretation if the first principle had been an "if...and only if..." statement.

Consider for example Pielou's argument that the Brillouin index must be used, rather than the Shannon-Weaver index, to measure the diversity of a finite population for which a complete census exists. Her argument against the use of the Shannon-Weaver index is that since, in information theory "...the Shannon-Wiener formula is not appropriate for finite collections, only for infinite ones..." (p. 304, Pielou, 1974) another index of diversity must be found for finite populations. This is precisely the type of misinterpretation of the first principle described in the last paragraph.

Pielou's argument against the Shannon-Weaver index also suffers from contradicting the second principle. The Shannon-Weaver index is a valid information measure for a finite collection, as well as for infinite ones. The conclusion that it is not a valid measure for finite collections is based on a set of arguments from the communication theory/frequency approach to information theory, which are incorrect. This has been shown quite clearly and in some detail by Jaynes in his discussion of the Brandeis Dice Problem (p. 47-77, Jaynes 1979, particularly in reference to the Rowlinson urn problem p.56-59). So even if diversity measures had to be valid information measures, Pielou's arguments against the Shannon-Weaver would be incorrect.

Her argument for the Brillouin index is flawed by the one mistake which, Jaynes has repeatedly pointed out, is often made. That is, she fails to observe the third principle stated earlier; clearly define who the observer is and what he knows. In this case a measure of the observer's average uncertainty about what species an individual will

belong to, given the proportion of individuals in each species is known, is what is sought. The Brillouin index measures the information gained (per individual counted) from doing the COMPLETE census of the species and discovering the proportion of individuals in each species. (p. 5-8, Brillouin 1962). This does NOT, in general, measure the AVERAGE information gained from detecting an INDIVIDUAL of a SPECIFIC species. Only when the total number of individuals become very large is the Brillouin index a satisfactory approximation to the sought after measure. However, theoretically, the Brillouin index is not the sought after measure. (It should be noted that these arguments do not necessarily imply that Pielou's discussion of estimating the diversity from samples of the population is incorrect. This is an entirely different problem having to do with sampling without replacement).

#### MEASURE OF RESOURCE NICHE BREADTH

The second example is of Colwell & Futuyma's (1971) measure of resource niche breadth. In their paper they go to some lengths to deal with the third principle.

Suppose that there are  $r$  resource states and  $s$  species. The probability that an individual is associated with resource state  $j$ , given that it is of species  $i$ , is  $p_{ij}$ . The  $p_{ij}$  are calculated using the proportion of the  $i$ th species which are found associated with resource state  $j$ . Given that these proportions are known, the average uncertainty about which resource state an individual of species  $i$  will be found to be associated with is given by (1):

$$B_i \equiv \sum_{j=1}^n -p_{ij} \log p_{ij} \quad (7)$$

Given  $Q_i$ , the probability that an individual is of species  $i$ , then (2) gives:

$$H \equiv \sum_{i,j=1}^n -Q_i p_{ij} \log p_{ij}$$

This is the average uncertainty as in (7) except averaged over all species as well as over all resource states.

Colwell & Futuyma argue that (7) measures the niche breadth of a species with respect to the resources, in that it measures the diversity with which the population of the  $i$ th species is distributed amongst the resource states. They point out that this

measure is very observer dependent since it depends completely on how the observer defines the resource states. They spend some time discussing how to define the resource states.

## THE NEED FOR MEASURES OF BIOLOGICAL MECHANISMS

Use of the entropy measure in the context of populations has in the past succumbed to a number of theoretical misinterpretations. These include the failure to differentiate between information measures and diversity measures, and the failure to correctly interpret whose and what average information the entropy measures, measure. Goodman (1975), in his definitive paper on species diversity, points out a more important problem with all these measures. "None of the commonly used diversity indices reflect a biological mechanism." (p.242, Goodman 1975).

Consider the Shannon-Weaver index (6) again. As an information measure, it assumes that the experimenter, who detects an individual, knows only the distribution of individuals amongst the species. It assumes that the experimenter cannot infer anything from where, when, and how the individual is detected. Thus no information is used which reflects the ecology of the situation. Only census information is used.

As a diversity measure, the Shannon-Weaver index only indicates the diversity with which individuals are distributed amongst the species. It indicates nothing about the diversity with which individuals or species interact with each other or their environment. In other words, it does not reflect the diversity of any ecological interactions. One is forced to wonder, as Goodman does, how such a measure could possibly be expected to infer anything about such fundamental ecological phenomena as ecological stability.

Colwell & Futuyma's measure (7) does reflect some form of biological interaction. As an information measure it indicates the average uncertainty about which resource state an individual of a specific species will be found to be in contact with. The only information used is, again, census information. Nothing is implied about the degree of interaction or the importance of the interaction represented by the contact. Perhaps most importantly, the proportion of the total resources used by the species, which comes from the different states contacted is not taken into account. Thus the measure only reflects information, about whether or not contact will occur between an individual of a specific species and a specific resource state.

In terms of diversity, the measure only reflects the diversity with which the species has contact with the resource states. It indicates nothing about the diversity of the degree of interaction or the diversity of the importance of the interaction between the individuals of the species and the resource states. Thus it measures niche breadth only in terms of the number of contacts which occur between the species and the given resource states. (In all fairness to Colwell & Futuyma, they do point out this problem and spend some time discussing how to pick resource states and weight the populations to compensate accordingly).

To be useful in theoretical ecology, information theory based measures must be applied in a mathematically correct way. They must also reflect something about the degree of ecological interaction which is occurring in a system. If the only information used to generate these measures is census data, or data which counts the number of contacts which occur as versus how much interaction occurs with each contact, then the measures cannot hope to reflect any biological mechanisms.

### **3-4 MEASURES OF FOOD WEB STRUCTURE**

In the remainder of this chapter discussion focuses on the use of information theory measures to describe the organization of the food web in an ecosystem. The ecological interaction being described is the exchange of mass and energy between the species which make up the ecosystem. From a systems-theoretic perspective it is the production-consumption<sup>6</sup> structure of the system which is being described. In particular characterization of the self-organization<sup>7</sup> of this structure is of interest.

Goodman (1975) in his review of the historical development of species diversity measures and the diversity-stability hypothesis, points out that the original impetus behind the use of the Shannon entropy as a species diversity measure came from the work of MacArthur (1955). MacArthur used the entropy to measure the diversity of the trophic interaction in the community. His premise, based on Odum (1953), is that "The

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<sup>6</sup> See Chapter 2 or Kay (1978) [Summarized in Kay, J., 2002, "On Complexity Theory, Exergy and Industrial Ecology: Some Implications for Construction Ecology" in Kibert, C., Sendzimir, J. (eds), Guy, B., Construction Ecology: Nature as a Basis for Green Buildings, Spon Press, pp.72-107. <http://www.fes.uwaterloo.ca/u/jjkay/pubs/IE>

<sup>7</sup> This term is defined in Chapter 2 and will be explored in more detail later in this chapter.

amount of choice which the energy has in following the paths up through the food web is a measure of the stability of the community." (p.534, MacArthur, 1955). The truly staggering amount of material written on species diversity<sup>8</sup> is a digression from MacArthur's original line of thinking.

The measures discussed herein represent a return to MacArthur's line of thinking. Population information is not used in the measures and they should not be mistaken for measures of species diversity. Rather they reflect the interaction between species through the exchange of mass and energy via the food web. The measures are meant to characterize only the organization of this aspect of ecosystems.

