

Please cite as:

Ulanowicz, R.E. 1997. Limitations on the connectivity of ecosystem flow networks. pp. 125-143. In: Rinaldo, A. and A. Marani (Eds.). Biological Models. Istituto Veneto de Scienze, Lettere ed Arti. Venice.

CHAPTER 4

LIMITATIONS ON THE CONNECTIVITY OF ECOSYSTEM FLOW NETWORKS

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ABSTRACT

The question of whether or not the diversity of interactions among the components of an ecosystem contributes to its stability has been a major issue in ecology for over three decades. Early discussions on the subject employed information theory to quantify the complexity of networks of energy and/or material exchanges. That thrust failed to produce unequivocal results, and information theory was eventually abandoned as attention turned toward a dynamical theory of random matrices, which demonstrated that an excessive number of interactions per system compartment actually leads to instability. However, a revised application of information theory to *quantified* ecological networks reveals that the complexity of interactions can function either to stabilize or to destabilize the system, depending upon the nature of the perturbation acting upon the system. Furthermore, a homology to the May-Wigner stability criterion cast in terms of information variables predicts a value for the greatest upper bound on the complexity of natural networks of exchanges. The range of complexity observed in 33 ecosystems resembles a "window of vitality" sandwiched between a domain of internal instability on the high side and a region of vulnerability to external disruptions below.

Key Words: average interaction strength, complexity, connectance, diversity, ecosystem flow networks, foodweb theory, information theory, network analysis, persistence, stability.

BIOLOGICAL MODELS

edited by

ANDREA RINALDO and ALESSANDRO MARANI

ISTITUTO VENETO DI SCIENZE, LETTERE ED ARTI
Venice, 1997

1. INTRODUCTION

More than any other single issue, the one that has dominated the field of theoretical ecology over the past three decades has been the search for a relationship between the level of an ecosystem's "connectedness" and its conjugate degree of "stability". Hutchinson, and later Odum (1953), suggested that parallel pathways of interaction connecting any two elements of an ecosystem imparted stability to communication between those elements. That is, if a chance external perturbation were to disturb one or more of the parallel pathways, any remaining, less-impacted routes could potentially grow to compensate for the disrupted flows. It is significant to note that the first prominent effort to quantify the degree of parallelism in ecosystem flow networks was made by MacArthur (1955), who proposed that the Shannon-Wiener index of uncertainty be used for this purpose.

Data on the magnitudes of ecological interactions and exchanges have always been notoriously difficult to collect, whereas information on population levels is often relatively more accessible. Therefore, it made sense in the years immediately following MacArthur's paper to experiment with applying the Shannon-Wiener measure to population densities instead of interspecies flows in an attempt to see if some connection could be drawn between the diversity of population levels and the stabilities of the communities those populations comprised. Unfortunately, this alluring diversion occupied much of ecology for over a decade without yielding more than equivocal results (e. g., Woodwell and Smith 1969).

Research on the issue of ecosystem stability took a decidedly sharp turn in the early seventies when May (1972, 1973) entertained the counterproposition that increased complexity *decreased* the likelihood that a linear system would remain stable. (An arbitrary system can be approximated as a linear one in the neighborhood of any of its stationary states.) May based his arguments on a significant set of Monte-Carlo experiments conducted on randomly-assembled matrices by Gardner and Ashby (1970). In brief, Gardner and Ashby studied the stability of linear dynamical systems as the connectance of such systems is increased. The behavior of a linear system is determined by the eigenvalues of its matrix of interaction coefficients, A . Gardner and Ashby assumed that each system element was stable in isolation (i.e., the diagonal entries in the matrix A were all assumed to be negative), and in each trial the magnitudes of a specific fraction of the interaction terms

(off-diagonal elements) were chosen at random from the interval $(-1, +1)$. If the largest eigenvalue of such a randomly assembled matrix exceeded zero, the system was assumed to succumb to a "self-generating catastrophe".

