Ecosystem Flow Networks: Loaded Dice?

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ABSTRACT

An information-theoretic comparison of the topologies of observed ecosystem trans-
fers and randomly constructed networks reveals that it is not easy to separate the
members of the two sets. The distribution of ecosystem flow magnitudes, however, is seen
to differ markedly from ordinary probability functions and to resemble the Cauchy or
Pareto distributions. The agencies that impart such structure to ecological flow networks
are not obvious, but one strong possibility is that autocatalysis, or indirect mutualism,
promotes certain pathways at the expense of others, thereby enlarging the tail of the
distribution of flow magnitudes.

BACKGROUND

The focus of ecology is upon the *relationships* among populations of
organisms and their surrounding environment. As such, theoretical ecolo-
gists seek to discover that which is common to all ecosystem configurations
and to elucidate the factors that bring these relational structures into being.

For at least two decades investigations of ecosystem structures were
dominated by attempts to relate the degree of trophic connectance in an
ecosystem to the "stability" exhibited by that community. Hutchinson, and
later Odum [20], argued that the redundant pathways that connect the
elements of an ecosystem provide routes for compensatory communication
whenever major arteries of flow are accidentally disrupted. One of the first
efforts to quantify the configuration of ecosystem flow networks was made
by MacArthur and Ranch [18], who proposed that the Shannon–Wiener
index of uncertainty [27] be used to measure the degree of parallelism
among flow pathways. Unfortunately, the Shannon–Wiener measure was

then applied to population densities, instead of interspecies flows, in what is now regarded to have been a largely futile attempt to draw a connection between the diversity of population levels and the stability of the communities the populations comprised (see [35]).

One of the several reasons why the diversity–stability issue foundered appears in hindsight to have been that MacArthur's identification of diversity with Shannon's index was premature. Shannon's version of information theory had only recently appeared in relatively inchoate form when MacArthur attempted to apply it to ecosystem networks. It is not apparent whether or not MacArthur was aware of later refinements in information theory such as the "average mutual information" or the "conditional uncertainty," or, if he were, that he ever tried to amend his treatment of compensatory pathways to include these new concepts.

Two decades after MacArthur attempted to quantify system diversity in terms of the Shannon–Wiener measure of average uncertainty, Rutledge et al. [26] reasoned that this index was not specific enough to quantify the extent to which parallel pathways are present in a network. It is necessary to distinguish between that part of the overall diversity that is constrained by the obligate coupling of the nodes and the remainder that represents the latitude for "choice" among alternative pathways out of or into a typical node. Ulanowicz [30, 31] argued that the appearance of constraints is tantamount to what should be regarded as the "growth and development" of an ecosystem, that is, the system's becoming ever more organized. He modified Rutledge's measures to draw a quantitative and comprehensive narrative of the direction in which ecosystem networks evolve.

We wish to investigate ecosystem organization along a different, but closely related, avenue and show how the calculation of information indices corresponding to weighted networks of flows is useful for investigating how, if at all, ecosystem networks are nonrandom in nature. Below, we give details on how appropriate information indices can be calculated both for randomly assembled, weighted networks and for a collected ensemble of estimated ecosystem networks. The resulting comparison of the measures of the two groups reveals how they differ in both qualitative and quantitative ways that are not apparent from a knowledge of their connection topologies (i.e., qualitative data) alone.

QUANTITATIVE FORMULATIONS

To be more concrete and quantitative, the magnitude of the exchange from node (species) i to node (species) j within a system containing n nodes will be denoted by T_{ij}. The total amount emanating from i is then determined by summing the outputs from i over all possible destinations j and is designated by T_i. Rutledge et al. [26] suggested that the inputs to

j from all possible sources i could be added to arrive at the total input to j, or T_j'. (At steady-state, $T_i = T_i'$ for all i, but the analysis that follows does not require such an assumption.) Finally, all the compartmental outputs or all of their inputs can be summed to calculate a unique measure of total exchange transpiring in the system. This latter index is called the total system throughput and is denoted simply by T.

Rutledge et al. observed that one could employ various quotients of these flow measures as likelihood estimators for the joint and conditional transfer probabilities. For example, the *joint* probability that an arbitrary quantum both leaves i and enters j can be estimated by the quotient T_{ij}/T. The *conditional* probability that a particular quantum enters j, given that it already left i, is estimated by the quotient T_{ij}/T_i. The unconditional probability that an input is flowing into j would be approximated by T_j'/T, and so on.

Using such probability estimators, one can approximate all the information variables pertaining to a given weighted network. In particular, the average mutual information is usually defined as

$$A = H(y) + H(x) - H(x, y),$$

where A is the mutual information and H is the Shannon uncertainty[1] as calculated on the input (x) and output (y) variables, respectively. $H(x, y)$ is the joint uncertainty, or total flow diversity. Rewriting A in terms of Rutledge's likelihood quotients gives

$$A = \left[- \sum_{i=1,\ldots,n} \frac{T_i}{T} \log\left(\frac{T_i}{T}\right) \right] + \left[- \sum_{j=i,\ldots,n} \frac{T_j'}{T} \log\left(\frac{T_j'}{T}\right) \right]$$
$$- \left[- \sum_{i,j=1,\ldots,n} \frac{T_{ij}}{T} \log\left(\frac{T_{ij}}{T}\right) \right]$$
$$= \left[- \sum_{i,j=1,\ldots,n} \frac{T_{ij}}{T} \log\left(\frac{T_i}{T}\right) \right] + \left[- \sum_{i,j=1,\ldots,n} \frac{T_{ij}}{T} \log\left(\frac{T_j'}{T}\right) \right]$$
$$- \left[- \sum_{i,j=1,\ldots,n} \frac{T_{ij}}{T} \log\left(\frac{T_{ij}}{T}\right) \right]$$
$$= \sum_{i,j=1,\ldots,n} \frac{T_{ij}}{T} \log\left(\frac{T_{ij}T}{T_i T_j'}\right). \tag{1}$$

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[1]Shannon gave the name "entropy" to his measure of uncertainty, and most texts on information theory persist in using this term. However, this term easily can be confused with the thermodynamic state variable of the same name, and its use in information theory should be discontinued.

