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The balance between adaptability and adaptation

Robert E. Ulanowicz *

Chesapeake Biological Laboratory, Center for Environmental Sciences, University of Maryland, PO Box 38, Solomons, MD 20688-0038, USA

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Abstract

In his 1983 book, *Adaptability*, Michael Conrad explored the quantitative relationship between adaptability and adaptation using the conditional ‘entropy’ of information theory as his primary tool. The conditional entropy can be used to estimate the connectivity of the network of system exchanges, a key indicator of system stability. In fact, the May-Wigner criterion for the stability of linear dynamical systems can be recast using the conditional entropy to help identify the boundary along which adaptability and adaptation are exactly in balance—the ‘edge of chaos’ as it is popularly known. Real data on networks of ecosystem flows indicate that in general these systems do not exist nigh upon the edge of chaos, but rather they populate a much wider ‘window of vitality’ that exists between the realms of chaotic and deterministic dynamics. It appears that the magnitudes of network flows within this region are distributed in power law fashion. The theory also suggests that an absolute limit to the connectivity of natural self-organizing systems exists, at approximately 3.015 effective connections per node. © 2002 Elsevier Science Ireland Ltd. All rights reserved.

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1. Introduction

Michael Conrad’s (1983) tome, *Adaptability*, is notable both for its ecological vision and for the attention he paid to hierarchical interactions. He attempted to formalize what many ecologists long had been preaching, namely that emphasis in biology had too long has been focussed upon the regular, the mean, and the predictable, practically

to the exclusion of the noisy, the stochastic, and the indeterminate inherent in the system. These latter attributes often are regarded as useless and undesirable characteristics to be overcome or obviated in order to discern more clearly the underlying dynamics. Even contemporary evolutionary theory appears to emphasize adaptation over adaptability. To help redress this imbalance, Conrad intentionally skewed his narrative to focus on adaptability, for he believed, that as much, if not more, of the evolutionary story lies in the nature of systems noise and irregularity as in any purported dynamical regularities.

* Tel.: +1-410-326-7266; fax: +1-410-326-7378.

E-mail address: ulan@cbl.umces.edu (R.E. Ulanowicz).

Not that Conrad neglected the necessary role of adaptation in evolution, for he made it quite clear that both regularity and chance were necessary elements for system survival and persistence. The problem arises, however, that within any given level, the constraints that keep a system adapted to prevailing circumstances usually interfere with its freedom to adapt to novel changes in those conditions. That is, at any specified level, adaptation and adaptability are in conflict, yet some degree of each is necessary for persistence. Conrad resolved the conflicting needs for both traits by introducing a process he called ‘hierarchical compensation’—the idea that adaptation could predominate at one level and adaptability predominate at another level.

I am not prepared to consider in quantitative fashion the trans-hierarchical nature of compensation that Conrad outlined, but I note instead that neither constraint nor freedom can be excluded from any particular level of the hierarchy. What I wish to elaborate here is the balance between adaptability and adaptation as it may be constrained within any single level. How does one identify the limits to freedom at any level—the ‘edge of chaos’ as it were (Langton, 1992)? While this problem has received notable attention as it pertains to linear dynamical theory (May, 1972), the results have not been as broadly applicable or as definitive as might have been desired. Therefore, I wish to approach the problem from a different perspective—the connectivist viewpoint of someone interested in informational constraints. Furthermore, I will employ as my primary tool in this inquiry the same one that Michael Conrad used throughout his book, namely the statistical measure called the conditional ‘entropy’¹.

2. Quantifying adaptability

In the narrower context of connectivism, adaptability is related directly to the connectivity of a system, because the number of pathways between any two arbitrary components rises dramatically as a function of the degree to which the system is connected. Should a novel disturbance disrupt any subset of pathways connecting two arbitrary nodes, a system with high connectivity will retain more pathways on average over which compensatory flow or communication can occur (Odum, 1953). Whence a quantitative measure of connectivity should serve as a reliable surrogate for the potential for adaptability.

Regarding the connectivity of natural systems, Wagensberg et al. (1990) have remarked that there seems to be a ‘magic value of about 3 bits per emitter as an actual upper limit to connectivity in real stationary ecosystems’. Their observation is consonant with that of Pimm (1982), who noted that the connectivity of his collection of ecosystem food webs averaged about 3.1. Kauffman (1991), in treating the stabilities of genetic networks, also related how persistent networks usually possessed between two and three connections per node.