Gardner and Ashby found that for systems having only a few elements, the probability of its being stable declined with increasing connectance (the fraction of non-zero interaction terms.) More interesting still was their finding that, for systems of larger dimension (say $n > 10$), there appeared a distinct threshold in the connectance below which the randomly generated systems were almost always stable and above which they invariably fell apart. May (1972) described this breakpoint using Wigner's (1969) "semi-circle law" in terms of the number of elements, n , their connectance, C , and the average interaction strength, α . He concluded that whenever

$$\alpha < (nC)^{-\frac{1}{2}}, \quad (1)$$

the system in question was almost certainly stable and otherwise had virtually zero probability of stability.

The immediate effect of May's counter demonstration was to cool the ardor of ecologists for any quick and crisp judgment on the proposition "diversity begets stability". A secondary consequence (unintended by May) was to cause many ecologists to forswear any further use of information theory in ecosystems analysis. The initiative which was begun so promisingly by MacArthur ended abruptly and ignominiously in the light of May's demonstrations. In the minds of a majority of ecologists information theory had become tainted by what appeared to have been the enormous wasted efforts of the sixties.

On the positive side, May's work spawned numerous daughter articles on the connectance-stability issue (e.g., DeAngelis 1975, Gilpin 1975, Rejmanek and Stry 1979, Yodzis 1981, Hogg et al. 1989) and, in conjunction with some early topological observations by Cohen (1978), gave rise to an entire subdiscipline of theoretical ecology that eventually came to be known as "foodweb theory".

It is difficult to do justice to foodweb 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 (Cohen 1977, Briand 1983, Briand and Cohen 1987) 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 issues debated have included: "What, if any, relationship exists between foodweb connectance and number of elements?" (Pimm 1982). "What determines the maximum length of a food chain within a foodweb?" (Pimm and Lawton 1977). "What lies behind the apparent constancy in the average number of predators per species of prey resource?" (Briand and Cohen, 1984).

Perhaps mindful of their earlier disappointment with how the diversity-stability controversy played out, many ecologists today remain skeptical of the utility of foodweb theory, asking whether the whole effort might not resemble the construction of "a ladder for picking strawberries" (Strong 1988). Perhaps most poignantly, Paine (1988) criticizes foodweb theory for relying on data that has been subjected to considerable "editing" (intentional or otherwise).

The strongest objection Paine raises is that qualitative data on foodwebs 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 used in all the foodweb narratives.

Actually, Paine's concern implicitly is directed against the qualitative nature of the assembled foodwebs, i.e., 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. (One is reminded of a Ukrainian fable: The recipe for meatloaf called for equal parts of rabbit and horse, so the peasant added one rabbit and one horse!) Clearly, some way to quantify interactions and to combine their magnitudes into a surrogate for connectance is required. Furthermore, the resulting connectance should be relatively insensitive to the magnitude of the observational threshold. Also, once interactions have been weighted, it may become possible to estimate the magnitude of the average interaction strength, α , which Paine says is unknown in almost all foodweb endeavors to date and which he fears may remain "unknowable".

Finally, Paine is uneasy about the amount of attention given to the network connectance, sensitive as that measure is to the number of components, n , in the chosen depiction of the system. Pimm (1982) and Rejmanek and Sary (1979) both remark upon the hyperbolic relationship

between C and n and on how the product nC appears to exhibit an upper bound. Pimm says that, on the average, the available data seem to satisfy the relationship $nC = 3.1$, whereas Rejmanek and Sary cite the data of McNaughton (1978) and others to place the range on observed values of nC to be between 2 and 6. Like Paine, they lament that they were "unable to estimate the α values."

I wish to argue in the remainder of this essay that: (1) The abandonment by most ecologists of information theory because of its ostensible failure to resolve the diversity-stability issue was both premature and ill-considered. (2) When properly applied, information theory can provide an alternative set of homologous variables to use in foodweb theory that obviate Paine's well-formulated criticisms. (3) Furthermore, when the May-Wigner criterion is recast in terms of the homologous properties, a distinct greatest upper bound on the effective number of connections per node results.

2. INFORMATION THEORY RECONSIDERED

As remarked earlier, MacArthur's intention to use information theory to quantify the degree of parallelism in interaction pathways was soon forgotten in the rush to measure the diversity of populations. Also, it is no affront to MacArthur's keen intuition to note that Shannon's (1948) version of information theory had only recently appeared in relatively inchoate form when the former attempted to apply it to ecosystem networks. It is not apparent to me whether or not MacArthur was ever 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.