Ulanowicz and Norden [33] argue that $H(x, y)$ is the most appropriate measure of the total flow diversity. The mutual information, A, quantifies the amount of that diversity that is encumbered by structural constraints. The remainder, $\Phi = H(x, y) - A$, represents the amount of "choice" (conditional uncertainty) pertaining to both the inputs and outputs of an average node in the network. After simplification, Φ becomes

$$\Phi = - \sum_{i,j=1,\ldots,n} \frac{T_{ij}}{T} \log\left(\frac{T_{ij}^2}{T_i T_j'} \right). \tag{2}$$

Dividing Φ into two terms reveals more about its mathematical meaning.

$$
\begin{aligned}
\Phi &= - \sum_{i,j=1}^{n} \frac{T_{ij}}{T} \log\left(\frac{T_{ij}}{T_i} \right) - \sum_{i,j=1}^{n} \frac{T_{ij}}{T} \log\left(\frac{T_{ij}}{T_j'} \right) \\
&= \sum_{i=1}^{n} \frac{T_i}{T} \left[- \sum_{j=1}^{n} \frac{T_{ij}}{T_i} \log\left(\frac{T_{ij}}{T_i} \right) \right] + \sum_{j=1}^{n} \frac{T_j'}{T} \left[- \sum_{i=1}^{n} \frac{T_{ij}}{T_j'} \log\left(\frac{T_{ij}}{T_j'} \right) \right] \\
&= \sum_{i=1}^{n} \frac{T_i}{T} H_i + \sum_{j=1}^{n} \frac{T_j'}{T} H_j',
\end{aligned}
\tag{3}
$$

where

$$H_i = - \sum_{j=1,\ldots,n} \frac{T_{ij}}{T_i} \log\left(\frac{T_{ij}}{T_i} \right)$$

and

$$H_j' = - \sum_{i=1,\ldots,n} \frac{T_{ij}}{T_j'} \log\left(\frac{T_{ij}}{T_j'} \right)$$

represent, respectively, the output diversity at node i and the input diversity at node j. Thus, one sees that the first and second terms (denoted by Φ_1 and Φ_2, respectively) of Equation (3) are, respectively, the average output diversity weighted by the total outputs T_i and the average input diversity weighted by the total inputs T_j'. The average diversity over both outputs and inputs thus can be written as $\Phi/2$.

It should be recalled from information theory that the diversity of pathways through a decision tree is an exponential function of the number of branch points or "decisions" that generate the tree. Accordingly, the

mean, or effective number of flows, m, impinging upon or emanating from a typical node in the network should be [16]

$$m = b^{\Phi/2}, \tag{4}$$

where b is the base to which the logarithms are referred (usually 2, e, or 10; in our calculations we shall put $b = e$ and $\log \Rightarrow \ln$). Because $m = b^{\Phi/2} = \sqrt{b^{(\Phi 1 + \Phi 2)}} = \sqrt{b^{\Phi 1} b^{\Phi 2}} = \sqrt{m_1 m_2}$, it becomes clear that m is the geometric mean of the input and output connectances.

To show that Equations (3) and (4) yield values of m that appeal to the intuition, the reader should refer to the hypothetical network shown in Figure A1 (Appendix A). There each node has exactly two inputs and two outputs, all of equal magnitude. The reader should substitute the uniform values for the T_{ij} into (3) and (4) to confirm that $m = 2$ for this limiting case (see also Table A1). In real, weighted flow networks, the exchanges are virtually never all equal in magnitude, as in Figure A1a, so the effective connectance per node, m, will almost never take on an integer value. But weightings serve to impart more meaning to m than is possessed by any connectance that could be calculated from qualitative linkages alone. For example, 600 units of flow are configured three ways in Figure A1. In Figure A1a, medium is distributed as eight equal flows. In Figure A1b, two-thirds of all medium flows along the four innermost channels; and in Figure A1c, almost all medium egresses compartment 1 to reach node 2, while only minute amounts flow along the remaining seven routes. In a qualitative sense, two outputs exit node 1 in each case. However, when one reckons the log mean number of outputs using Equations (3) and (4), one arrives at $m = 2$ for configuration (a), but $m = 1.889$ for the one in Figure A1b, and $m = 1.096$ for the third one. The last value accurately reflects the fact that the flow in the third case is dominated by a single output. Hence, m is seen to represent the *effective connectance* per node.

Rutledge's measures pertain only to closed networks. Hirata and Ulanowicz [10] show how these indices can be extended to open systems as well. They define three virtual compartments to provide sources and sinks for exogenous transfers. For example, the node 0 denotes the source of an external input, while $n + 1$ and $n + 2$ refer to the sinks that receive exports of useful and dissipated medium, respectively. (The distinction between useful and dissipated exports is subjective to a degree, but it is not altogether essential to this analysis.) Thus, T_{0j} represents the amount of medium flowing into j from outside the system, whereas $T_{i,n+2}$ is the amount of medium dissipated by i per unit time. Simply by extending all the summations in Equations (1), (2), and (3) to run from 0 to $n + 2$, one thereby calculates the values of $H(x, y)$, A, and m as they apply to open systems.

There is a minor complication in applying Equations (3) and (4) to open systems to calculate the effective connectance per node, m, in that the resulting value will usually be inflated by what often is a large number of flows emerging from node 0 and entering nodes $n + 1$ and $n + 2$. As these nodes are purely hypothetical, it is best not to include their respective output and input fractions in the calculation of m. An amended conditional uncertainty obviates such inflation of m by including only the input and output diversities of the n system nodes. The modified measure of choice will be denoted by Φ' and calculated as

$$\Phi' = - \sum_{i,j=1,\ldots,n} \frac{T_{ij}}{T} \log\left(\frac{T_{ij}^2}{T_i T_j'} \right) - 2 \sum_{j=1,\ldots,n} \frac{T_{0j}}{T} \log\left(\frac{T_{0j}}{T_j'} \right)$$
$$- 2 \sum_{i=1,\ldots,} \frac{T_{i,n+1}}{T} \log\left(\frac{T_{i,n+1}}{T_i} \right) - 2 \sum_{i=1,\ldots,n} \frac{T_{i,n+2}}{T} \log\left(\frac{T_{i,n+2}}{T_i} \right). \quad (5)$$