In contrast to these, more or less definitive limits, May’s analysis of linear dynamical systems provided no absolute upper bound on connectivity. Rather, he formulated a hyperbolic relationship that has become known as the May-Wigner stability criterion. It states that the average intensity of interaction between system components must be less than the reciprocal of the square-root of the average number of connections per node (May, 1972). I wish to explore whether or not May’s analysis can be recast using the quantitative language that Conrad used to describe adaptability so as to achieve a more definitive statement of the necessary balance between freedom and constraint, or between adaptability and adaptation. To begin the search, I turn to the formalisms of information theory (Rutledge et al., 1976).

From a connectivist viewpoint, the upper bound on the options available for system re-configuration is given by the diversity of the network connections (Ulanowicz and Norden, 1990).

¹ I reluctantly follow the unfortunate convention in statistics of referring to uncertainty as ‘entropy’. I emphasize, however, that no connection with thermodynamical entropy is thereby implied.

Hence, if T_{ij} represents the flow from component i to node j , then the Shannon formula for the diversity of systems processes can be written as

$$H = - \sum_{i,j} \left(\frac{T_{ij}}{T} \right) \ln \left(\frac{T_{ij}}{T} \right)$$

where $T = \sum_{p,q} T_{pq}$, is the total flow occurring in the system, and \ln signifies the natural logarithm. Not all of this diversity is available for adaptability, however, as a certain amount is encumbered by internal system constraints and must be subtracted from H . This amount may be estimated by comparing the apriori and aposteriori probabilities of flow from i to j . The probability that a quantum of medium is leaving i is estimated by the quotient $\sum_k T_{ik}/T$, while the probability that a quantum is entering j is reckoned as $\sum_m T_{mj}/T$. If i and j exert no constraint upon each other, then the apriori probability of transfer from i to j would be the simple product of these two estimators, or $(\sum_k T_{ik} \sum_m T_{mj})/T^2$. But the observed (aposteriori) probability of transfer from i to j under the influence of existing constraints is T_{ij}/T . Whence from information theory, one may measure the constraint that i and j exert upon each other as the difference between the logarithms of these two probabilities. When this logarithmic difference is weighted by its corresponding aposteriori probability and the result is summed over all possible combinations of i and j , the outcome is known as the average mutual information, which here takes the form

$$I = \sum_{i,j} \left(\frac{T_{ij}}{T} \right) \ln \left(\frac{T_{ij} T}{\sum_k T_{ik} \sum_m T_{mj}} \right).$$

From information theory it can be proved that $H \geq I \geq 0$, whence one may subtract I from H to yield a nonnegative remainder called the *conditional entropy*², Φ ,

$$\Phi = H - I$$

$$\Phi = - \sum_{i,j} \left(\frac{T_{ij}}{T} \right) \ln \left(\frac{T_{ij}^2}{\sum_k T_{ik} \sum_m T_{mj}} \right).$$

This conditional entropy quantifies the degrees of freedom that the system possesses. Furthermore, the connectivity per unit node can be calculated as an explicit function of Φ in the form $m = \exp(\Phi/2)$, where m is the *effective* number of connections per node (Ulanowicz 1997a). To convince oneself that m captures the connectivity per unit node, the reader should try substituting the values of T_{ij} shown in Fig. 1 into the formulae for m and Φ to discover that m equals exactly 3.0 in this instance. The reader is invited to test any other network configuration wherein, (a) the flows are all equal in magnitude and (b) the same number of links enters and leaves each node so as to convince oneself that the correct integer is always generated. Whenever either (a) or (b) does not hold, the value of m will not be an integer, but instead will denote the *effective* number of links per node. For example, when the formulae for m and Φ are applied to the network in Fig. 2, the resulting $m = 1.023$. This makes intuitive sense, because, despite the fact that three links enter and leave each node, two of them are inconsequential in magnitude in comparison to the one dominant flow.