### 3.4.1 THE PROBABILITY DISTRIBUTIONS

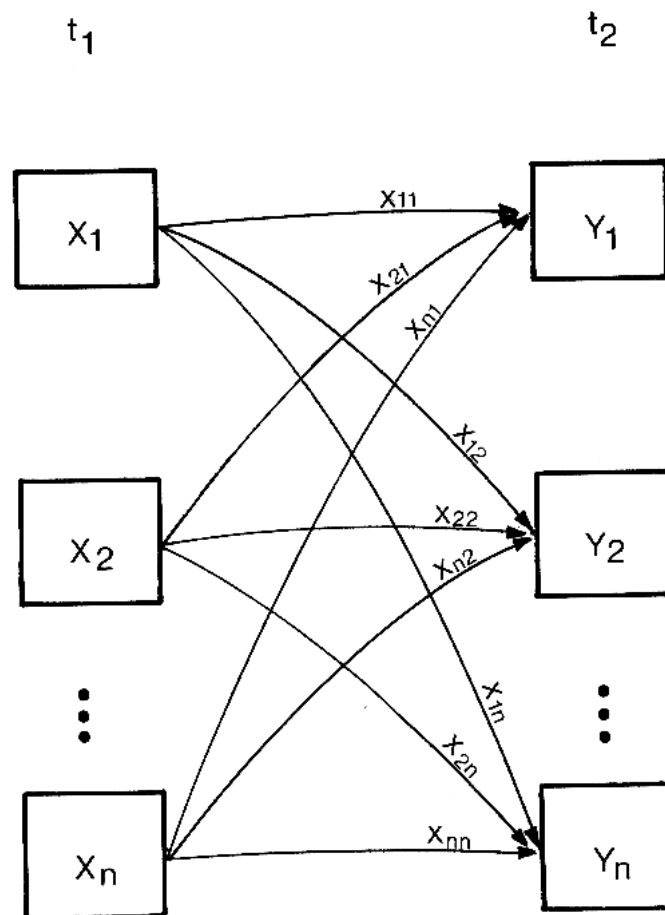
#### THE EXPERIMENT

Atlan (1974) and Rutledge (1974) independently developed a model (see Figure 1) which can be applied to ecosystem structure and used to define some information measures. In this model, the system is divided into N compartments which exchange resources (i.e. mass and energy). The ecological interaction being examined is this exchange of resources.

In order to investigate this exchange the movement of a specific quantum of resource (i.e. mass and energy) from compartment to compartment is examined. Two experiments X and Y are considered. Experiment X consists of discovering which compartment (indicated by subscript i) a quantum of resource is flowing out of at time  $t_1$ . The probability that the resource flows from compartment i is denoted by  $P_{i\downarrow}[X]$ . Experiment Y consists of discovering which compartment (indicated by subscript j) the quantum of resource has flowed into at a later time  $t_2$ . The probability that the resource flows to compartment j is  $P_{j\uparrow}[Y]$ .

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<sup>8</sup> See Grassle and others 1979 for a bibliography containing over 1000 articles.



**Figure 1:** Structural model used by Rutledge

PROBABILITY	THIS THESIS	ATLAN (1974)	RUTLEDGE (1974,1976)	ULANOWICZ (1979)	ULANOWICZ (1980)
$P_i(X)$	$X_i$	$X_i$	$Q_i$		$Q_i$
$P_i(X/Y_j)$	$X_{ij}$			$g_{ji}$	
$P_j(Y)$	$Y_j$	$Y_j$	$P_j$	$Q_i (?)$	
$P_j(Y/X_i)$	$Y_{ji}$		$f_{ij}$		$f_{ij}$

? It is ambiguous whether  $Q_i=P_i(X)$  or  $P_j(Y)$  in Ulanowicz 1979.

**TABLE 1:** Notation used by Atlan (1974), Rutledge (1974), Rutledge et al. (1976), Ulanowicz (1979,1980).

**RUTLEDGE:**

$Q_i$  = percentage of the total energy and material flow through the ecosystem at time  $t_1$  which passes through the  $i$ th compartment.

$P_j$  = percentage of the total energy and material flow through the ecosystem at time  $t_2$  which passes through the  $j$ th compartment.

$f_{ij}$  = percentage of the total energy and material flow through the  $i$ th compartment which passes to the  $j$ th compartment between times  $t_1$  and  $t_2$ .

**ULANOWICZ (1979):**

$Q_i$  = fraction of the total system throughput associated with compartment  $i$ .

$g_{ij}$  = fraction of  $Q_i$  which flows from compartment  $j$ .

**ULANOWICZ (1980):** A steady-state is assumed so that the throughput equals the total input or output of a compartment.

$Q_i$  = same as in 1979 paper.

$f_{ij}$  = probability of any quantum of flow leaving compartment  $i$  directly contributing to the sustenance of compartment  $j$ .

**THIS CHAPTER:** See text

**TABLE 2:** Definitions of the probability distributions.

The structure of the ecosystem is given by either of the conditional probability distributions.<sup>9</sup> The distribution  $P_i[X/Y_j]$  indicates the probability that a quantum came from a particular compartment (i) at  $t_1$ , given that it is known which compartment (j) it has flowed to at  $t_2$ . In effect  $P_i[X/Y_j]$  tells us how the compartments are interconnected. (Alternatively  $P_j[Y/X_i]$ , the probability that a quantum has flowed into compartment j at  $t_2$ , given that it was in compartment i at  $t_1$ , can be used).

The notation used to denote these probabilities vary from author to author and paper to paper. This makes comparison of measures quite difficult. This difficulty is compounded by the use of different ways of associating the probabilities with actual ecosystem variables. Table 1 contains the different notations used and Table 2 contains the different definitions of the variables.

#### PROBLEMS WITH THE DEFINITION OF ECOSYSTEM VARIABLES

Atlan's discussion of organization is meant to be completely general. Thus he does not define the probability distributions used. This makes it quite difficult to discuss the applicability of his measures. (As pointed out earlier, the meaning of information measures is highly dependant on the the specific observer involved). For arguments sake his definitions will be assumed to be consistent with the other authors.

Rutledge's definitions are more specific. His definitions are meant to be used in a communication theory context. The times  $t_1$  and  $t_2$  are meant to designate when a resource is transmitted and when it is received. In practice  $t_1$  and  $t_2$  have no meaning and add a conceptual complication to the definitions. Another difficulty with the time difference is that a quantum of resource may have been in compartment i at time  $t_1$  and moved through several compartments before coming to compartment j at  $t_2$ . This however does not appear to be taken into account in models of actual systems as only direct connections between compartments are accounted for.

A more serious difficulty with Rutledge's definition is the quantification of the flow "through" a compartment. Does one use the input or output of the compartment? Rutledge uses the "content" of the compartment multiplied by the "turnover time" of the

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<sup>9</sup> Bayes Theorem allows one distribution to be determined from the other, if  $\{P_i[X]\}$  and  $\{P_j[Y]\}$  are known.

compartment to yield its "throughput". This "throughput" does not appear to be a directly measurable characteristic of the flows in the system.

A final problem, not dealt with by Rutledge's definitions, is how to handle resources which are either flowing into or out of the whole ecosystem (i.e. sunlight).

Ulanowicz (1980) circumnavigates all of these problems by imposing a steady state on the system. In this case The flows through the system are identical at  $t_1$  and at  $t_2$ . Nothing is stored in any compartment. Thus input equals output equals throughput, and the open nature of ecosystems is not a consideration as total input equals total output. However, what is to be done for the more typical non-steady-state situation?

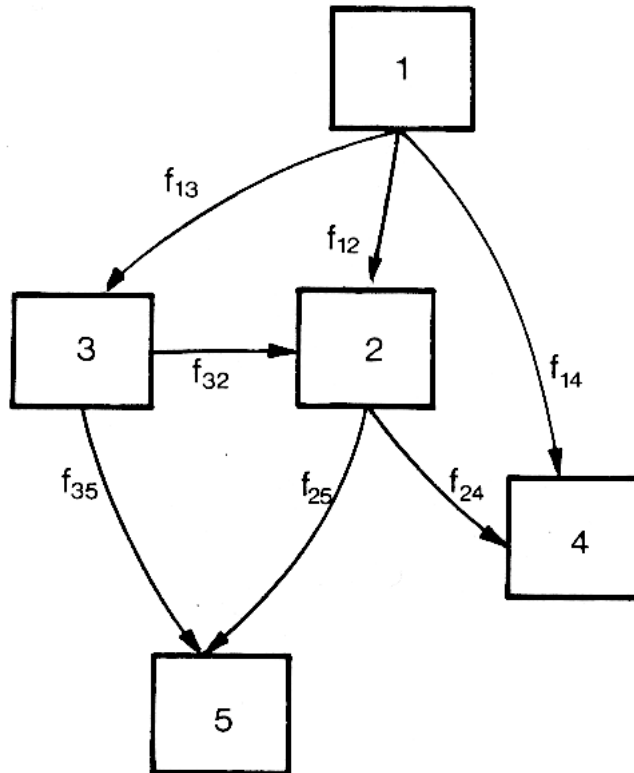
#### PRODUCTION-CONSUMPTION MODEL

The following model is meant to address these problems. Consider Figure 2. Each compartment can be considered as a producer of resources and as a consumer of resources. Each compartment exchanges resources with other compartments. The flow of resources out of a compartment, which is consumed by other compartments, is referred to as the OUTPUT of the compartment. The flow of resources into a compartment, which is produced by other compartments, is referred to as the INPUT to the compartment. The term FLOW OF RESOURCES is meant to indicate the flows of mass and energy in the ecosystem which move directly from a producer to a consumer without flowing through any intermediate compartments. Each compartment which produces (i.e. has an output) a specific [resource]<sup>10</sup> is a SOURCE of the resource. The RESOURCE NICHE of a compartment refers to the set of sources used by the compartment.