Fully two decades were to elapse before anyone seriously reconsidered MacArthur's treatment of flow diversity. Mulholland (1975, see also Rutledge et al. 1976) reasoned that the diversity (Shannon-Wiener measure of average uncertainty) of the flows was not specific enough a measure to quantify the extent to which parallel pathways are present in a network. Some of the overall diversity is constrained by the obligate coupling of the nodes, while the remainder represents the latitude for "choice" among alternative pathways out of or into a typical node.

To become more concrete and quantitative it is useful to denote as T_{ij} the magnitude of the exchange from species i to species j . The total amount emanating from i is determined by summing the outputs from i over all possible destinations j and is designated by T_i . One could as easily have added the inputs to j from all possible sources i 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, one can sum either all the compartmental outputs or all of their inputs to calculate a unique measure of total exchange transpiring in the system. This index is called the total system throughput and is denoted simply by T .

Mulholland astutely observed that one could employ various quotients of these flow measures as likelihood estimators for the joint and conditional transfer probabilities. For example, of all the medium exchanged during a unit of time, the joint probability that a particular quantum both leaves i and enters j can be estimated by the quotient T_{ij}/T . Similarly, the conditional probability that a particular quantum enters j , given that it already left i , is estimated by the quotient T_{ij}/T_i , and the conditional probability that a quantum known to be entering j came from i is approximated by T_{ij}/T_j' .

Using such probability estimators one can approximate all the information variables pertaining to a particular weighted network. Ulanowicz and Norden (1990) have argued that the best measure of the total flow diversity is the joint uncertainty¹, H , about both the origins and destinations of all flows calculated as

$$H = - \sum_{i=1}^n \sum_{j=1}^n \left(\frac{T_{ij}}{T} \right) \log \left(\frac{T_{ij}}{T} \right) \quad (2)$$

A particular fraction of this diversity derives from structural constraints and is quantified by A , the average mutual information,

$$A = \sum_{i=1}^n \sum_{j=1}^n \left(\frac{T_{ij}}{T} \right) \log \left(\frac{T_{ij} T}{T_i T_j'} \right) \quad (3)$$

¹ Shannon gave the name "entropy" to his measure of uncertainty, and most texts on information theory persist in using this term. However, such usage causes unwarranted confusion with the thermodynamic state variable of the same name and should be studiously avoided.

The remainder represents the amount of "choice" (conditional uncertainty), pertaining to both the inputs and the outputs of an average node in the network. Subtracting (3) from (2) and regrouping terms yields

$$\Phi = - \sum_{i=1}^n \sum_{j=1}^n \left(\frac{T_{ij}}{T} \right) \log \left(\frac{T_{ij}^2}{T_i T_j} \right) \quad (4)$$

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

$$\begin{aligned} \Phi = & - \sum_{i=1}^n \sum_{j=1}^n \left(\frac{T_{ij}}{T} \right) \log \left(\frac{T_{ij}}{T_i} \right) \\ & - \sum_{i=1}^n \sum_{j=1}^n \left(\frac{T_{ij}}{T} \right) \log \left(\frac{T_{ij}}{T_j} \right). \end{aligned} \quad (4')$$

The argument of the logarithm in the first term of (4') is the fraction of the total output from i that flows to j . The logarithm is weighted by the fraction of total exchange activity that is comprised by T_{ij} . Summing over all combinations of i and j , it is seen that the first term in (4') is the logarithmic mean output fraction. Similarly, the second term is the logarithmic mean input fraction. Because each flow T_{ij} appears twice in (4'), the mean fraction that an arbitrary flow serves *either* as input *or* output is $\Phi/2$.

Focusing upon $\Phi/2$ as a measure of "choice" or degrees of freedom, it should be recalled from information theory that the number 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:

$$m = b^{\frac{\Phi}{2}}, \quad (5)$$

where b is the base to which the logarithms are referred (usually 2, e or 10).

To show that equations (4) and (5) yield values of m that appeal to the intuition, the reader should refer to the hypothetical network shown in Figure 1a. 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 (4) and (5) to confirm that $m = 2$ for this particular case.