THE TOPOLOGICAL CONNECTANCE

As part of our investigation into the nature of ecosystem structure, it will prove useful to quantify the information one gains by estimating the magnitudes of ecosystem connections, that is, by upgrading from qualitative to quantitative data. Toward this end we devise an alternative measure of topological connectance cast in the same idiom as m, that is, using information theory. The examples in Appendix A provide a clue as to how one should proceed. We define the topological connectance per node, m^*, as the value that m would take on if all the nonzero flows in the network were assumed equal in magnitude (as is implicitly done when one works with qualitative data). To calculate m^*, one simply sets all T_{ij} in (3) or (5) to the same value, call it T^*, and proceeds to calculate a value Φ^* for the conditional uncertainty. This value of Φ^* can then be substituted into (4) to obtain m^*. [In the example in Figure A1a, $m^* = m$. As soon as any two values of T_{ij} become unequal, then $m^* > m$. See Appendix A.]

To recapitulate, m measures the effective connectance per node as averaged over all nodes and all flows in the network. Because flows are virtually never uniform in a system, its effective connectance per node will always be less than its topological connectance per node, that is, $m < m^*$. The difference, $m^* - m$, is related to the amount of information one gains about the system configuration once the various magnitudes of the transfers are known. As any arbitrary network will yield a couplet (m^*, m), the relationship between its topological and effective connectances can be graphed as a point on a plane defined by m^* and m axes. Because

$m^* \geqslant m \geqslant 1$, all possible networks will map into the positive octant defined by the diagonal line $m = m^*$ and the horizontal line $m = 1$.

PLAN OF INVESTIGATION

In what follows we seek to identify and compare the regions of the feasible octant populated by randomly assembled and observed networks, respectively.

Creating a randomly assembled, weighted network involves two steps. First, one must employ a random number generator to assign locations in a matrix to nonzero flows according to a given level of overall connectivity. In this study we assigned flows both to $n \times n$ matrices and to $(n+3) \times (n+3)$ matrices, where in the latter cases the last three rows and columns represented imports, exports, and respirations, respectively. (All the elements of the respiration column, were filled with nonzero flows to interject the effects of the second law of thermodynamics.) The results were not appreciably influenced by whether we included or excluded exogenous transfers, as long as we were careful to use (5) whenever exogenous flows were present.

The second step in constructing a random net is to assign a magnitude to each nonzero flow in the topology just defined. We tested the effects of using five different ordinary probability distribution functions (pdf's) to assign magnitudes: uniform random (white noise), (one-sided) Gaussian with zero mean and unit variance, negative exponential (Laplacean) with unit mean, Poisson with mean of 100, and log-normal calculated on the Gaussian. To test the distribution of each pdf on the m^*m plane, we generated 490 random networks: for each dimension n from 2 through 50 inclusive, we created 10 networks with connectivities equally spaced between 10% and 100% inclusively.

To see where observed or estimated ecosystem networks stand in relation to the random networks, we have assembled a set of 37 examples of weighted webs that have been estimated by at least 17 different investigators for a wide variety of ecosystems. The number of compartments, n, in the flow webs ranges from 4 to 36. Prior to the analysis we made no effort to assess the relative accuracies of the reported flows, either within a given ecosystem representation or among their numerous authors. Most of the data have been reported elsewhere in the literature, although a few were communicated directly to the first author.[2]

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[2]Copies of the Fortran source code used to generate the random networks, as well as the data comprising the 37 estimated networks, can be obtained from either author via electronic mail (ulan%cbl.umd.edu@umd2 and toe002@djukfa11, respectively on BitNet) or by forwarding a diskette of the reader's choosing to one of the authors.

RESULTS

When all the random networks generated by a particular pdf are plotted in the m^*m plane, the results are at first startling. The points representing the random networks converge very quickly to a straight line,

$$m = \alpha m^*, \tag{6}$$

where α is a constant characterizing the generative pdf. In Appendix B we demonstrate analytically that networks generated by ordinary pdf's that are normalized and possess finite means should converge to a ray on the m^*m plot. Furthermore, the slope α of each ray is independent of the mean of the generating pdf and depends only on its higher-order moments. The values range from a high of 0.99 (virtually 1.00) for the Poisson distribution to a low of 0.61 for the log-normal. A random uniform distribution yields a value of $\alpha = 0.82$, the Gaussian a value of 0.75, and the Laplace distribution converges to a ratio of 0.65. The five sets of randomly generated networks are shown in Figure 1, where each radial is labeled according to its generating pdf.

When the points corresponding to the 37 observed networks are mapped onto the same axes (see Figure 2), many of the networks with low m^* fall
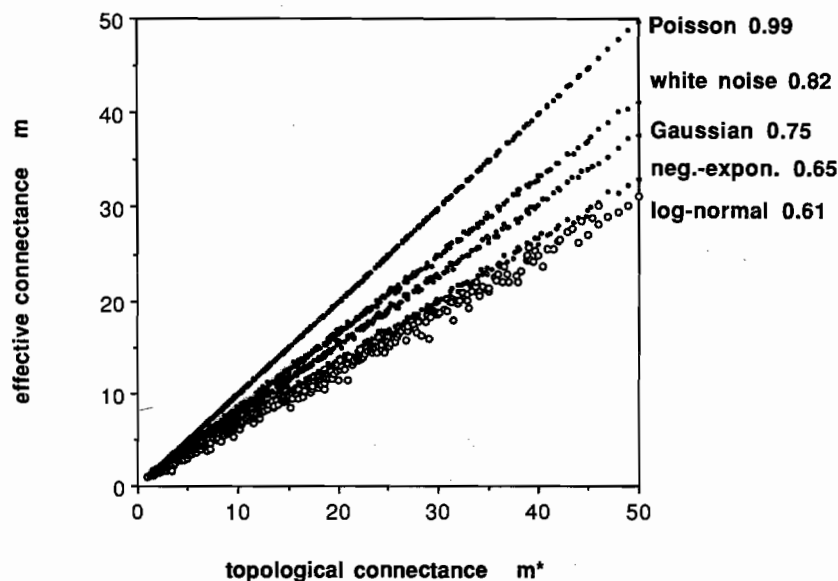