The properties of the Shannon entropy dictate that Φ will increase whenever the magnitudes of the flows are more evenly distributed. It follows that for any topological configuration of flows, Φ

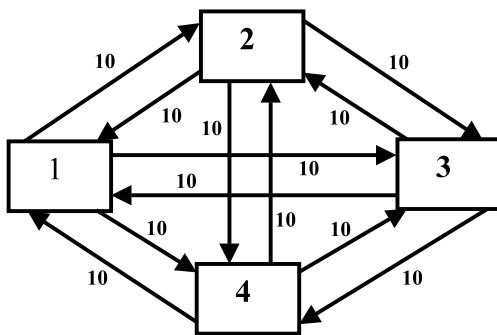


Fig. 1. Equiponderant transfers among four hypothetical compartments. Topological connectivity is calculated to be exactly three links per node.

² This form of the conditional entropy is not identical to the one used by Conrad. He used the entropy of the compartmental throughflows as his reference point, whereas, my reference point is the joint entropy. One is free to specify the reference point with respect to which entropy will be reckoned.

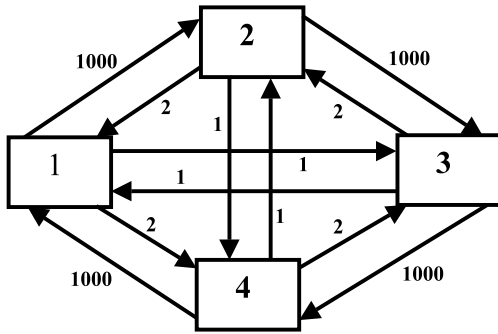


Fig. 2. Transfers among four hypothetical compartments. Topological connectivity equals exactly 3.0 links per node, but effective connectivity (m) is calculated to be only 1.023 links per node.

will achieve its local maximum, Φ^* , whenever all the flows have exactly the same value. For obvious reasons, Φ^* is called the topological conditional entropy, and $\Phi^* \geq \Phi$. The corresponding value $m^*(\geq m)$ is called the *topological connectance* per node.

Of course, networks of actual systems will almost always be open (contain non-trivial exchanges with the external world), unlike the closed examples presented in Fig. 1 and Fig. 2. It is not difficult to amend the formulae for Φ , Φ^* , m and m^* to yield values for open networks that accord with intuition. The amended formula is given in the Appendix A.

3. Adaptabilities of hypothetical and actual networks

Having quantified system adaptability using the measures just defined, we now ask how the adaptabilities of observed networks of ecosystem exchanges compare with randomly assembled networks? Randomly constructed networks having randomly chosen magnitudes of flow should possess the highest adaptabilities possible. Such networks are rather easy to construct. One first specifies both the dimension of the network and the approximate level of topological connectivity that one wishes the system to have. Ecosystem networks found in the literature usually consist of about 4–60 compartments, but it is difficult to

treat the statistics of networks with fewer than at least seven elements, so I chose to construct networks with dimensions corresponding to each integer from 10 to 60. For each dimension, ten trials with approximate topological connectivities ranging evenly from 0.1 to 1.0 were constructed, yielding a total of 500 trial networks.

Each network was constructed in three passes. One begins the construction of a network of dimension n by setting each of the n^2 possible links to zero. Then each possible link is visited in turn, and if a random number generator yields a number less than the specified nominal topological connectivity assigned to that trial, the value of the link is reset to one. This specifies the topology of the network (recorded as zeroes and ones in what is known as the adjacency matrix) that has a topological connectivity (m^*) close to the specified nominal value. On the final pass each entry with a one is visited and assigned a magnitude between zero and one using the random number generator. The effective connectivity (m) of this weighted network can then be calculated.

When the 500 random networks thus generated were plotted on a scatter diagram of m versus m^* , they fell close upon a line having a slope of 0.832. The first 359 such points are shown plotted in Fig. 3. That is, the effective connectivities (m) of randomly assembled flow networks are closely proportional to their topological connectivities (m^*).

We now wish to compare this linear distribution with how a collection of observed ecosystem networks fall on the same plot. For this purpose the author collected a set of 41 ecosystem networks. They ranged in dimension from 4 to 125 and were taken from 25 separate projects in which a host of investigators participated. They represent ecosystems from a multitude of different habitats—aquatic, marine, estuarine, wetland, and terrestrial. These 41 networks are shown in Fig. 4 plotted on the m^*-m plane. Towards the lower-left-hand corner of Fig. 4 one notices that the lower-dimensional ecosystem networks lie close to the extrapolated line defined by the random networks. The higher-dimensional ecosystem networks had higher topological connectivities (m^*), but their effective connectivities (m) fell radically below their counterparts among the ran-