Experiment X is now taken as determining which source a quantum of resource flow came from. In the absence of any other information,  $P_i[X]$  is determined by the proportional contribution of the  $i$ th compartment to the total flow of resources out of all the source compartments. This proportional contribution will be referred to as  $X_i$ .

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<sup>10</sup> The term RESOURCE will be used to signify the basic energy and material required by a species for metabolism, for example: water, nitrogen, phosphorous, solar energy (including stored forms), oxygen, etc.. A SOURCE refers to a reservoir from which species can extract a needed resource. (One of the species eaten by the studied species would be a source.)



$$IN_i = \sum_{j=1}^n f_{ji}$$

$$P_i(Y) = \frac{IN_i}{\sum_{j=1}^n IN_j} = Y_i$$

**Figure 2:** Production-Consumption Model

Experiment Y is now taken as determining which compartment consumes a quantum of resource flow. In the absence of any other information,  $P_j[Y]$  is determined by the proportion of the total flow of resources into all the compartments which enters compartment j. This proportion will be referred to as  $Y_j$ .

The conditional probability  $P_i[X/Y_j]$  is the probability that a quantum of resource came from compartment i, given that it is known to be consumed by compartment j. This

probability is determined by the proportion ( $X_{ij}$ ) of the total input to compartment  $j$  which comes from compartment  $i$ .  $P_j[Y/X_i]$  is the probability that a quantum of resource is consumed by compartment  $j$  given that it is known to be output from compartment  $i$ . This probability is determined by the proportion ( $Y_{ji}$ ) of the total output of compartment  $i$  which is consumed by compartment  $j$ . Either  $X_{ij}$  or  $Y_{ji}$  can be used to describe the production-consumption structure or in other words the food-web of the ecosystem.

#### ADVANTAGES OF THE MODEL

This model has several advantages. It is cast in terms of experiments rather than in terms of the transmission and reception of energy. It is conceptually clearer in that there is no mention of throughput. The "idea" of a trophic level is not introduced. There is no reference to times  $t_1$  and  $t_2$ . Only direct links between producers and consumers are considered. Thus the problem of an open ecosystem does not arise. A steady-state situation does not have to be assumed. Finally, and most importantly, the model more closely describes how the probabilities are actually calculated in practice.

Measures of the uncertainty about experiments  $X$  and  $Y$  can be generated by substituting the appropriate probability distributions in (1), (2) and (3). The fundamental information variables  $H[X]$ ,  $H[Y]$ ,  $H[X/Y]$  and  $H[Y/X]$  can be interpreted as follows. Given that a quantum of resource flow is detected,  $H[X]$  measures the observer's average uncertainty about which compartment produced the resource.  $H[Y]$  measures the observer's uncertainty about which compartment will consume the resource.  $H[X]$  can also be interpreted as the diversity with which the individual sources contribute to the resource flow in the system.  $H[Y]$  can similarly be interpreted as the diversity with which the compartments contribute to the consumption of the resource flow. Given that a quantum of resource flow is detected entering a specific compartment  $H[X/Y]$  measures the observer's average uncertainty about which source the resource came from.  $H[X/Y]$  can be interpreted as the average diversity with which consuming compartments utilize their sources. Given that a quantum of resource flow is detected leaving a specific compartment,  $H[Y/X]$  can be interpreted as the diversity with which the resource flow

from a source is distributed amongst the consuming departments. These interpretations will be discussed in more detail later.

This production-consumption model of an ecosystem lends itself to definitions of experiments. These definitions in turn lend themselves to the development of the fundamental measures of uncertainty about the flow of mass and energy between compartments in the ecosystem. The model allows us to associate the probabilities with specific ecosystem variables. However the definition of compartments or resource flow, and the assignment of actual values to the probabilities in specific situations still remains to be investigated. As it stands, the model provides a sufficient basis for discussing the measures of structural organization proposed by Atlan, Rutledge and Ulanowicz.

### **3.4.2 THE MEASURES**

In this section a review of previously proposed measures of structural self-organization is undertaken. In order to clearly compare the measures proposed by the various authors, they will be expressed in terms of the fundamental variables:  $H[X]$ ,  $H[Y]$ ,  $H[Y/X]$ ,  $H[X/Y]$ .

This review assumes that the probability distributions are those of the production-consumption model. This will simplify comparison of measures and is justified because actual measurements may appear to be consistent with this model.

The purpose of this section is to explore the choice of measures made by other authors. This choice cannot be discussed without referring to the hypothesis concerning self-organization made by these authors. However, in this chapter no judgement<sup>11</sup> is made about the relative merits of the hypothesis. Only the relative merits of the measures themselves will be discussed.

#### **RUTLEDGE**

Rutledge (1974) and Rutledge, Basore, & Mulholland (1976) examine how energy is distributed amongst compartments in an ecosystem. The associated information measures are given by equations (1), (2) and (4) with experiment A being

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<sup>11</sup> See Chapter 5

associated with experiment Y and experiment B with experiment X. With this association made Rutledge defines three measures:

$$D \equiv H [X] \quad (8)$$

This, he claims, measures the diversity of throughput in the ecosystem or alternatively the uncertainty about how energy is distributed amongst the compartments in the ecosystem.

$$I \equiv I [X,Y] = H [X] - H [X/Y] \quad (9)$$

This, he claims, measures the uncertainty resolved by knowledge of the food web structure.

Finally:

$$S \equiv D - I = H [X] - ( H [X] - H [X/Y] ) = H [X/Y] \quad (10)$$

Rutledge claims that S is a measure of ecological stability. As S increases the ecosystem becomes more stable. In effect S is a measure of self-organization of the food web. Self-organization is occurring when  $dS/dt > 0$ .

Rutledge defines ecological stability as the ability of an ecosystem to resist changes in the presence of perturbations. His arguments concerning stability are a version of the "diversity implies stability" hypothesis. Following Odum (1953), MacArthur (1955), he reasons that ecological stability is related to the choice of pathways for energy flow in the ecosystem. Underlying this reasoning is the idea that if a species has a large reservoir of potential sources to choose from, a disruption in any one source can be compensated for by choosing another source. He also suggests that a measure of food web complexity would reflect the stability of the ecosystem. He claims that S is a measure of "the effective freedom to exercise choice in a system" (p.17, Rutledge 1974) and is "an index of complexity" (p.24, Rutledge 1974). Hence he proposes S as a measure of ecological stability.

Rutledge backs this claim up by showing that S measures the sensitivity of species to disruptions in their food supply. Intuitively, as S increases the relative proportion of the total energy flow into a compartment, from every other compartment, becomes more equal. Thus, as S increases, it would be reasonable to expect changes in the flow from any one compartment, on average, to have less impact on the other compartments.

Rutledge's line of argument can be extended one step further. He states that "long term changes in a stability measure would indicate the direction of succession" and "succession is a process of self-organization" (p.2, Rutledge 1974). Thus increases in S could be interpreted as indicating ecosystem self-organization.

In terms of the production-consumption model S measures the average uncertainty about which compartment a resource has come from, given that it is known which compartment it is in. Another interpretation is that S measures the diversity with which the input of a compartment is made up of the outputs of other compartments. Thus, according to Rutledge, self-organization corresponds to an increase in the diversity with which consuming compartments use their sources.