Mulholland's measures pertain only to closed networks. Hirata and Ulanowicz (1984) show how the Mulholland 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 (zero) 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 not absolutely 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 (2), (3), and (4) to run from 0 to $n+2$, one thereby calculates the values of H , A , and Φ as they apply to open systems.

"There is a minor complication in applying equations (4) and (5) 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 efferent to node 0 and afferent to 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 that obviates such inflation of m will be denoted by Φ' and calculated as

$$\begin{aligned} \Phi' = & - \sum_{i=1}^n \sum_{j=1}^n \left(\frac{T_{ij}}{T} \right) \log \left(\frac{T_{ij}^2}{T_i T_j} \right) \\ & - 2 \sum_{i=1}^n \sum_{j=1}^n \left(\frac{T_{0j}}{T} \right) \log \left(\frac{T_{0j}}{T_j} \right) \\ & - 2 \sum_{i=1}^n \sum_{j=1}^n \left(\frac{T_{i,n+1}}{T} \right) \log \left(\frac{T_{i,n+1}}{T_i} \right) \\ & - 2 \sum_{i=1}^n \sum_{j=1}^n \left(\frac{T_{i,n+2}}{T} \right) \log \left(\frac{T_{i,n+2}}{T_i} \right). \end{aligned} \quad (6)$$

The hypothetical network in Fig. 1b has exactly two internal flows and one exogenous flow (all equal) incident to each node. Substitution of the flow values first into (6) and then into (5) yields $m=3$, as expected.

2. EFFECTIVE CONNECTANCE PER NODE

I now wish to compare the variables used in foodweb analysis with those encountered in flow analysis. It should be noted here that flow analysis is limited to considering only palpable exchanges. In dynamical foodweb theory more general interactions are allowed, such as spatial interference, ethological communication, and a host of other processes that are difficult to quantify. Those trafficking in foodweb analysis are usually well aware that they are dealing with only a necessary subset of all possible interactions, but they argue 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. Furthermore, it should be noted that the input and output quotients are not unrelated to a dynamical analysis of the system. If one writes the dynamical balance equations for the medium under scrutiny, the input and output quotients (i.e., T_{ij}/T_j' or T_{ij}/T_i , respectively) become the (positive and negative) coupling coefficients in a set of first-order differential equations describing the time rate of change in each pool of medium as normalized by the throughput of that compartment.

In real, weighted flow networks the exchanges are virtually never all equal in magnitude, as in Figure 1, so that the effective connectance per node, m , will almost never take on an integer value.

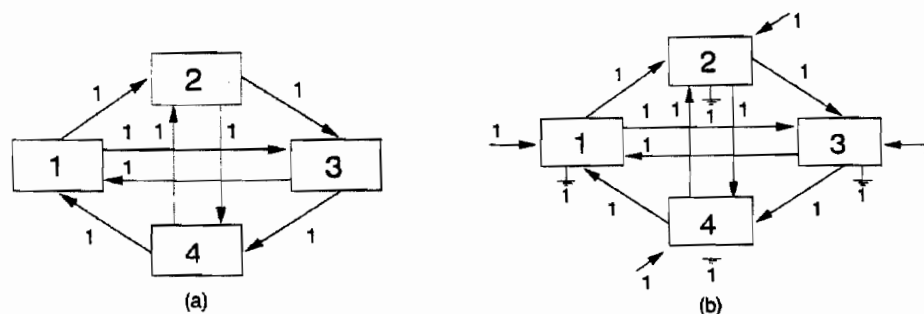


Fig. 1 - Hypothetical uniform flows among four components (a) of a closed system (b) of an open system.

But weightings serve to impart more meaning to m than is possessed by any connectance calculated from qualitative linkages. For example, 900 units of output from compartment i are configured two ways in Figure 2.

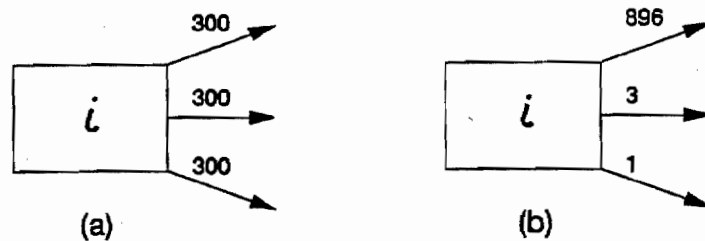


Fig. 2 - Three sample outputs from arbitrary compartment i (a) equi-partitioned, (b) heavily skewed towards top flow.