FIG. 1. Distributions of effective connectance m versus topological connectance. Each ray is labeled according to its generating pdf together with its slope α from Equation (6).
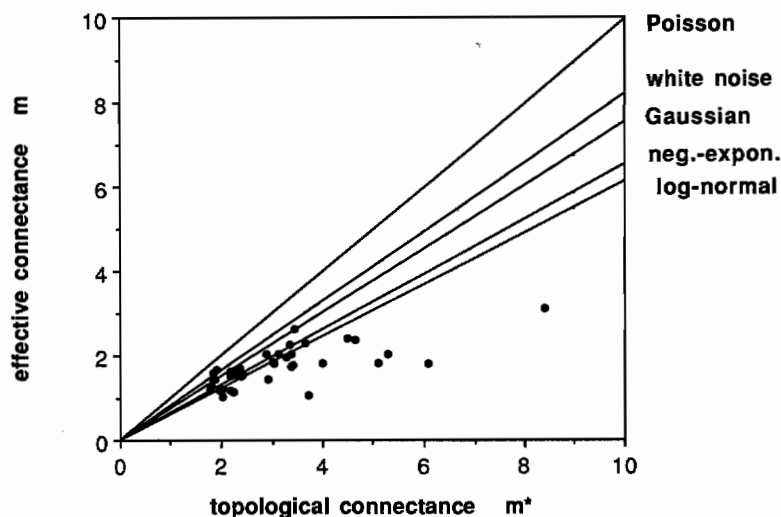
FIG. 2. The 37 observed networks are mapped against the same five rays as in Figure. 1.

among the pdf radials. However, as m^* increases, virtually all the observed networks are situated well below the radial of least slope (the log-normal). There are two possible reasons behind this divergence: (1) The networks in question belong to a class of random networks generated by pdf's with radically skewed higher moments or (2) they belong to a class that cannot be generated by ordinary pdf's. The latter circumstances would have strong implications for future work on randomly assembled ecosystem networks.

We have strong reason to believe that "well-researched ecosystem networks" do not belong to the class that can be generated by ordinary pdf's. To present the evidence behind this claim, we note that all pdf's with definite means and variances generate random networks that are character-ized by a single, universal relationship. In Appendix C we show that all ordinary pdf's generate networks for which the following relation is asymp-totically fulfilled:

$$e^A = n/m. \tag{7}$$

This relationship implies that on a plot of $\exp(A)$ versus n/m, networks generated by ordinary pdf's yield points close to the diagonal. On Figure 3 the 490 networks generated by the uniform-random distribution (shown as black dots) cluster near the diagonal

Also plotted in Figure 3 are the 37 sample ecosystem networks (open circles). We gauged the scatter of the random networks around the diago-
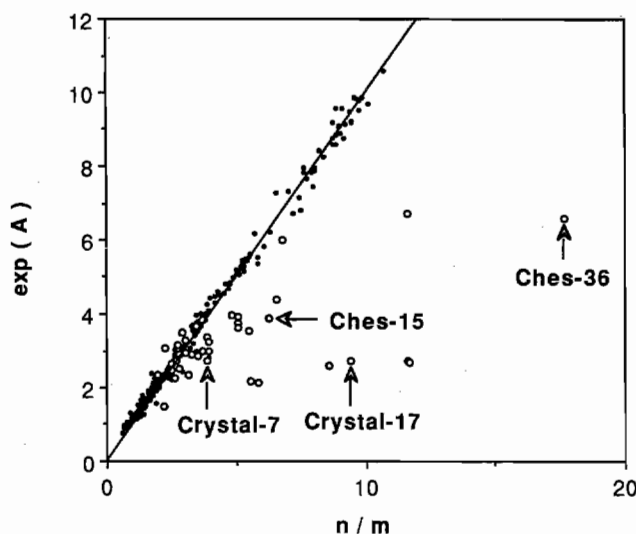
FIG. 3. The 490 networks generated by the uniform-random distribution (white noise) are shown as black dots; the 37 sample ecosystem networks are shown as open circles. The four marked sample networks are explained in the text.

nal using the distance

$$D = \frac{1}{\sqrt{2}} \left| \left(\frac{m}{n} \right) e^A - 1 \right|. \tag{8}$$

The distribution of random-uniform networks reveals that only nine of the sample networks fall within the 95% confidence interval and an additional four fall within the 99% interval. Thus, a substantial fraction of the observed networks lie well beyond the scatter of the generated random nets, and we conclude that it is most improbable that the outlying ecosystems have configurations that belong to the class of networks that can be generated using ordinary pdf's.

The divergence of the distribution of the magnitudes of observed flows from random types has both practical and theoretical implications. If, for example, the distance of a network from the diagonal in Figure 3 is related to the information inherent in the configuration of its flows, then one should design ecosystem accounting projects so as to have a moderate chance of capturing such information. That is, from the beginning one should resolve the system into a sufficient number of compartments that there remains a reasonable probability that the resultant n/m will exceed, say, 4. Because effective connectivities of real systems are always greater

than 1, this means that one should not begin a study with only four or five compartments. (It is slightly embarrassing to note that the five-compartment Cone Spring network, used widely as an exemplar by one of the authors and by many others, lies closer to the diagonal of Figure 3 than *any* of the other 36 networks!)

We note that aggregating compartments will lower both n/m and $\exp(A)$ and, in addition, will decrease the relative distance separating the aggregated network from the diagonal. Our collected data contain two specific examples that may further illustrate this point: The flow networks of the ecosystems inhabiting the mesohaline part of Chesapeake Bay and the Crystal River (Florida), respectively. The 36-compartment network for Chesapeake Bay [1] has been condensed to 15 compartments (labeled Ches-36 and Ches-15, respectively, in Figure 3) to match exactly a previously established compartmental structure of the Baltic Sea ecosystem [36]. Most of this aggregation involves lumping 14 compartments of Chesapeake finfishes into two categories according to whether they are filter-feeding or carnivorous. Similarly, seven benthic compartments are combined into filter-feeding or deposit-feeding aggregates. In the second aggregation example, a 17-compartment Crystal River ecosystem network [14] has been consolidated into seven compartments [11] (see Crystal-17 and Crystal-7 in Figure 4). Unlike the ad hoc aggregation of the Chesapeake ecosystem, the Crystal River compartments were iteratively combined in pairwise fashion so as to minimize the (inevitable) decrease in the average mutual information at each step (see below). The values for $\exp(A)$, n/m, and the relative distance D away from the diagonal [calculated from Equation (8)] are given in Table 1. Both aggregation schemes, although very different in methods and purpose, result in comparable and, more important, substantial losses of information, as exemplified by the lower values of D in the aggregated networks.