#### ATLAN

Atlan (1974) examines how changes in the structure of the ecosystem affect the average information<sup>12</sup> an observer gains by performing experiment X and Y, given that the structure is known a priori. This is done by considering two experiments A and B. Experiment A is carried out by an observer who knows the system structure. He monitors the system via a noiseless communication channel in order to obtain the outcomes of events X and Y. Experiment B consists of determining the outcomes of X and Y directly. Therefore<sup>13</sup>  $H[B] = H[X, Y] = H[X] + H[Y/X]$  and, because of the definition of a noiseless communication channel,  $H[B/A]=0$ .

From (4):

$$I [A,B] = H [B] - H [B/A] = H [X,Y] = H [X] + H [Y/X] \quad (11)$$

and using the inequality from (2):

$$\max I [A,B] = \max ( H [X] + H [Y/X] ) = H [X] + H [Y]. \quad (12)$$

(The maximization process is over all possible structures, that is all possible values of  $Y_{ji}$  with  $X_i$  remaining fixed.)

From (5):

$$R = \frac{(H [X] + H [Y]) - (H [X] + H [Y/X])}{H [X] + H [Y]} = \frac{I [X, Y]}{H [X] + H [Y]} \quad (13)$$

<sup>12</sup> The average information gained by doing an experiment equals the uncertainty prior to performing the experiment.

<sup>13</sup>  $H[X] = -\sum X_i \ln X_i$ ,  $H[X/Y] = -\sum Y_j X_{ij} \ln X_{ij}$ , etc. using  $P_i[A] = P_i[X]$  or  $P_i[Y]$  as is appropriate in (1)

Using the inequality in (4)  $0 \leq R \leq 1/2$ . (This assumes that  $H[X] = H[Y]$ , if  $H[X] \neq H[Y]$  then  $0 \leq R \leq$  the lesser of  $1/(1 + H[X] / H[Y])$  or  $1/(1 + H[Y] / H[X]) < 1/2$ .)

Atlan defines  $H \equiv H[X,Y]$ ,  $H_{\max} \equiv H[X]+H[Y]$  and consequently<sup>14</sup>

$R = (H_{\max} - H) / H_{\max}$  This leads to:

$$\frac{dH}{dt} = (1-R) \frac{dH_{\max}}{dt} - (H_{\max}) \frac{dR}{dt} \quad (14)$$

Atlan claims that  $H$ ,  $H_{\max}$  and  $R$  characterize the structure of the system. He argues that organization occurs when  $dH/dt > 0$ . A noisy environment corresponds to  $dH_{\max}/dt < 0$  and  $dR/dt < 0$ . (14) indicates that it is possible for  $dH/dt > 0$  in a noisy environment. This case is called self-organization by Atlan. "This case corresponds to self-organization since it shows an increase in complexity, apparently spontaneous, while it is due in fact to the effect of random factors on the system. ...we propose to call self-organization a process where the change in organization with increased efficiency, although it is induced by the environment, is not directed by a programme but occurs under the effects of random environmental factors." (Atlan 1974, pp. 299-300)

What do  $H$ ,  $H_{\max}$ , and  $R$  measure about the ecosystem?  $H$  measures an observer's average uncertainty about the resource flow (that is both inputs and outputs) through the ecosystem structure, given that he knows the structure.  $H$  is made up of two components. The first is the average uncertainty  $H[X]$  the observer has about the output flows (the  $X_i$ ). This uncertainty reflects the diversity with which the total resource flow in the system is contributed to by the output from each compartment. The second component is the average uncertainty  $H[Y/X]$  about how the resources will flow from one compartment to another. (This flow is given by  $Y_{ji}$ .) This uncertainty is determined by the average diversity with which the total output of each compartment is distributed, as input, amongst the consuming compartments.  $H_{\max}$  measures the same uncertainty except the observer does not know about the system structure, that is he does not know how the components are interconnected. Thus he must assume that  $Y_{ji}=Y_j$ , that is the

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through (5). Also  $H[X,Y] = H[Y] + H[X/Y]$ ; see Table 3

<sup>14</sup> Because of how Atlan defines experiments A and B,  $I[A,B] = H[B]$  and  $\max I[A,B] = \max H[B]$ . This is NOT true in general.

proportion of the total output from the  $i$ th compartment which flows to the  $j$ th is the same as the proportion of the total resource flow which is input to the  $j$ th compartment.

Increases in  $H$  indicate that both the diversity of the output flow contributions to the total flow, and the diversity of the distribution of each compartment's outputs amongst the consuming compartments are increasing; or one of these two diversities is increasing more quickly than the other is decreasing. Decreases in  $H_{\max}$  indicate that either both the diversity of input and output flows are decreasing, or one of these two diversities is decreasing faster than the other is increasing. Decreases in  $R$  will always occur if  $H$  is increasing and  $H_{\max}$  is decreasing. Thus, according to Atlan, self-organization ( $dH/dt > 0$ ) in a noisy environment ( $dH_{\max}/dt, dR/dt < 0$ ) occurs when some aspects of the diversity of flows is increasing while other aspects decrease in diversity. How each specific aspect of an ecosystem's structure is changing in diversity is left ambiguous by Atlan's description.

#### ULANOWICZ

Ulanowicz (1979a) follows reasoning similar to Atlan, but his experiments A and B are different. Experiment A corresponds to experiment Y, that is ascertaining which compartment the resources are flowing to. Thus  $H[A] = H[Y]$ . Experiment B consists of determining where the resources are flowing from. ( $H[B] = H[X], H[B/A] = H[X/Y]$ ). He examines how changes in the system structure effect the knowledge an observer has about where resources came from, given he knows where they are.<sup>15</sup>

Using the same analysis as led to (11), (12), and (13), except using Ulanowicz's definition of A and B, leads to:

$$I [A,B] = H [X] - H [X/Y] \quad (15)$$

$$\max I [A,B] = H [X] \quad (16)$$

$$R = \frac{H [X] - (H [X] - H [X/Y])}{H[X]} = \frac{H [X/Y]}{H [X]} \quad (0 \leq R \leq 1) \quad (17)$$

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<sup>15</sup> Experiments A and B are the same as Rutledge's. However Ulanowicz chooses to examine changes in the system structure differently than Rutledge. This is evidenced by the different measures he uses.

Ulanowicz defines  $C \equiv H[X]$ ,  $I \equiv H[X] - H[X/Y]$  and consequently  $R = (C - I)/C$ . This leads to:

$$\frac{dI}{dt} = (1 - R) \frac{dC}{dt} - \frac{dR}{dt} \quad (18)$$

In analogy to Atlan, Ulanowicz claims that  $I$ ,  $C$ , &  $R$  characterize ecosystem structure. He argues that self-organization occurs for  $dI/dt > 0$ . He also suggests that environmental disturbances will decrease the number of compartments and disturb the flows between them. This, he claims, is characterized by  $dC/dt < 0$ . Ulanowicz poses the question; "Can the system compensate for the disturbance so as to still be able to maintain structural self-organization?". He argues that the system can be self-organizing (i.e.  $I$  increases) even if  $C$  decreases, if  $R$  can decrease appropriately.

According to Ulanowicz's definitions, the amount of information gained from knowing the system structure, about which compartment the resources came from, is measured by  $I$ .  $I$  is a measure which combines  $H[X]$  and  $H[X/Y]$ . The latter uncertainty is determined by the average diversity with which the total input to each compartment is made up of outputs from the other compartments.  $C$  measures  $H[X]$ , that is the diversity of the contributions made by each compartment, through their output, to the total resource flow in the system.  $R$  measures the ratio of  $H[X/Y]$  to  $H[X]$ .

Increases in  $I$  correspond to an increase in the diversity of the output flow contributions to the total flow, and a decrease in the average diversity with which the total input to each compartment is made up of the outputs from other compartments. Increases in  $I$  can also correspond to the former diversity increasing more rapidly than the the latter, or the former diversity decreasing less rapidly than the latter diversity. Decreases in  $C$  correspond to decreases in the former diversity. Thus in words, Ulanowicz claims that self-organization in a noisy environment, corresponds to the average diversity ( $H[X/Y]$ ), with which the total input to each compartment is made up of outputs from other compartments, decreasing more rapidly than the diversity ( $H[X]$ ) with which the total resource flow, in the system, is made up of the output flows from each compartment.