In Fig. 2a medium exits i as three equal flows. In Figure 2b almost all medium egresses along the first channel, and only minute amounts leave via the remaining two routes. In a qualitative sense three outputs exit node i in each case. However, when one reckons the log mean number of outputs using equations (4) and (5), one arrives at $m=3$ for configuration 2a, but $m=1.0315$ for the one in Fig. 2b. The latter value more accurately reflects the fact that output in the second use is dominated by a single output. Hence, m is seen to represent the *effective* connectance per node.

In the foodweb literature the connectance, C , can be calculated 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 quantity m likewise depicts a connectance per node, but one wherein the contribution of each flow is weighted according to its relative magnitude.

I 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. In using m one avoids the pitfalls that Paine cites. Of course, data on weighted interactions in ecosystems will still remain incomplete—it is inevitable that some small interactions will remain beyond detection by the observer (see also Cohen and Newman 1988). 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 minimally from what would result by their inclusion.

As for the concern that connectance, C , is a strong function of n , it already has been noted by Rejmanek and Stary (1979) and Pimm (1982) how the product nC (the connectance per node) varies much less than does C alone. It should be obvious from the averaging scheme used to calculate Φ that m will be almost independent of the number of nodes, n , and indeed evidence will be presented below showing that m is even less sensitive to changes in n than is the product nC .

Most important, however, is the fact that information on the mean level of interaction between components is implicit in the calculated value of m . If one can devise a way to make that interaction strength explicit, then some criterion for the stability of flow configurations might be ventured. Towards this goal, it is useful to define a topological connectance per node, m^* , as the value that m would take on if all the non-zero 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 (4) or (6) 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 (5) to obtain m^* . (In the examples in Figure 1 $m^*=m$ for both cases. As soon as any two values of T_{ij} become unequal, then $m^*>m$.)

A mean level of interaction, a , now can be defined as that constant value which, when it multiplies each input fraction (T^*/T_j) or relative output (T^*/T_i) in the formula for Φ^* , yields the identical value that one would obtain using the actual weighted data. That is,

$$\Phi = - \sum_{i=1}^n \sum_{j=1}^n \left(\frac{aT^*}{T} \right) \log \left(\frac{a^2 T^{*2}}{T_i T_j} \right). \quad (7)$$

or,

$$\Phi = -2a \log a - a \sum_{i=1}^n \sum_{j=1}^n \left(\frac{T^*}{T} \right) \log \left(\frac{T^{*2}}{T_i T_j} \right). \quad (7')$$

But the double summation in (7') is recognized to be Φ^* , whence (7') becomes

$$\Phi = a (\Phi^* - 2 \log a). \quad (7'')$$

For open systems one would employ eqn. (6) instead of (4) to calculate Φ^* , but the final result (7'') would still obtain. Knowing the flow magnitudes one can calculate Φ using either (4) or (6). After setting each flow in the network to the same arbitrary value, say 1, one then employs the same formula to calculate Φ^* . Thereafter, the mean interaction strength, a , remains the only unknown in the transcendental equation (7''). Any one of a number of iterative techniques can be used to solve (7'') for a .

It will prove useful to recast (7'') in terms of connectances per node, m^* and m . Equation (5) may be used for this purpose and yields:

$$\log m = a(\log m^* - \log a). \quad (8)$$

For example, if Figure 2b represents an observed situation ($m=1.0315$), and Figure 2a its qualitative counterpart ($m^*=3$), then a works out to be approximately 0.00482. This value is central (in a logarithmic sense) to the three output fractions in Figure 2b (0.9956, 0.0033 and 0.0011, respectively).

4. RECASTING THE MAY-WIGNER CRITERION

I now wish to explore whether it might prove useful to recapitulate the May-Wigner stability analysis in terms of the variables just defined. Two homologous pairings have been noted: Although May's mean square interaction term, α , is calculated differently than the log-mean value of exchange magnitude, a , there probably is a strong correlation between the two quantities. Likewise, despite numerical differences between the product nC and the topological connectance per node, m^* , a significant correlation between those cognates is to be expected.