Ecological data tend to be relatively scarce, so that the need seldom arises to aggregate system compartments; but the converse is true in economics, and criteria for aggregating nodes are most useful. Theil [29] and Hirata and Ulanowicz [11] have suggested that minimizing the decrease in the average mutual information of the flows, A, is a very effective

TABLE 1

Ecosystem Flow Network	n/m	$\exp(A)$	D
Chesapeake Bay (36 compts.)	17.68	6.592	0.443
Chesapeake Bay (15 compts.)	6.263	3.885	0.268
Crystal River (17 compts.)	9.413	2.730	0.502
Crystal River (7 compts.)	3.885	2.718	0.212

aggregation criterion. However, the results of this analysis indicate that minimizing the drop in the distance from the diagonal in Figure 3 might be even more effective in preserving the fundamental traits of the system. Because of the geometry of the diagonal (slope = 45°), this criterion translates into minimizing the decrease in the absolute value of the difference, $1 - (m/n) \exp(A)$.

One of the most common excuses given for not resolving ecosystem budgets into more compartments is the increased time and cost associated with *precisely* measuring so many exchange rates. We remark here that if a network lies close to the diagonal in Figure 3, striving for measurement precision is likely to prove futile, as the resulting configuration will probably still fail to portray essential characteristics of the network. Conversely, it appears that flow magnitudes in a highly resolved network need be known only to order-of-magnitude precision before the network begins to capture the essential trophic characteristics of the system (i.e., a highly resolved and roughly estimated network is likely to lie farther off the diagonal than a poorly resolved, but precisely known set of flow measurements). We hope this observation will encourage more colleagues to attempt the estimation of high-resolution (i.e., many-compartment) flow networks.

A plot of n/m^* versus $\exp(A^*)$ for randomly assembled networks also yields a straight line (see Appendix C). Unlike the distribution of weighted networks in Figure 3, however, the topological structures of the 37 sample networks all lie close to the diagonal, intermingled among the random, topologies (cf. Figure 4). In other words, the observed topological networks are indistinguishable from their randomly constructed counterparts when gauged by information-theoretic indices. (In hindsight, this property also justifies the first step in our procedure for constructing artificially assembled networks.) Knowing the topology of a system certainly can be useful, but one should be aware that a marginal amount of further effort to attach rough magnitudes to the indicated exchanges is likely to pay handsome rewards by revealing characteristics about the system that otherwise would go unnoticed.

In light of the virtual certainty that real ecosystem configurations do not belong to the grand ensemble of networks generated by ordinary probability distributions, the reader may wonder whether stochastic distribution functions do exist that will generate randomly assembled webs that more closely resemble real ecosystem networks. In fact, it is quite easy to construct random networks that populate the octant below the diagonal in Figure 3. For example, if the arc magnitudes of a flow network are generated as the ratios of paired samples from the random-uniform distribution [15], the networks that result are dispersed throughout the allowed octant of the m^*m plane, as shown in Figure 5. We demonstrate in Appendix D that the distribution function for these quotients remains flat
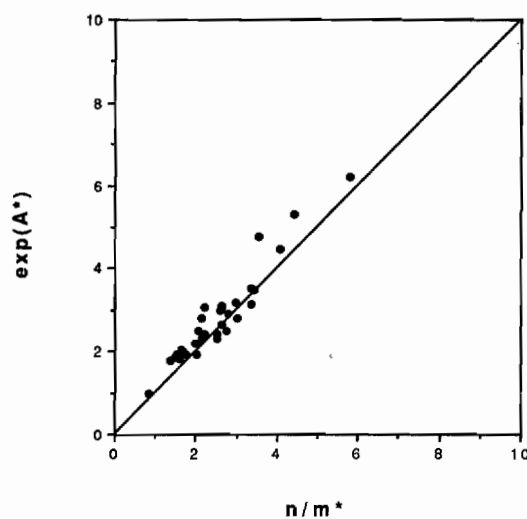
FIG. 4. The same information-theoretic indices as in Figure 3 are plotted for *unweighted* networks.
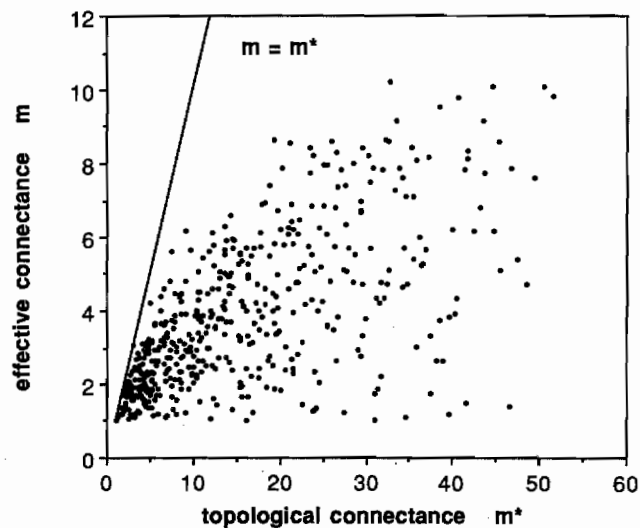

FIG. 5. Plot of *m* versus *m** for networks generated by the random quotient distribution. (Note the different scales of the axes.)

like white noise until the mean of the uniform distribution used to generate
the numerators and denominators. Thereafter, the distribution falls off as
$1/x^2$ (like the Pareto and Cauchy distributions). This distribution function
can be normalized, but it does not possess a finite mean (or higher
moments). The probability that a finite sample drawn from this distribution
will possess one or a few unusually large values always remains palpable,
and it is these outlier flows that drive the network away from the diagonal
in Figure 5 (see also the examples in Appendix A).