AUTHOR	VARIABLE NAME	DEFINITION IN TERMS OF EXPERIMENTS X & Y	DEFINITION IN TERMS OF EXPERIMENTS A & B
Atlan	H	$H[X,Y] = H[X] + H[Y/X]^*$	$I[A,B]$
	$H_{max}$	$H[X] + H[Y]$	$\max I[A,B]$
	$R = \frac{H_{max} - H}{H_{max}}$	$\frac{I[X,Y]}{H[X] + H[Y]}$	$\max I[A,B] - I[A,B]$
Ulanowicz	I	$I[X,Y] = H[X] - H[X/Y]$	$I[A,B]$
	C	$H[X]$	$\max I[A,B]$
	R	$\frac{H[X/Y]}{H[X]}$	$\frac{\max I[A,B] - I[A,B]}{\max I[A,B]}$
Rutledge	I	$I[X,Y] = H[X] - H[X/Y]$	$I[A,B]$
	D	$H[X]$	$\max I[A,B]$
	S	$H[X/Y]$	$\max I[A,B] - I[A,B]$

\* NOTE: In order to discuss and compare Atlan's and Ulanowicz's hypotheses this definition is used. However it is equally correct to state that  $H[X,Y]=H[Y]+H[X/Y]$ . This form is not used because it obscures the intuitive discussion and comparison with Ulanowicz's hypotheses.

**TABLE 3:** Definitions of Atlan's, Ulanowicz's, and Rutledge's measures of ecosystem structure in terms of experiments X and Y and experiments A and B.

AUTHOR	ORGANIZATION	NOISY ENVIRONMENT
ATLAN	$dH/dt > 0$	$dH_{max}/dt < 0, dR/dt < 0$
ULANOWICZ	$dI/dt > 0$ $dR/dt < 0$ (Self-organization)	$dC/dt < 0$
RUTLEDGE	$dS/dt > 0$	Not Defined

**TABLE 4:** Rutledge's, Atlan's, and Ulanowicz's selforganization hypotheses in terms of their own variables.

### 3.4.3 COMPARISON OF THE MEASURES AND HYPOTHESIS

In Table 3, the sets of variables used by Rutledge, Atlan, and Ulanowicz to describe ecosystem structure are defined in terms of the uncertainty associated with experiments X, Y, A and B. In terms of their purely mathematical definitions (i.e. in terms of experiments A and B) Atlan's measures H, Hmax, and R and Ulanowicz's corresponding measures I, C, and R are identical. Thus they have the same mathematical properties. However, what they describe ecologically, that is about experiments X and Y, is quite different. On the other hand Rutledge and Ulanowicz's measures are the same both ecologically and mathematically except that Ulanowicz uses R where Rutledge uses S.

The author's hypotheses about structural self-organization are summarized in Table 4. Each author characterizes organization using a measure which is quite different in an ecological context, that is in terms of what is measured about the uncertainties associated with experiments X and Y. There is clearly no consensus on how to characterize structural self-organization.

Not only do the authors use different variables to characterize structural organization, but the changes in the fundamental variables,  $H[X]$ ,  $H[Y/X]$ , and  $H[X/Y]$ , which they predict will occur with self-organization are quite different. To see these differences more clearly consider a steady-state situation. In a steady state the input to each compartment must equal the output, that is  $X_i = Y_i$ . Therefore  $H[X] = H[Y]$  and, from (4),  $H[X/Y] = H[Y/X]$ . Atlan's hypothesis about self-organization in a noisy environment becomes  $dH[X]/dt < 0$  and  $dH[X/Y]/dt > 0$ . Ulanowicz's hypothesis becomes  $dH[X]/dt < 0$  and  $dH[X/Y]/dt < 0$ . Rutledge's hypothesis is  $dH[X/Y]/dt > 0$ . Clearly these different hypotheses predict changes in the fundamental variables which are the antithesis of each other.

All three authors use only one variable to characterize structural organization. (This should not be confused with the three variables used to characterize ecosystem structure.) In Atlan and Ulanowicz's cases their single variable is a composite of two fundamental variables. Since each fundamental variable describes a well defined aspect of the diversity of the food web, changes in the composite organization measures do not clearly reflect changes in distinct aspects of the diversity of the food

web. Thus, as is evidenced by the discussion of each author's hypothesis in the last section, it is impossible to unambiguously associate their self-organization hypotheses with changes in the various aspects of the structural diversity of the ecosystem.

On the other hand, Rutledge measures self-organization in terms of one fundamental variable. Thus he characterizes structural self-organization by changes in a single aspect of the diversity of the food web. It is not clear that changes in structural self-organization in fact do not involve changes in other aspects of the food web.

From this examination of the literature it is clear that there is no agreement on how to examine the structural self-organization of ecosystems. The question of which ecological interactions are important to focus on has not been settled. Nor has the question of how to formulate descriptions of these interactions (i.e. the use of composite variables which lump together individual fundamental variables vs use of the fundamental variables themselves). The manner in which the ecological interactions are expected to develop with self-organization is an unresolved issue. The remainder of this chapter is devoted to the first two issues.

The starting point for resolving these issues is to more clearly define what is meant by structural self-organization. Once this is done, an investigation into which of the fundamental variables or combination of variables can be used to characterize structural self-organization, can be undertaken.

### **3-5 STRUCTURAL SELF-ORGANIZATION**

Self-organization<sup>16</sup> of a system refers to the process by which the function of the system's components and the interconnections between the components (the structure) are modified in order to more effectively carry out some overall function of the system. The prefix "self" implies that these modifications are generated from within the system. These modifications can be in the direction required to keep the system in a steady state<sup>17</sup>. They can also serve to move the system to some new steady state. The former is called homeostasis and the latter homeorhesis. (Sahal, 1979) These modifications

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<sup>16</sup> For a more detailed discussion see Chapter 2.

<sup>17</sup> i.e. Optimum Operating Point.

can occur in response to environmental changes (adaptation) or spontaneously (evolution).

Living systems have many different functional goals (e.g. reproduction, feeding, evasion of predators, etc.). The effectiveness of any one of these functions may only be maximized at the expense of another. Thus the process of self-organization is one of optimizing rather than maximizing the effectiveness of any particular function. This process of optimization is further complicated by the existence of a constantly changing environment in which living systems must survive. The implication of a changing environment is that the optimum operating point for the system will be constantly altered. This will require constant modifications on the part of the system. Thus it seems unrealistic to expect there to be one mathematical function whose maximization will describe the path of self-organization.

Organization should be discussed relative to the system's function whose effectiveness is being improved. (i.e. What is the purpose of the organizational process?) (Wicken, 1980, Cottrell, 1977, Saunders and Ho 1976, Mayr, 1976). It should also be specified whether homeorhesis, homeostasis, evolution, or adaptation is being studied. Organization also has structural and functional elements. These are usually studied separately.

In Chapter 2 a paradigm concerning self-organization in living systems was presented. According to the paradigm life is a solution to the problem of maximizing energy degradation in a changing and sometimes unpredictable environment. It has been hypothesised that an ecosystem's organizational goals are to increase its energy degradation and survival potential. This is reflected in the species organizational goals, which are to maximize their offspring, subject to the constraint that they preserve the microenvironments of other species. In this way they maintain the internal stability of the ecosystem while degrading energy. The individuals of a species must survive at least until the survival of the next generation is assured. At all hierarchical levels organization will occur so as to minimize the disruption caused by an environmental change. No single goal is predominant.

Of significant importance to the survival and reproductive capabilities of species is the availability of an adequate and dependable food supply. The ability of the

ecosystem to furnish each species with the opportunity to maximize its offspring is dependent on the ecosystem's providing for the fullest possible use of the available resources. Therefore it can be concluded from the hypotheses concerning ecosystem organization that **THE PURPOSE OF STRUCTURAL SELF-ORGANIZATION IS TO PROVIDE A DEPENDABLE FOOD SUPPLY AND TO ALLOW FOR THE FULLEST POSSIBLE USE OF THE AVAILABLE RESOURCES.**

Structural self-organization refers to changes in the way in which material and energy flows between the individuals in the system. These changes reflect the response of the species to the environmental and thermodynamic forces<sup>18</sup> acting on them. The species response will be to modify the way in which they utilize the set of sources available to them<sup>19</sup>. In other words, their response will be a modification of their resource niche. **STRUCTURAL SELF-ORGANIZATION, IN THE CONTEXT OF AN ECOSYSTEM FOOD WEB, CAN BE LOOKED AT AS THE PROCESS BY WHICH THE RESOURCE NICHE ARE MODIFIED. MEASURES OF STRUCTURAL SELF-ORGANIZATION, THEREFORE, MUST DESCRIBE CHANGES IN THE RESOURCE NICHE.**

Any description of the resource niche must characterize each of the individual sources and the total set of sources used by the consumers. The individual sources are characterized by the quantity and quality of resources extracted from them. The set of sources are characterized by the relative sustenance provided by each source to each consumer. The use of the set of sources, from the perspective of the whole ecosystem, must also be characterized.