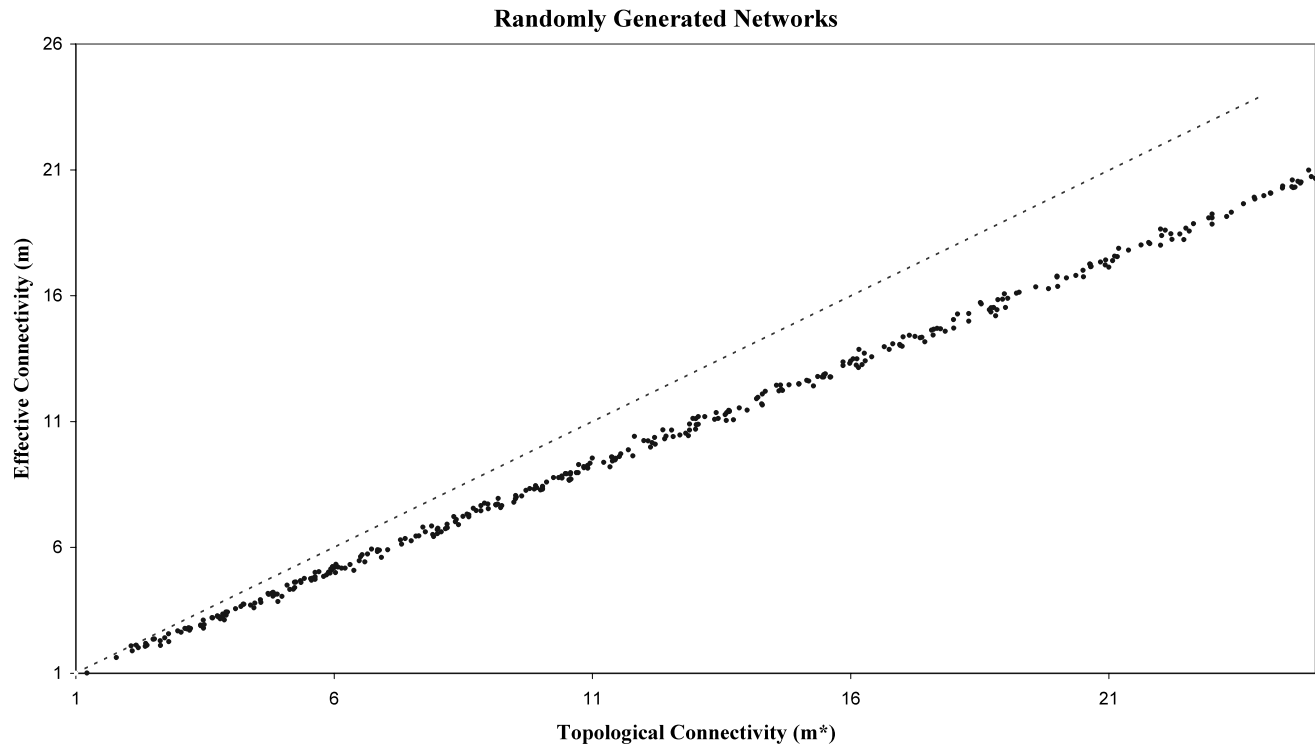


Fig. 3. The topological connectivities (m^*) and effective connectivities (m) of 359 randomly constructed networks plotted on the m^*-m phase plane. Combinations above the dotted line ($m = m^*$) are mathematically infeasible.

dom networks. Presumably, the differences in effective connectivities are due to the organizational constraints inherent in the ecosystem networks, which represent, at least in part, adaptation by the constituent populations both to the external environment and to the other populations within the system.

4. The balance between adaptability and adaptation

That ecosystem networks should show evidence of organizational constraints is hardly surprising, but the wide discrepancy between the effective connectance of ecosystem networks and their random counterparts prompts one to ask where ecosystems stand with respect to the tradeoff between degrees of freedom (adaptability) and in-

herent constraints (adaptation)? In other words, exactly where does the ‘edge of chaos’ lie on the plot of m versus m^* ? Conrad suggested that adaptability plays a larger role than adaptation in the evolution of organisms (and presumably of ecosystems as well). His opinion would tend to support the conjecture by Langton (1992) and Kauffman (1995) that living systems teeter upon the brink of chaos.