There is no a-priori reason why May's stability criterion (1) written in terms of the logarithmic variables, i.e.

$$a < (m^*)^{-\frac{1}{2}} \quad (9)$$

must hold. However, the "dimensions" of each pair of homologous variables are identical, so that a dimensional analysis should reveal that the actual criterion would at least be similarly scaled. Most importantly, one should bear in mind that criterion (1) arose from empirical observations by Gardner and Ashby. Therefore, it is quite legitimate to test how effectively (9) serves to delimit the stability of observed networks of ecosystem exchanges. The actual line of demarcation between stable and unstable configurations will be described by rewriting the inequality (9) as an equality, i.e.,

$$a = (m^*)^{-\frac{1}{2}} \quad (10)$$

If (10) is substituted into (8), the result is an equation for m in terms of m^* ,

$$\log m = \frac{(3 \log m^*)}{\left(2(m^*)^{\frac{1}{2}}\right)}, \quad (11)$$

that separates a domain of probably stable combinations of m^* and m from another wherein the pairings are likely to be unstable.

Three regions of the m^* - m plane are depicted in Figure 3.

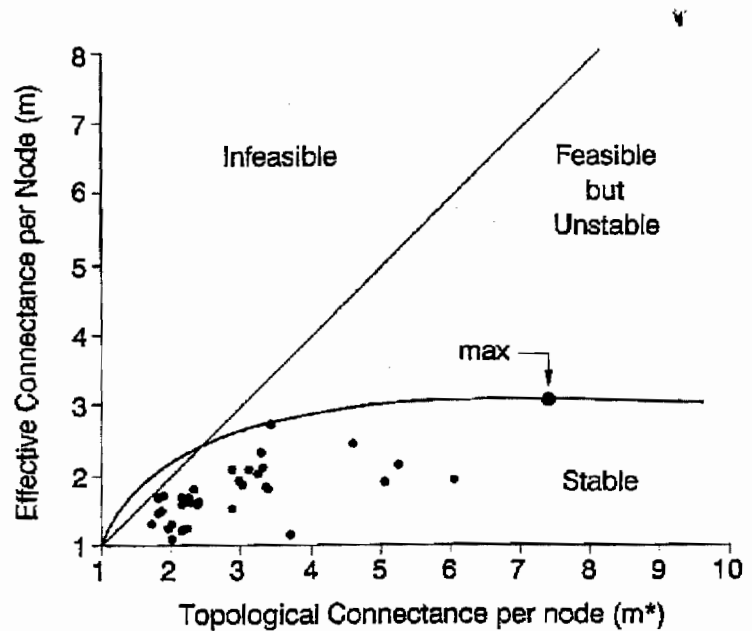


Fig. 3 - Plot of the topological connectance per node (m^*) vs. the effective connectance per node (m) for 33 different networks of ecosystems flows. Straight line separates feasible from infeasible combinations; curve delimits stable region.

The area above the 45-degree line represents all combinations of m^* and m that are unfeasible because of the requirement that $m^* \geq m$. The domain bounded by the curved line and the m^* axis [actually the line $m^*=1$, because the graph has its origin at $(m^*, m) = (1, 1)$] contains all combinations of topological connectance and effective connectance that would be stable under criterion (9). Presumably, observed networks of ecosystem flows would populate this domain. Any combination of m^* and m falling between these two regions identifies a class of flow networks that are feasible, but unlikely to be stable.

To see where observed or estimated ecosystem networks stand on Figure 3, I have collected a set of 33 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. I have made no effort to assess the relative accuracies of the reported flows, either within a given ecosystem representation or among the numerous authors--the quality of the data is almost certainly uneven. Despite such variability, when the values of m^* and m were calculated for each of the networks, they plotted without exception into the stable region of the m^* - m plane, as indicated by the dots in Figure 3. Of course, 33 points is a small number of observations upon which to base an empirical principle, but the fact that all the configurations fell within the hypothesized stable zone leads one to speculate that: (1) there probably exists an information theory counterpart to the May-Wigner stability criterion, and (2) the functional form of that criterion is not likely to be much different from inequality (9).