When a suite of networks created by the random quotient distribution is
plotted on the m^*m plane as in Figure 5, one notices that the envelope of
the generated points closely resembles the plot of $(m^*)^{1/2}$. The existence of
such an envelope suggests that, as topological connectivity increases, the
disparity between measured configurations and those generated in ordinary
random fashion grows even faster.

DISCUSSION AND SPECULATIONS

Most readers are probably aware that the comparison of stochastic and
observed ecosystem configurations also has been a central theme in the
development of a field of theoretical ecology now known as "food web
theory" [8, 9, 12, 19, 25, 37 and, particularly, 6 and 28].

It is difficult to do justice to food web theory in a single paragraph;
suffice it here to characterize the effort as the examination of *qualitative*
data on predator–prey interactions in a wide variety of communities
[2, 4, 5] for underlying regularities. The central variables in most discussions
are the connectance of the web, C, the number of elements in the web, n,
the length of the trophic chain, and the ratio of predators to prey. Some of
the other issues debated have included: "What, if any, relationship exists
between food web connectance and number of elements?" [22]; "What
determines the maximum length of a food chain within a food web?" [23];
"What lies behind the apparent constancy in the average number of
predators per species of prey resource?" [3].

There are significant differences between the assumptions underlying
"flow analysis" as presented here and those encountered in food web
theory. For example, flow analysis is limited to considering only palpable
exchanges. In food web theory, more general interactions are allowed, such
as spatial interference, ethological communication, and a host of other
processes that are difficult to quantify. Food web analysis usually deals only
with a necessary subset of all possible interactions, but it can be argued that
through the myriad of feedback processes at work in the system, the effects
of the nonpalpable interactions are made implicit in the observed flow
magnitudes that they treat.

In the food web literature the connectance, C, is quantified in one of
several ways, but all methods of reckoning involve dividing the number of

observed interactions by a quantity that is proportional to the square of the number of nodes, n. Thus, the product nC represents an average number of flows per node, or an average connectance per node. The effective connectance, m, likewise depicts a connectance per node, but one wherein the contribution of each flow has been weighted according to its relative magnitude.

We wish to suggest that the effective connectance per node, m, is more useful than the product nC for evaluating the overall status of ecosystem interactions. Paine [21], for example, has been highly critical of the data used in food web analysis. He cites how data on food webs are always incomplete. That is, it is never possible to study an ecosystem with so fine a resolution that all the species and all their interactions can be enumerated. One must always aggregate species to some degree (usually more so at lower trophic levels) and stop counting interactions below some nebulous threshold. Both of these approximations can strongly affect the perceived values of n and C (and their product nC) used in all the food web narratives.

At its root, Paine's concern is directed against the binary nature of qualitative food webs, that is, either a connection exists or it does not. Once an interaction is assumed to be present, its effect upon the connectance is the same regardless of whether it represents a dominant interchange or a minute one. However, the values of m in quantified networks should remain relatively insensitive to the magnitude of the observational threshold. Of course, data on weighted interactions in ecosystems will likewise remain incomplete; it is inevitable that some small interactions will remain beyond detection by the observer (see also [7]). However, by virtue of the small weightings that would be assigned to these neglected flows and/or nodes (species), the value of m calculated in their absence will differ only minimally from what would result by their inclusion. As a result, m will always remain less sensitive to incomplete data than will its food web counterpart, nC.

The observation that estimated *topologies* are indistinguishable from randomly constructed ones (see Figure 4) provides evidence to support the hypothesis that ecosystem food webs cannot easily be separated from stochastically assembled communities [17]. However, this negative result does not mean that it is impossible to define some conditional properties that could be used to subdivide the class of random topologies. One might then identify observed topologies with a given subclass, for example, the interval food webs of Cohen [6] or the tightly packed simplicial complexes of Sugihara [28].

Our conclusion as regards quantified ecosystem networks is quite another matter. On the basis of the available evidence, we feel it not premature to assert that real ecosystem networks of material and energy

flows, when sufficiently quantified and resolved, are not ordinary stochastic systems. Having drawn this inference, we remain at a loss to identify conclusively those factors that actually impart structure and definition to real ecosystem networks. At this time we can only speculate, and we wish to share our inclinations with the reader in the hope of initiating productive dialogue.

Real flow networks are not the results of unconditional stochastic allocations in the same way as, say, throws of a pair of dice or even the frequencies of species in an ecosystem [24]. Enlightened by hindsight, we now see how it was unreasonable ever to have expected flows to be distributed so simply. Flows by their very nature are *conditional*. That is, how much flows from i to j is always conditional upon circumstances at both i and j. In trying to envision a stochastic scenario, one might assume that the activities of the donor compartments were apportioned according to the random-uniform distribution. The activities of the recipients might be likewise distributed. Then the amounts leaving a particular donor and arriving at a chosen recipient would involve conditional probabilities, that is, Bayesian quotients resembling those that define the random-quotient distribution discussed in the last section and in Appendix D. (We note in passing that the Cauchy distribution often is referred to as the "conditional" distribution.)

It remains conceivable that the uncommon distribution of ecosystem flow magnitudes derives from some systematic bias in the way ecologists are inclined to identify ecosystem compartments (i.e., it is an artifact of how the system is aggregated). We believe that this possibility is remote. To test this issue conclusively would require that one compare sets of randomly constructed networks with collections of observed networks under the constraint that all networks in both sets have the same number of compartments. There simply are not enough estimated networks having large dimensions to attempt such a comparison. (Exercises in aggregating and disaggregating existing networks show only that the former process moves the network closer to the $m-m^*$ diagonal and vice versa). But the key indication that the Cauchy-like distribution of flows is not an artifact of aggregation comes from the fact that the associated stocks are *not* distributed in similar fashion. It should further be noted that the family of probability functions with long tails and without definable means was introduced first by Pareto to describe the distribution of incomes among individuals in an economic community. We note that (1) the question of aggregation in Pareto's ensembles was moot, and (2) incomes are flow variables quite analogous to ecosystem transfers. One could even regard the conclusions presented here as an extension of Pareto's results into ecology.