As mentioned above, May (1972) proposed a criterion that delimited the transition between stable and unstable linear systems, or the chaotic and the well-behaved, for randomly assembled linear dynamical systems. He did so by invoking Wigner’s criterion that is written in terms of the topological connectance and the strength of interaction. To be more precise, the test for a stable system is whether

$$a < (nC)^{-1/2}$$

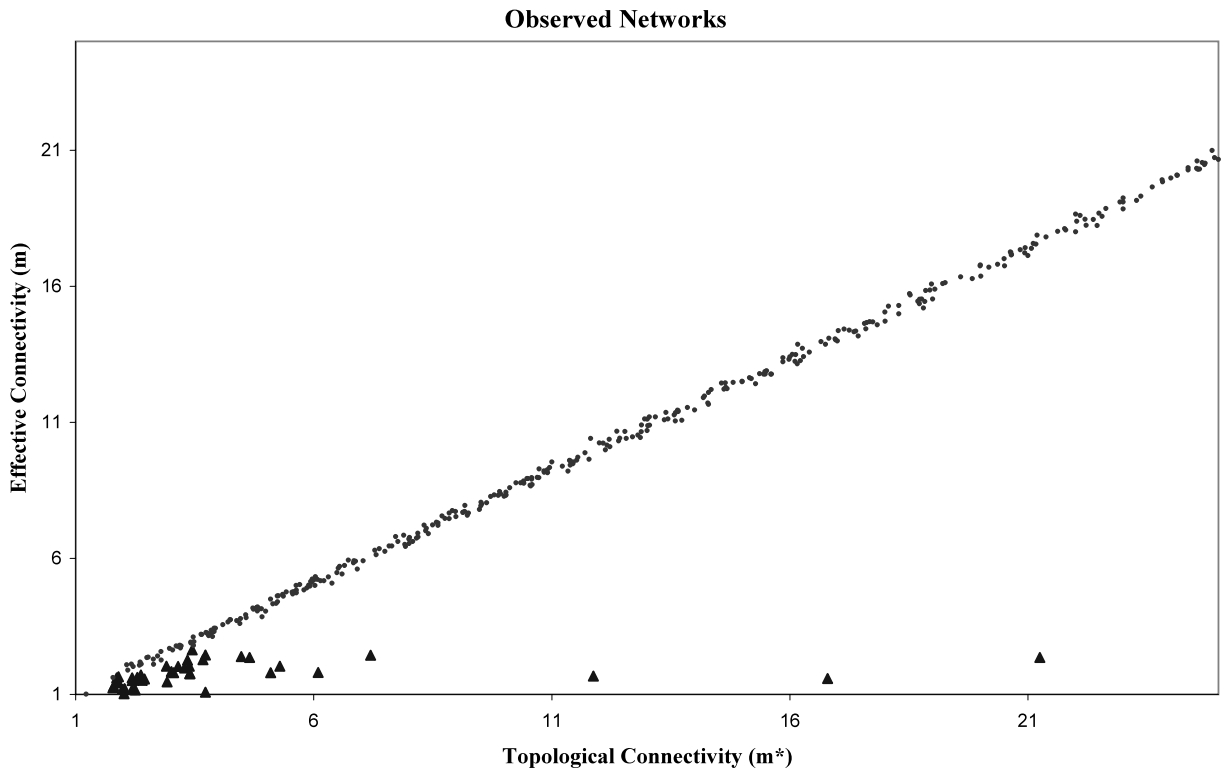


Fig. 4. Plot of randomly connected networks (small dots) along with 41 observed ecosystem networks (triangles) on the m^*-m phase plane.

where a is the average strength of interaction; n , the system dimension; and C , the topological connectance of the system. It was shown above that the topological connectance, m^* , is a function of the conditional entropy of the topological connections (Φ^*) and serves as an intuitive surrogate for the product nC . This allows us to rewrite the criterion as

$$a < (m^*)^{-1/2}.$$

The actual ‘edge of chaos’ or border between the domains of the stable and the unstable will be crossed whenever the inequality is replaced by an equality, i.e.