### **3-6 MEASURES OF RESOURCE NICHE**

#### **DEFINITION OF X AND Y**

The ecological meaning of the fundamental uncertainty measures associated with experiments X and Y ( $H[X]$ ,  $H[X/Y]$ ,  $H[Y]$ ,  $H[Y/X]$ , given by (1) and (2)) are now explored to see if they describe the resource niche. The first consideration is the

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<sup>18</sup> Environmental forces have both an abiotic and biotic component (see Chapter 2) and thermodynamic forces refers to the demands placed on the species by the second law of thermodynamics.

<sup>19</sup> The point is that the species have some control over what they eat. The species do not respond to the forces by changing who eats them. It is for this reason that the focus is on the consumption pattern of the

definition of experiments X and Y. These definitions consist of specifying the compartments and what proportional flow rate into and out of the compartments will constitute the probability distributions. The structure portrayed by the compartment model can be drastically altered by changing these specifications. As stated above, it is the information about the sources and how they are used by the species which is important.

The consuming compartments should be chosen such that each one corresponds to an individual species. This is done because the species are the basic reproductive unit whose behavior is shaped by the environmental and thermodynamic forces and whose survival is promoted by self-organization. It is the species choices about what they will eat which determines the structural organization of the ecosystem.

The producing compartments should be chosen so that the individuals which make it up are thermodynamically equivalent. (By thermodynamically equivalent is meant, that from a consumer's perspective, the resources which are available from each individual, are stored in the same manner and are equally difficult to obtain and consume.) If this is done, any unit of resource extracted from a particular source (i.e. compartment) will appear to be the same to the consumer. If the production compartments are chosen so that each one corresponds to an individual species then this criteria will be met.

The flows out of each source must be characterized by the amount of resources which are being extracted. Thus not only is the flow rate important, but so is the available work<sup>20</sup> and material density in the flow. If these quantities are known then the actual amount of usable resources being consumed can be determined.

In summary the components should correspond to the individual species and the probability distributions should reflect the proportional amount of available work and material flowing through each interconnection between the species.

Unfortunately, it is usually impractical to obtain sufficiently detailed information to choose the compartments as individual species. Instead the species are often lumped

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species.

<sup>20</sup> Available work refers to the maximum work which can be extracted from stored energy. Availability (Keenan 1951) and Exergy (Brzustowski and Golem, 1978, Ahern 1980) is a measure of available work

together into convenient units. It is equally difficult to obtain information about the flows. Usually the mass or calorie flow is the best that can be hoped for, it being quite often impractical to experimentally ascertain the availabilities. In spite of these practical difficulties, for the purpose of theoretical discussion it is assumed that ideal conditions exist, that is the components are the individual species and the probability distributions reflect the proportion of available work and material flowing through the component interconnections.

## THE MEASURES

In light of these definitions, the experiment  $X$  can be loosely interpreted as ascertaining which species is eaten from and experiment  $Y$  as which species does the eating. Thus  $H[X]$  measures the diversity with which species are used as sources by other species. As the utilization of species as sources becomes more evenly distributed over all the species acting as sources,  $H[X]$  increases.  $H[X]$ , in a sense, indicates the degree to which the potentially available sources of resources are utilized in the particular ecosystem being examined.

$H[X/Y]$  measures the diversity of sources utilized by each species, averaged over all consuming species. When  $H[X/Y]$  is large, the species are on average generalists, that is, they use many sources of food evenly. When  $H[X/Y]$  is small, the species are on average specialists. They have a small number of sources, one of which is used heavily. In effect,  $H[X/Y]$  measures the average amount of choice, in picking sources, exercised by each species during the time the ecosystem is observed.  $H[X/Y]$  measures the average resource niche breadth in the ecosystem during the time it was observed.

If the flow rates do reflect the proportion of available resource coming from each source, then  $H[X/Y]$  measures the average relative amount of sustenance provided each species by each source. In this sense  $H[X/Y]$  indicates the average dependance of any one species on the available sources. (The larger  $H[X/Y]$ , the less the species depend on any one source.)  $H[X/Y]$  measures the diversity of ecological interaction between the species which occurs through the food web.

Together  $H[X/Y]$  and  $H[X]$  characterize the resource niche, that is which sources are being utilized by the species.

As discussed earlier, the object of structural self-organization is to provide the species with a dependable food supply and to make the fullest possible use of the available resources. The structural organization of an ecosystem is determined by the choices made by the species about what they will eat. The pressures which shape structural organization act by modifying the choices made by the individual species about the sources they utilize. These choices can be monitored by  $H[X/Y]$ . (Rutledge, 1974). The pressures will also affect the overall utilization of sources in the ecosystem. This can be monitored by  $H[X]$ . Therefore the structural self-organization of the ecosystem can be monitored using  $H[X]$  and  $H[X/Y]$ .

$H[X]$  and  $H[X/Y]$  were called  $D$  and  $S$  respectively, by Rutledge. These designations are appropriate in the context of this work.  $D$  measures the diversity of the distribution of the contribution of each compartment's output to the total resource flows in the system.  $S$  measures the average resource niche breadth and hence indicates how specialized the species are.

(Why not use  $H[Y]$  and  $H[Y/X]$ ? While  $H[X]$  and  $H[X/Y]$  characterize what is being eaten,  $H[Y]$  and  $H[Y/X]$  characterize who is eating. The two sets of variables are looking at the system structure from opposite perspectives. In a steady-state situation (that is a compartment's inputs equal its outputs) both perspectives yield the same result. In general, however, the perspectives will yield different results.

$H[Y]$  measures the diversity with which the total available resources flowing through the ecosystem structure are distributed amongst the consuming species. This would be useful in ascertaining if any species were dominating the consumption of resources. However it does not reveal in any way how the sources are being utilized.  $H[Y/X]$  measures the average diversity of consumers using each source. As such it indicates the average dependance of all species on any one source. This would be useful in assessing, on average in the ecosystem, if the disruption of a source will effect many species or a few. However  $H[Y/X]$  does not indicate anything about the dependancy of a individual species on a source. Therefore, it cannot be used to determine the significance to the species of a disruption of a source. Neither measure tells us anything directly useful about the resource niche, that is about the way in which each of the species is choosing to use the available sources.)

STATE NUMBER	Y <sub>1</sub>	Y <sub>2</sub>	Y <sub>3</sub>	Y <sub>4</sub>	Y <sub>5</sub>	D (=H[X])
1	0.200	0.200	0.200	0.200	0.200	1.068902
2	0.100	0.100	0.200	0.300	0.300	1.007215
3	0.050	0.060	0.080	0.400	0.410	0.954891
4	0.020	0.050	0.090	0.150	0.690	0.890264

**TABLE 5:** Examples of the values of D for a 5 compartment system.

	S	$\frac{(S_{\max} - S)}{S_{\max}} \times 100$	$\left\langle \frac{ (X_{ij})_{\max} - (X_{ij}) }{(X_{ij})_{\max}} \right\rangle \times 100$
Case 1: (S <sub>max</sub> )	1.09861	0	0
Case 2:	1.09428	0.39%	8.3%
Case 3:	0.39440	64%	113%

**Table 6:** Comparison of the difference in S to the spread in the X<sub>ij</sub>. (See the text for the various values of X<sub>ij</sub> for the three cases.)

#### QUANTITATIVE BEHAVIOR OF D AND S

Table 5 gives four different probability distributions that could be associated with a five compartment system. The value D is also given in this Table. Notice that for distributions which represent substantially different systems the value D changes by a small amount. This is because D is a logarithmic function.