It is more likely that the unusual distribution of flow magnitudes is the effect of some natural bias (i.e., is ontological rather than epistemic in

nature). There are any number of factors that could impart order to ecosystem flow networks and thereby distinguish them from ordinary stochastic ones. Natural selection, of course, heads the list of agencies believed to impart order to evolving communities. However, natural selection commonly is regarded to act on species separately, and in that context is unlikely to account for the distributions seen in Figure 3.

A minority of naturalists believe that selection can act on larger units of the ecosystem. For example, Wicken [34] and Ulanowicz [31, 32] believe that autocatalytic feedback serves to coalesce populations into coherent units that compete with each other for resources. Ulanowicz [30–32] has suggested that the end result of cybernetic feedback is to increase the articulation of the flow network, that is, to decrease the effective connectance per node, m. It is hardly surprising, therefore, that we should regard the tendency for large natural systems to deviate from simple stochastic networks as evidence favoring the hypothesis that selection is acting on units larger than the individual population. We make no claim that autocatalytic feedback is the exclusive agent imparting coherence to flow networks, and invite the reader to speculate on other possible factors.

If left unchecked, cybernetic feedback, and in particular its autocatalytic form, would result in highly specialized communities—communities with values of m only slightly greater than unity. Although our collection of estimated networks includes only a handful of systems with moderate topological connectance, m^*, it is obvious that none of them resembles a configuration of entirely monospecific trophic interactions. Rather, one sees the beginnings of what might be called a "window of viability"—a region of the feasible m^*m octant that is withdrawn from the frontiers of the purely stochastic realm (of higher m) but also does not approach the limit of $m = 1$ where sustenance flows over very narrow channels.

The emerging picture of the development and persistence of trophic patterns makes the earlier notion of "diversity begets stability" appear simplistic by comparison: Systems with large numbers of components are unlikely to behave as if composed of independent entities—competitive advantage accrues to constellations of interacting elements. Neither are they likely to appear as deterministic automata, for such rigidity or "brittleness" [13] renders them incapable of responding to unexpected changes in their environments. Real patterns of trophic interactions appear to be the result of a true dialectic—a balance between separate tendencies toward organization and disorganization that are at the same time obligately inclusive and mutually exclusive.

APPENDIX A

We wish to consider several examples that illustrate the behavior of the conditional uncertainty, the topological and effective connectances, and the average mutual information. We begin with a topological structure identical to that shown in Figure A1. Although the topology and the total system throughout will remain fixed, the *relative* magnitudes of the flows will be varied to demonstrate how the indices respond.

In the first example, Figure A1a, all flows are equal; for example, $T_{ij} = 75$, such that the total system throughput is $T = 600$. In the second, Figure A1b, the four innermost flows ($T_{13}, T_{31}, T_{24}, T_{42}$) are twice the outer ones (i.e., equal to 100 and 50, respectively). In the last example, Figure A1c, all flows are equal to 5.66, except the flow from node 1 to node 2: $T_{12} = 560$, such that 99% of the output of compartment 1 leaves via the arc
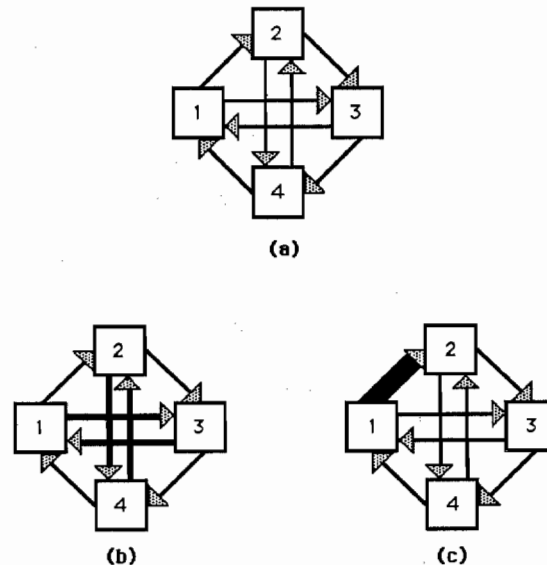

(a)

(b)   (c)

FIG. A1. The hypothetical flow networks used as an example.

TABLE A1

	Example A	Example B	Example C
Total system throughput T	600	600	600
Conditional uncertainty Φ	$2\ln 2 = 1.39$	1.27	0.182
Effective connectance m	2	1.889	1.09
Topological connectance m^*	2	2	2
Aveg. mutual information A	$\ln 2 = 0.693$	0.7498	0.188
$\exp(A)$	2	2.116	1.206
n/m	2	2.117	3.65

to node 2. The values of the various indices for each example are given in Table A1.

We see in the first example, where all flows have the same value, that the effective and topological connectances are equal. In the other two examples the topological connectance exceeds the effective connectance. In fact, it can be shown rigorously that the topological connectance always exceeds its effective counterpart, that is, $m^* > m$, except for $m^* = m$ when all flows T_{ij} have the same value. Comparing the last two rows in Table A1, we note that in Example A, $\exp(A) = n/m$, whereas in the remaining two examples $\exp(A)$ is always less than n/m.

APPENDIX B

We now wish to demonstrate that all networks generated randomly by the same ordinary pdf yield effective connectances that are linearly related to their topological counterparts, that is, they plot along the ray $m = \alpha m^*$, where α is characterized by the higher moments of the given simple distribution. We begin by assuming that the magnitudes of the flows, T_{ij}, are distributed according to an ordinary pdf $P(t)$, $t > 0$, with mean $\langle t \rangle$ and variance s. The existence of a well-defined mean $\langle t \rangle$ implies that as the network becomes sufficiently large (and not too sparsely populated), all row and column sums asymptotically approach a value equal to the number of flows (pn) within each row or column times the mean value of the flows $\langle t \rangle$, that is,

$$T_i \approx T_j' \approx pn\langle t \rangle, \tag{B1}$$

where n denotes the size of the network (i.e., the number of nodes), p is the fraction of existing flows (such that pn^2 is the total number of flows), and $\langle \ \rangle = \int \ldots P(t)\,dt$. Accordingly, the total system throughput is given by

$T \approx pn^2\langle t \rangle$. The conditional uncertainty under these assumptions becomes

$$\Phi = -\frac{2}{pn^2\langle t \rangle} \sum_{i,j} T_{ij} \ln T_{ij} + 2\ln(pn\langle t \rangle). \tag{B2}$$