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

If a could somehow be expressed in terms of m and m^* , then the May-Wigner criterion would describe the transition between the stable and unstable domains of the m – m^* plots. With an eye on this possibility, we define a to be that constant value, which, when it multiplies each input fraction $T^*/\sum_i T_{ij}$, or output fraction $T^*/\sum_j T_{ij}$, in the formula for Φ^* , yields the corresponding value of Φ . That is,

$$\Phi = - \sum_{i=1}^n \sum_{j=1}^n \left(\frac{aT^*}{T} \right) \ln \left(\frac{a^2 T^{*2}}{\sum_p T_{pj} \sum_q T_{iq}} \right)$$

$$\Phi = -2a \ln(a) - a \sum_{i=1}^n \sum_{j=1}^n \left(\frac{T^*}{T} \right) \ln \left(\frac{T^{*2}}{\sum_p T_{pj} \sum_q T_{iq}} \right)$$

or

$$\Phi = a(\Phi^* - 2 \ln[a]).$$

Substituting the definitions of m and m^* in the last formula recasts it as

$$\ln(m) = a(\ln[m^*] - \ln[a]).$$

The strength of interaction, a , can be obtained from either of the last two transcendental equations by any number of iterative solution techniques. Doing so, we discover that a , for the network in Fig. 1 is 1.0 (by definition), while that for the network in Fig. 2 is approximately

0.003345 (a value that is logarithmically central to 0.997, 0.002, and 0.001).

Substituting the May-Wigner demarcation Eq. (1) into this last equation eliminates the parameter a and defines the separatrix between the stable and unstable domains of the m – m^* quadrant as,

$$\ln(m) = \frac{3 \ln(m^*)}{2(m^*)^{1/2}} \quad (2)$$

The solution couplets to transcendental equation Eq. (2) are depicted on Fig. 5, plotted on the m – m^* plane along with the random and observed networks.

Fig. 5 exhibits several interesting features. First of all, the observed networks show no evidence of crowding upon the ‘edge of chaos’. Most networks fall well between the separatrix and the horizontal line, $m = 1$. One concludes that ecosystems do not appear to exist at the edge of chaos, but rather they inhabit a broader ‘window of vitality’, remaining sufficiently removed both from the edge of chaos and from the ‘frozen’ or maximally constrained configurations represented by the line $m = 1$.

Secondly, one notices that the separatrix exceeds the diagonal line $m = m^*$ for all values of m^* below 2.25. Since, $m \leq m^*$ for all possible network configurations, one may infer that all networks with $m^* < 2.25$ are inherently stable. Kauffman (1991) reported what appeared to be a transition point as the dimensionalities of his genetic networks were reduced. Most of the networks he probed were unstable until a point somewhere near two connections per node, below which they became predominately stable.

Lastly, one’s eye is drawn to the very flat nature of the separatrix beyond the value of ca. $m^* = 5$. In fact, the boundary appears to curve downwards beyond $m^* = 8$. That this in fact is the case can be demonstrated analytically. Differentiating Eq. (2) with respect to m^* reveals that a global maximum for the separatrix exists at $m^* \cong 7.389$, at which point m takes on the value $e^{(3/e)}$, or ca. 3.015—very close to the ‘magical number’, three.