5. IMPLICATIONS OF RESULTS

One cannot help but notice in Figure 3 the relative thinness of the zone of stability. None of the available networks possessed an unusually high value of topological connectance per node, m^* , but equation (11) implies that even had one been observed, its effective connectance per node would have remained low. In fact, it is easy to demonstrate using (11) that the boundary curve on m possesses a single maximum of $m=e^{3/e}$ (about 3.015) when $m^*=e^2$ (around 7.389). Thus, a greatest upper bound on the effective connectivity of natural exchange networks appears to exist. Criterion (9) says that naturally occurring flow networks cannot grow arbitrarily complex. Whenever the value of the effective connectivity per node approaches 3, it seems likely the system will succumb to a self-generating catastrophe.

An absolute limit to effective ecosystem connectance would support and even fortify the earlier remarks by Margalef (1968) and May (1972) to the effect that internal stability considerations impose a hierarchy upon the suite of interactions possible within a natural system. On the average, a component of a system can interact strongly with a very few other compartments and very weakly with many others, but situations where a component interacts evenly (either weakly or strongly) with many other taxa are likely to be rare (but not prohibited, as long as they are stabilized by other parts of the system.)

There are other factors that mitigate the complexity of networks of exchanges. I have argued elsewhere that autocatalysis (Ulanowicz 1986) and competition (Ulanowicz, 1989) both serve to increase the degree of

articulation, coherence and constraint present in a network. That is, in the absence of major perturbations there is a natural tendency for the average mutual information of a network, as defined in eqn. (3), to increase at the expense of the conditional uncertainty (4). In Figure 3, this tendency works as if to move the points nearer to the m^* axis. However, the approach of a system to $m=1$ also signifies that it is becoming too constrained, too brittle (Holling 1986) and thus vulnerable to catastrophe initiated by chance perturbations originating outside the system.

After many years, a coherent and self-consistent picture of the relationship between stability and complexity in ecosystems is beginning to emerge: Natural stochastic processes (immigrations, mutations, etc.) cause the system to accrue even more variety and complexity. However, as the system approaches the limits discussed here, the likelihood increases that the system will fall apart due to *endogenous* perturbations. (The magnitude of such catastrophe need not radically alter the system's identity. It may involve the extirpation of only one or a few minor taxa.) Against this tendency towards ever more complex systems operate the order-building drives, such as autocatalysis or competition, that act to increase system efficiency and streamline the topology of its constituent interactions. But as the system reaches low values of effective connectance (i.e., as m approaches 1), it begins to lose those parallel pathways that, according to Hutchinson and Odum, could potentially buffer it against external perturbations. Hence, it becomes evermore probable that system structure will change catastrophically in response to a novel *exogenous* perturbation.

It appears, then, that dynamical structures persist by populating a "window of viability"—the middle ground set between susceptibility to disordering agents from within on the one hand and unexpected impacts from without on the other. Endurance of dynamical form seem to require something resembling a dialectic—to persist a system must possess adequate portions of two mutually exclusive properties. The data presented in Figure 3 are too sparse and too unreliable to demonstrate unequivocally such a tradeoff, however one does discern in them a tendency for the estimated systems to group towards the middle of the layer defined by the stability envelope and the m^* -axis.

The pieces in the puzzle that portray the relationship between diversity and stability are beginning to fit together. It is not a simple picture that is emerging, but there was never any reason to expect that an adequate narration of complexity would itself be simple! What matters is that the

description remain self-consistent, and consistency is often a consequence of how the subject is viewed. But the quantitative relationship between object and observer is the realm of information theory—the closest one can come to a mathematical formulation of epistemology. Information theory is a tool that has been eschewed now for too long by many ecologists, largely because of historical accident. If there is to be any hope of drawing a unified picture of the ecological world, this most unfortunate bias must be put aside. I commend information theory to ecologists as fundamental to their endeavors.

6. ACKNOWLEDGMENTS

I would like to thank Jacqueline McGlade and Bernardo Huberman for bringing to my attention their paper stressing the need for a better measure of network connectance. Ms. Jeri Pharis was most helpful with the typing and editing of the manuscript.

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