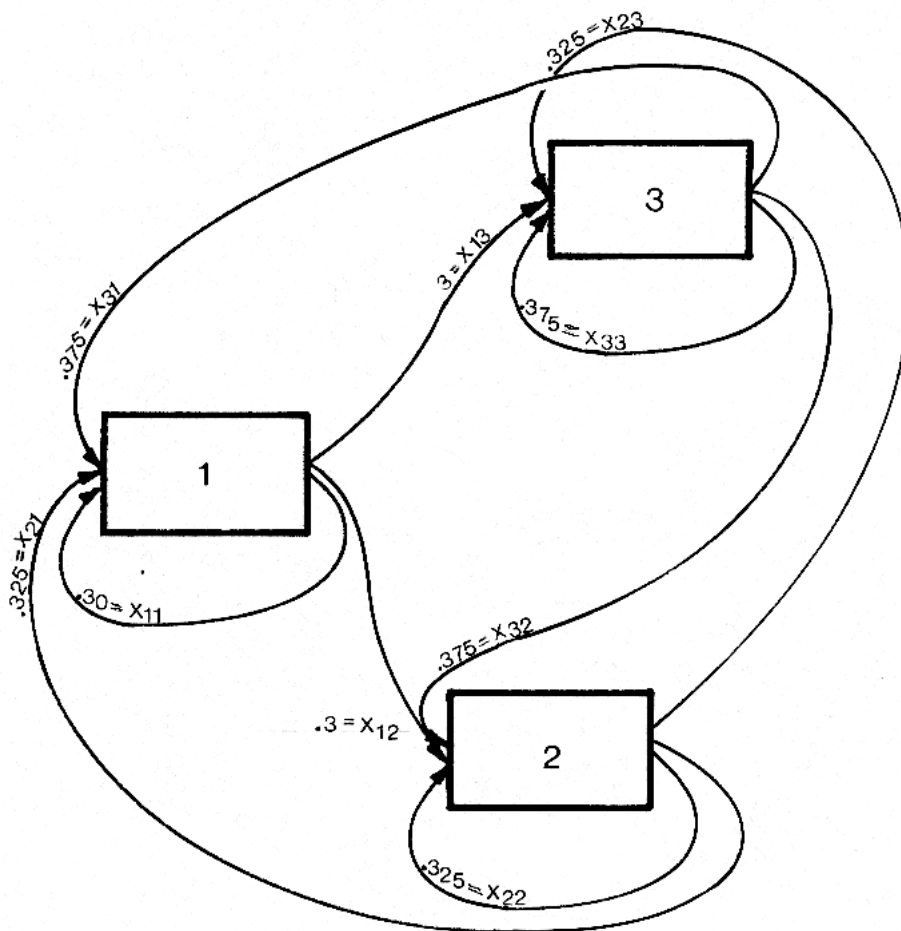
To better illustrate the properties of S consider the following simple system made up of three compartments. Assume that there is an even distribution of input flows amongst the compartments (i.e. Y<sub>j</sub> = 1/3). Consider three cases:

1. Each compartment is equally dependant on every other for food (X<sub>ij</sub> = 1/3);
2. Each compartment is almost, but not quite, equally dependant on every other compartment for food (X<sub>1j</sub> = .30, X<sub>2j</sub> = .325, X<sub>3j</sub> = .375);

3. Each compartment is essentially dependant on one other compartment for food  
 $(X_{1j} = .05, X_{2j} = .90, X_{3j} = 05)$

(It is assumed for simplicity that all of the compartments in each example have the same dependence on other compartments, Figure 3 shows this for Case 2.)

Table 6 shows the resulting values of S, the percentage difference between the maximum value of S and the value of S for the specific case, and the average percentage difference between the value of the  $X_{ij}$  for the specific case and the value of  $X_{ij}$  for the case when S is maximum. The point of this example is to demonstrate that small changes in S reflect much larger changes in the distribution of energy and mass flow (the  $X_{ij}$ ) through the system. This can be seen from examining the results in Table 6.



**Figure 3:** Food web for case 2 of the example systems.

Note also that the more evenly distributed the dependence of a compartment on other compartments (i.e. the more equal the  $X_{ij}$ ) the larger  $S$  is. Similarly  $S$  becomes larger as the energy and material output becomes more evenly distributed between the compartments.  $S$  also increases with the number of compartments.

### **3-7 THE ADVANTAGES OF USING $D$ AND $S$**

The most immediately obvious difference between the formulation presented in this paper and that of Rutledge, Atlan, or Ulanowicz is that the use of two measures to characterize structural self-organization is recommended. This is in contrast to one measure as suggested by the other authors. There are substantial theoretical arguments in favor of two measures.

From a purely statistical perspective, two experiments are being examined. Our knowledge about these experiments can be completely specified through either the  $\{P_i[X]\}$  and the  $\{P_j[Y/X_i]\}$  or the  $\{P_j[Y]\}$  and the  $\{P_i[X/Y_j]\}$ . With one set of these probabilities known, Bayes Theorem and the Completeness Axiom allow for the calculation of the other set. In order to completely describe the uncertainty associated with the situation, a measure of the uncertainty associated with conditional distribution, and a measure of the uncertainty associated with the unconditional distribution are required.

If less than two diversity measures are used, all the information the observer has about the flows in the system are not used. If more than two measures are used, the excess measures are simply re-expressing the information contained in two of the measures. The use of two measures, one incorporating a conditional probability and the other an unconditional probability will make use of all the information available about the ecosystem structure from the flow rates ( $\{X_i, Y_j, X_{ij}, Y_{ji}\}$ ).

Another way of stating this argument is from a systems theory viewpoint. Whether uncertainty or diversity is being measured, two levels in the system's hierarchy are being examined, the species level and the ecosystem level. Changes can occur in the diversity of flows as seen from the perspective of one level without affecting the diversity as seen from the other. Thus two measures are needed, one for each level. ( $D=H[X]$  measures changes at the ecosystem level,  $S=H[X/Y]$  measures changes at the species level.)

The obvious question these arguments beget is which two measures should be used? The argument given in the last two sections is that the measures which reflect "who is consumed", that is D and S are of immediate interest.  $H[Y]$  and  $H[Y/X]$  are measures of "who is consuming". These two sets of measures are complimentary in that one set looks at the outputs (D and S) and the other the inputs ( $H[Y]$  and  $H[Y/X]$ ). They are related by the symmetry property of  $I[X, Y]$ .

If Rutledge's formulation is examined in light of this discussion it becomes clear that S alone is not sufficient, on theoretical grounds, to characterize structural self-organization. It is also not adequate as a measure of stability, in the sense of sensitivity to external perturbations. The overall sensitivity of a system is quite different for a high value of D than for a low value, given that S remains constant. In the low value case, each species will depend highly on the same source. In the high value case, each species may depend highly on one source, but it will not be the same source for all species. Obviously these two different situation represent quite different overall systems sensitivities to disruptions in sources.

Atlan's and Ulanowicz's use of a single composite measure leads to ambiguities which do not occur with the use of two fundamental variables to characterize self-organization

For example, for Atlan's  $H (=H[X] + H[Y/X])$ ,  $dH/dt$  could be positive definite ( $> 0$ ) but  $dH[X]/dt$  and  $dH[Y/X]/dt$  would be indefinite (i.e. could be positive, negative or zero). Thus Atlan's definition of organization ( $dH/dt > 0$ ) does not place any definitive restriction on the fundamental variables. In Ulanowicz's case ( $dI/dt > 0$ ,  $I =H[X] - H[X/Y]$ ) organization can occur with either  $H[X]$  or  $H[X/Y]$  decreasing or increasing. If changes in  $H[X]$  or  $H[X/Y]$  are observed it is not possible to decide whether these changes are organizing or disorganizing (in Ulanowicz's sense), unless the changes in I are calculated.

In Appendix 3-I there is a numerical example. In this example  $dH[X]/dt < 0$  and  $dH[X/Y]/dt < 0$ . Yet the value of I does not change monotonically. More importantly for two quite different sets of values of  $H[X]$  and  $H[X/Y]$  (states 3 and 6), I has the same value. If I was used alone to measure the structural organization of the system, the conclusion would be that there is no difference in organization between states 3 and 6.