Randomly Generated Networks

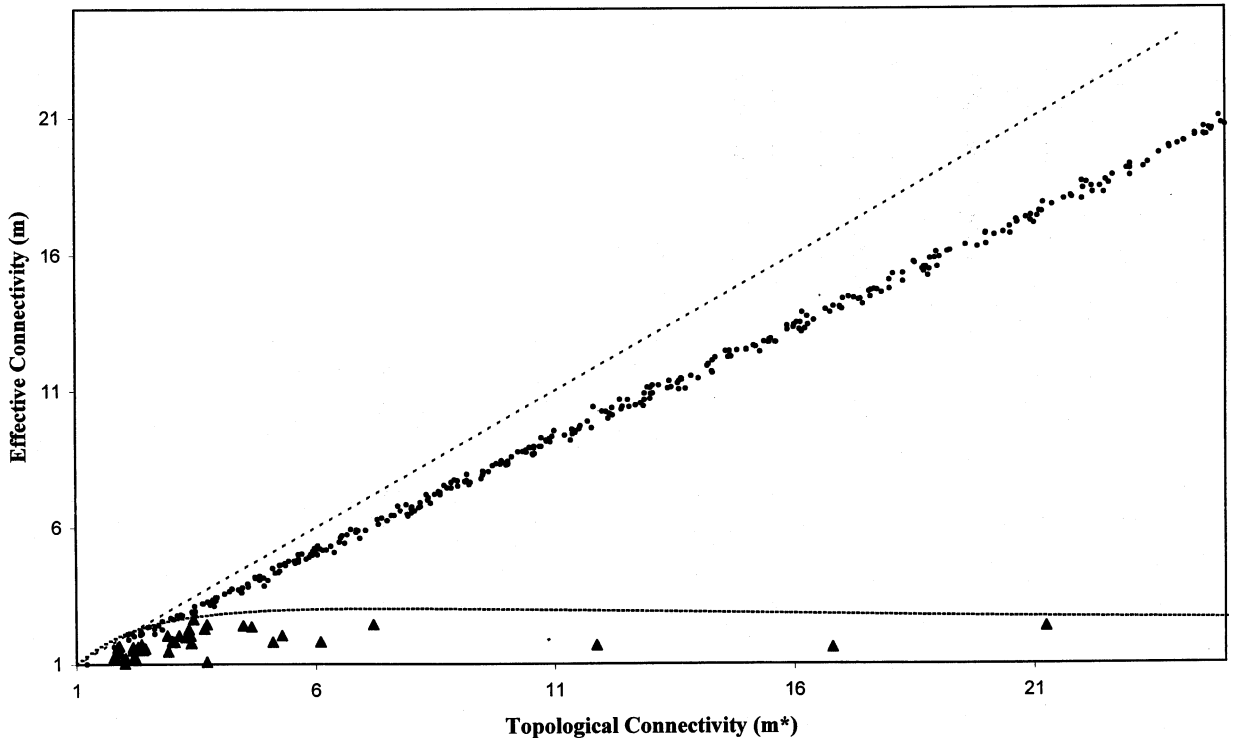


Fig. 5. Randomly constructed and observed networks plotted along with the boundary (tightly dotted line) that separates the domain of stable networks (below) from unstable ones (above).

5. Discussion and conclusions

Perhaps the first issue suggested by these results is how they reflect on the popular ‘edge of chaos’ hypothesis. It is relevant that the ‘edge’ hypothesis arose out of purely algorithmic models. Just as true randomness can be only approximated by algorithms, so also the ‘knife-edge’ character of the transition between the deterministic and chaotic could possibly be an artifact of an entirely mechanically synthesized creation. There is strong suspicion abroad that living systems cannot adequately be addressed by explicit algorithms (Popper, 1982; Rosen, 1999; Salthe, 1993; Ulanowicz, 1997b), and the data tend to support these doubts.

The results bear mixed implications for Conrad’s suggestion that adaptability predominates

over adapted (efficient) behavior. On the one hand, if adaptability were to play the dominant role in evolution, one might expect that systems indeed would evolve to retain as much adaptability as continued existence would allow. That is, they would crowd upon the edge of chaos. The data seem to indicate that such is not the case. On the other hand, neither do the actual systems crowd the m^* axis, which would have indicated an unrestrained drive towards determinate behavior. That real systems do give evidence of non-mechanical behavior argues for the necessity of adaptability as a very vital aspect of evolution. Furthermore, our approach, constrained as it is to a single level, has not begun to probe the implications of Conrad’s ‘hierarchical compensation’, whereby, adaptability and adaptation segregate themselves at different levels or among different

components—much like most of the human body is a marvel of adaptation, while the central nervous system exhibits extraordinary adaptability.

The evidence seems quite clear that networks of ecosystem processes are not assembled randomly in the manner described above. Although only the random uniform distribution was used in this exercise, there is good reason to believe that the application of any well-behaved probability distribution (one that can be normalized and possesses a definite mean) will give similar results (Ulanowicz and Wolff, 1991 Appendix A). As for the placement of the observed networks in the m^*-m plane, it has been demonstrated how flow magnitudes that are distributed according to power laws cause the networks to draw much closer to the m^* axis (ibid Appendix A). That they distance themselves so far from randomly assembled networks is an indication that adaptational constraints are very active in shaping ecosystems.

What might be the origin of these organizational constraints that impart structure to ecosystems? The conventional answer is that natural selection works to diminish certain processes with respect to others. It should be noted, however, that Darwinian selection is always exerted from *outside* the system and that it can work directly only *against* a feature and can favor others only in indirect ways. As mentioned in the previous paragraph, power law distributions seem more appropriate for describing how ecosystem flows are apportioned. The ‘fat tails’ of power law distributions imply the dominance of the system by a very few processes. It is a stretch to explain the growth of these predominate system elements solely in terms of a mechanism that can act directly only in a negative way.