Now, the first term can be estimated as

$$\frac{1}{pn^2} \sum_{i,j} T_{ij} \ln T_{ij} \approx \langle t \ln t \rangle, \tag{B3}$$

so that the conditional uncertainty becomes

$$\Phi = -\frac{2\langle t \ln t \rangle}{\langle t \rangle} + 2\ln\langle t \rangle + 2\ln(pn). \tag{B4}$$

The reader should note that the first two terms in (B4) are independent of the size of the network n and the fraction of existing flows p. Furthermore, for any ordinary pdf the sum of the first two terms in (B4) is always negative (which can be shown using Jensen's inequality). Thus, we arrive at the inequality

$$\Phi \leqslant 2\ln(pn), \tag{B5}$$

where the equality is achieved only when all flows become equal, $T_{ij} = t^*$, or equivalently, $P(t) = \delta(t - t^*)$. Therefore, the maximal value of Φ, denoted hereinafter as Φ^*, is given by

$$\Phi^* = 2\ln(pn). \tag{B6}$$

Using (B6), (B4) can be rewritten as

$$\Phi = -\frac{2}{\langle t \rangle} \langle t \ln t \rangle + 2\ln\langle t \rangle + \Phi^*. \tag{B7}$$

Exponentiating both sides of (B7), we obtain the linear relationship between the topological and effective connectances:

$$m = \alpha m^*. \tag{B8}$$

The coefficient α is given by

$$\alpha = \langle t \rangle \exp\left(-\frac{\langle t \ln t \rangle}{\langle t \rangle}\right) = \exp\left(-\left\langle \frac{t}{\langle t \rangle} \ln \frac{t}{\langle t \rangle} \right\rangle\right). \tag{B9}$$

Because α depends only on the normalized variable $t/\langle t\rangle$, it is independent of the mean of the pdf and can vary only with changes in the higher moments of the distribution.

We have checked the accuracy of the approximations involved in obtaining (B9). For example, for the random uniform distribution the expectation values in (B9) are given by

$$\langle t\rangle = 1/2, \qquad \langle t\ln t\rangle = -1/4, \tag{B10}$$

such that $\alpha = \sqrt{e}/2 \approx 0.8243$, which agrees well with the numerical value 0.8240 obtained for the slope of the Monte Carlo trials. Similar agreement results between values calculated using (B9) and the slopes of the plots of networks generated by other pdf's used in the trials, although the expected values in (B9) for the other pdf's are more difficult to calculate.

APPENDIX C

We wish to show that all networks generated by ordinary pdf's approximately satisfy the universal relationship (7) in the text. Combining the expressions for the average mutual information (2) and the conditional uncertainly (3) yields the equality

$$A + \frac{\Phi}{2} = \ln T - \frac{1}{2T}\sum_{i,j}T_{ij}\ln T_iT_j'. \tag{C1}$$

The same approximations used in Appendix B, in particular

$$T_i \approx T_j' \approx pn\langle t\rangle, \qquad T \approx pn^2\langle t\rangle, \tag{C2}$$

and

$$\sum_{i,j}\frac{T_{ij}}{T} = 1, \tag{C3}$$

can be used to reduce the right-hand side of (C1) to $\ln n$, whence

$$e^A = n/m. \tag{C4}$$

We emphasize that this result holds only if the mean $\langle t\rangle$ of the pdf is finite. This relationship may not necessarily hold for non-simple distributions, such as that considered below in Appendix D.

APPENDIX D

The nature of the distribution of ratios of arbitrary pairs of uniformly distributed random numbers can be outlined using simple geometric arguments. (See also Exercise 35.13, p. 140, in [38].) In Figure D1 the line
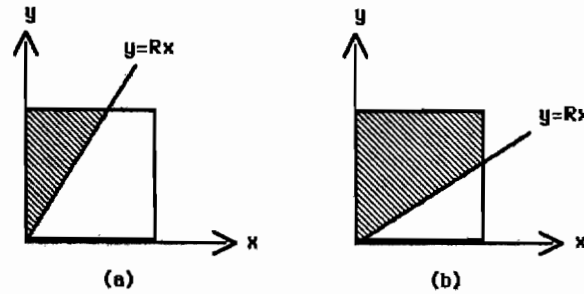
FIG. D1. Schematic representation of the probability space for quotients of arbitrary pairs of samples from the random uniform distribution: (a) $R > 1$; (b) $R < 1$.

$y = Rx$ divides a unit square into two separate regions. The upper left, hatched region contains all points (x, y) for which $y > Rx$ or $y/x > R$. The probability that y/x is greater than R, $P(y/x > R)$, is thereby given by the area of this region. The remaining area represents the probability $P(y/x < R)$, that is,

$$P(r > R) = \begin{cases} 1 - R/2, & R \leqslant 1 \\ 1/2R, & R \geqslant 1, \end{cases} \tag{D1}$$

where $r = y/x$. Because

$$P(r > R) = \int_R^\infty P(R)\, dR, \tag{D2}$$

we derive the desired distribution function by differentiating (D1) with respect to R as

$$P(R) = -\frac{d}{dR} P(r > R) = \begin{cases} 1/2, & R \leqslant 1 \\ 1/2R^2, & R \geqslant 1. \end{cases} \tag{D3}$$

$P(R)$ is normalized, $\int_0^\infty P(R)\, dR = 1$, but all higher moments do not exist. In particular, the mean is undefined, which is why the linear relationship between m and m^* derived in Appendix B does not hold for this distribution.

We note in passing that by considering the ratio $y/x^{1/\sigma}, 0 \leqslant \sigma \leqslant 1$, one may produce random numbers having the distribution

$$P(R) = \begin{cases} \sigma/(\sigma + 1), & R \leqslant 1 \\ \sigma/[(\sigma + 1)R^{1+\sigma}], & R \geqslant 1. \end{cases} \tag{D4}$$

Obviously, (D2) is the special case $\sigma = 1$. All distributions (D4) produce

qualitatively similar results whenever the effective connectance of the networks they generate is graphed against the topological values m^*. They populate most of the area under the rays in Figure 2.

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