Yet  $H[X]$  (=D) and  $H[X/Y]$  (=S) reveal that changes have occurred in the way in which resources flow in the system. The structural organization has changed.

Combining fundamental variables into a single composite variable results in a loss in ability to unambiguously associate changes in the system variables with changes in the patterns of source utilization by the species. A number of ecologically quite different changes in species patterns of utilizing sources could result in the predicted changes in Atlan's and Ulanowicz's variables. The gain in simplicity in having a single variable to characterize organization is, in my opinion, offset by the loss in fidelity of the description of what is occurring in the ecosystem, particularly from the species perspective.

In summary, the major advantage of the measures of structural organization presented here, over those of Rutledge, Atlan and Ulanowicz, is that two of the fundamental variables are used as measures instead of one variable. In this way all of the structural information about the different levels in the system hierarchy is made use of. As well the ambiguity which stems from using a single system variable is removed. Finally the measures D and S focus on "who is consumed" rather than on "who is consuming".

## **CONCLUDING COMMENTS**

In this chapter the theoretical basis for using information theoretic measures in the context of describing the food web of ecosystems has been explored. The differences between the probable inference and frequency approaches to probability and the communication vs experiment approach to information theory were explored. The definition of information theory measures was made in the context of the probable inference/experiment approach.

The Shannon-Weaver index of species diversity and Colwell & Futayma's measure of resource niche breadth were then explored. Three points about these applications of information theory were brought out. The first is the importance of differentiating between criteria for measures of uncertainty and criteria for measures of diversity. The second is that information measures are only meaningful in the context of a specific observer. Third, population measures can only indicate how frequently

contact is made and not the degree of biological interaction which is represented by each contact.

Information measures associated with the resource (mass and energy) flows in the ecosystem were then examined. These measures represent a return to the line of thinking put forward by MacArthur. A production-consumption model of the ecosystem was proposed. This model allows for a clearer ecological interpretation of experiments X and Y than the models proposed by Rutledge and Atlan. The various measures of ecosystem structure proposed by Rutledge, Atlan, and Ulanowicz were reviewed. This review led to the conclusion that there is no agreement on how to measure structural organization.

Structural self-organization refers to changes in the way in which material and energy flows between the individuals in the ecosystem. The object of structural self-organization is to provide the species with a dependable food supply and to make the fullest possible use of the available resources. The effect of the pressures which shape structural self-organization will be to modify the choices made by species about the sources they will utilize. That is, the pressures will modify the resource niche occupied by the species. The average resource niche breadth is measured by  $S (=H[X/Y])$ . The pressures will also affect how the sources are utilized overall in the system. This can be monitored by  $D (=H[X])$ .  $S$  and  $D$  can be used to characterize the structural self-organization of an ecosystem.

The employment of two measures has the benefit of using all the information about the ecosystem's structure. As well, the ambiguity associated with Atlan's and Ulanowicz's single measures is avoided.

Atlan, Rutledge and Ulanowicz put forward hypotheses about how structural self-organization will develop under certain environmental conditions. These hypotheses have not been critically examined in this chapter nor have hypotheses which use  $S$  and  $D$  been put forward. However this has been done elsewhere. (See Chapter 4).

A recurring theme in this chapter is that the measures must reflect some ecological interaction. The ecological interaction, measured by the measures discussed herein, is determined by the definitions of the probability distributions and experiments X and Y. It has been suggested that the distributions should reflect the availability of the

resources in the flows between species. There are theoretical and practical problems with this. Availability [20] is a rather new concept in thermodynamics. It has not been adequately developed to be useful in the context of ecosystems. Several difficult problems in theoretical physics and statistical mechanics need to be resolved before measures can be developed for use in an ecological context. These issues are discussed in later chapters.

On the practical side, the assignment of specific values to the distributions and definitions of compartments in specific experimental situations has not been discussed. Any wisdom on these issues is empirical in nature and awaits the application of the measures in sufficient situations to justify generalizations. This chapter has only laid the theoretical basis for developing measures of ecosystem structural organization.

The reader should realize that the measures discussed herein characterize only one set of aspects of the ecosystem and of a species niche. For example, the control structure of the ecosystem is not discussed. Nor is the range of physical environments habitable by species. The measures are meant to characterize only one aspect of self-organization in ecosystems. There are other aspects of self-organization which are at least as important as structural self-organization.

### **APPENDIX 3-I: A HYPOTHETICAL FOOD WEB**

This appendix contains a numerical example which demonstrates how use of  $I$  alone as a system variable can lead to erroneous conclusions about a hypothetical food web.

The hypothetical system consists of 5 compartments which are not in a steady state. The system is moved through 11 different states.  $H[X]$ ,  $H[X/Y]$ , and  $I$  are calculated for each state. (See Table A-1.)

The reader should note that as the state number increases both  $H[X]$  and  $H[X/Y]$  decrease. However  $I$  is not monotonic. The fourth column of Table A-1 clearly demonstrates this. The point is that the monotonic decrease in the diversity of source utilization and the resource niche breadth is not clearly reflected by changes in  $I$ .

Of greater importance is the fact that two quite different states (3 and 6) have the same value of  $I$ . The differences between the values of  $D$  and  $S$  are about 4% while the differences between the values of  $I$  are less than 0.001%. (Since we are dealing with logarithmic measures

small differences reflect large differences in the system.) If only the value of I had been used to monitor the system, no change in the system would have been detected.

#### DETAILS OF THE SYSTEM CHANGE

For each of the 11 states the values of the  $X_{ij}$  are the same. Only the  $X_i$  are varied. (The  $X_i$  are calculated from the  $Y_j$  using  $X_i = \sum X_{ij} Y_j$ .)

#### DETAILS OF STATE 3 AND STATE 6 DIFFERENCES

For state 3 the  $X_i$  are {0.043000, 0.072000, 0.058000, 0.115000, 0.712000}. For state 6 the  $X_i$  are {0.051800, 0.066240, 0.059120, 0.089400, 0.733440}. The average percentage difference between the  $X_i$  is 11.13%. The percentage difference between the values of  $H[X]$  is 4%. The percentage difference between the values of I is less than 0.001%. (All percentages are calculated relative to state 3)

State Number	H[X]	H[X/Y]	I	I Difference
1	1.068902	1.037368	0.031534	
2	1.007215	0.976510	0.030705	-
3	0.980459	0.949051	0.031408 *	+
4	0.978245	0.949745	0.028499	-
5	0.954891	0.927178	0.027713	-
6	0.943597	0.912189	0.031408 *	+
7	0.914017	0.885642	0.028375	-
8	0.901683	0.874900	0.026783	-
9	0.890264	0.864516	0.025749	-
10	0.863401	0.842588	0.020813	-
11	0.795710	0.790646	0.005064	-

**TABLE A-1:** Values of  $H[X]$  and  $H[X/Y]$  and I for each of the 11 states. The fourth column indicates whether I has increased (+) or decreased (-) from the previous state. (\* = same value of I.)

STATE NUMBER	Y1	Y2	Y3	Y4	Y5
1	0.200	0.200	0.200	0.200	0.200
2	0.100	0.100	0.200	0.300	0.300
3	0.100	0.100	0.100	0.300	0.400
4	0.050	0.060	0.200	0.350	0.340
5	0.050	0.060	0.080	0.400	0.410
6	0.156	0.044	0.100	0.100	0.600
7	0.050	0.060	0.080	0.200	0.610
8	0.020	0.090	0.050	0.200	0.640
9	0.020	0.090	0.050	0.150	0.690
10	0.050	0.050	0.050	0.050	0.800
11	0.010	0.010	0.010	0.010	0.960

**TABLE A-2:**  $P_i[Y]$  for each state. For example for state 5,  $Y_3 = 0.080000$ .

	i=1	i=2	i=3	i=4	i=5
j=1	0.10	0.10	0.10	0.10	0.60
j=2	0.05	0.06	0.08	0.20	0.61
j=3	0.02	0.09	0.05	0.20	0.64
j=4	0.02	0.09	0.05	0.15	0.69
j=5	0.05	0.05	0.05	0.05	0.80

**TABLE A-3:** For each state the same values of  $X_{ij}$  are used. This is the table of the  $P_i[X/Y_j] = X_{ij}$ . For example  $X_{23}$ , the proportion of the input to compartment 3 from compartment 2, is 0.090000.

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