It is noteworthy, therefore, that power law distributions lately have become a popular theme in self-organization theory (Watts, 1999; Johnson, 2000). The positive feedback or autocatalytic-like agency inherent in self-organization theory is capable of exerting selection that directly *favors* the growth of participating elements and acts *internal* to the system itself (Ulanowicz, 1997b). Biologists have been more than reluctant to allow the selection generated by the self-organization process as a legitimate parallel agency in the evolutionary

narrative (usually wielding Occam’s razor to excise it from any discussion). Conventional evolutionary arguments are growing progressively more indirect and unnaturally mechanical (Dennett, 1995), however, and there comes a point at which Occam’s razor eventually cuts those who apply it with such abandon (Ulanowicz, 2001).

Conrad (1985) was never enamored of the strictly mechanical, and often criticized the artificial intelligence endeavor for being too exclusively algorithmic. It was his *Adaptability* that first opened this author’s eyes to the possibility that a causally open universe could be just as amenable to quantitative description as one that is closed. It is my fervent hope that this exercise will stand as a fruitful exploration of the directions that Michael Conrad’s extraordinary intellect helped to pioneer.

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Appendix A

The conditional entropy, Φ , used to calculate the connectance of closed networks must be modified to apply to open systems. The problem is that when dealing with open systems, it becomes necessary to define artificial nodes to serve as the origin of inputs to the system and the sinks for useful exports and dissipations. The convention has been to define the nodes 0, $n + 1$ and $n + 2$ to accommodate these functions, respectively, (Hirata and Ulanowicz, 1984). The problem is that these artificial nodes emit and receive large numbers of flows to and from the whole system. To treat them exactly like the other system nodes would impart a positive bias to the average number of nodes per link. To avoid such

bias, the external exchanges are never regarded from the inward-facing perspective of the artificial nodes, but rather are counted twice from the outward-directed perspective of the compartments in the system with which they communicate. The entropy thus modified, denoted by Φ' , looks like

$$\begin{aligned} \Phi' = & - \sum_{i=1}^n \sum_{j=1}^n \left(\frac{T_{ij}}{T} \right) \ln \left(\frac{T_{ij}^2}{\sum_p T_{pj} \sum_q T_{iq}} \right) \\ & - 2 \sum_{j=1}^n \left(\frac{T_{0j}}{T} \right) \ln \left(\frac{T_{0j}}{\sum_p T_{pj}} \right) \\ & - 2 \sum_{i=1}^n \left(\frac{T_{i,n+1}}{T} \right) \ln \left(\frac{T_{i,n+1}}{\sum_q T_{iq}} \right) \\ & - 2 \sum_{i=1}^n \left(\frac{T_{i,n+2}}{T} \right) \ln \left(\frac{T_{i,n+2}}{\sum_q T_{iq}} \right) \end{aligned}$$

The reader is urged to substitute the flow magnitudes and topology shown in Fig. 6 to ascertain that this formula yields the intuitive connectivity of exactly 3 links per node. He/she is further invited to test other open network configurations

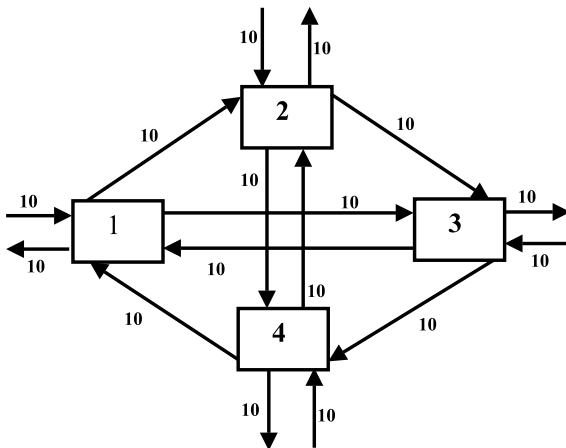


Fig. 6. Hypothetical configuration of equiponderant flows that include transfers with the external environment. Topological connectivity calculated according to Φ' is exactly 3.0 links per node.

to assure oneself that Φ' yields results that accord with intuition.

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