

Complexity, Stability and Self-Organization in Natural Communities *

Robert E. Ulanowicz

University of Maryland, Chesapeake Biological Laboratory, Solomons, Maryland 20688, U.S.A.

Summary. The search for a functional relationship between diversity and stability has thus far been futile. Recent advances in cybernetics suggest that progress may be achieved if diversity, stability and redundancy are considered to be cofactors in determining the key dependent variable – the capacity for self-organization.

The relationship between complexity and stability in natural communities has captivated the attention of ecologists for over 25 years (Odum, 1953). Observation indicates that many-specied, highly connected communities show less intense random fluctuations than their simpler counterparts. The idea that a redundant network of flows can better persist after disruption of some of its members than a corresponding linear chain has resulted in the intuition that “complexity infers stability.” In his influential treatise, *Stability and Complexity in Model Ecosystems*, May (1973) warns against too narrow a focus upon this hypothesis by offering counter examples of a random nature where, in fact, complexity infers instability in the local sense. Much of the reaction to May’s remarks has been chronicled by MacDonald (1978), and the results of the debate should have influence on the further course of investigation and action in the realms of ecological management, economics, and social science.

Most of the current discussions, however, still center about the couple complexity-stability. To avoid narrow focus on this relationship one should consider other system properties which may interact with these interesting features. For example, recent articles on the application of information theory to ecosystems and on cybernetic theory suggest that flow redundancy and the capability for self-organization may be combined with complexity and stability into a unified framework for the description of the structure and function of ecosystems.

To begin this synthesis it is useful to recall that Odum’s original hypothesis stressed that ecosystem self-regulation was dependent upon the choice of flow pathways within the trophic structure. Soon thereafter, MacArthur (1955) at-

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tempted to quantify the choice of pathways in ecosystems by applying the Shannon-Wiener measure of information to the diversity of flows in a trophic web. Diversity of flows, however, was soon replaced by the more easily-measured diversity of species, and a major digression from Odum's original concept was under way. Much later, Mulholland (1975) returned to the consideration of flows in the language of information theory and pointed out that complexity is not necessarily synonymous with choice of pathways. The complexity, as expressed by MacArthur, and the redundancy of pathways differ by a amount known in information theory as the average mutual information.

To be more specific, it is useful to consider the isolated measurement, T_i , of the total amount of energy flowing through the i^{th} compartment of an ecosystem with n compartments. The fraction of the total system throughput associated with compartment i thereby becomes

$$Q_i = T_i / \sum_{j=1}^n T_j. \quad (1)$$

Since these measurements were made in isolation, there is maximal uncertainty about the intercompartmental exchanges as expressed by the formula

$$C = - \sum_{i=1}^n Q_i \ln Q_i. \quad (2)$$

Now if the exchanges among compartments are observed over a convenient interval of time, it might be ascertained that the fraction g_{ij} of Q_i flows from compartment j . The amount of uncertainty about flows within the system has been reduced by an amount

$$I = \sum_{k=1}^n \sum_{j=1}^n g_{kj} Q_j \ln \left[g_{kj} / \sum_{i=1}^n g_{ki} Q_i \right] \quad (3)$$

as a consequence of measuring all the intercompartmental flows. This average mutual information may also be thought of as a measure of the information content of the system flow structure as viewed by an outside observer. The residual uncertainty

$$S = C - I \quad (4)$$

expresses the information associated with the choice of alternate pathways. In fact the redundancy, R , of the structure is expressed by the quotient S/C , and the information content of the flow structure may, therefore, be written

$$I = C(1 - R). \quad (5)$$

The effect of disturbance upon the system is generally to decrease the number of compartments and disturb the flows between them. How, then, does the system respond so as to maintain or increase its structural integrity?

This problem has been addressed by Atlan (1974), and its resolution is evident upon differentiation of (5) with respect to time

$$\frac{dI}{dt} = (1 - R) \frac{dC}{dt} - C \frac{dR}{dt}. \quad (6)$$

Providing the redundancy is high enough, the system can respond by “spending” its redundancy enough rate to compensate for the decrease in complexity.

This process can be further illuminated by assuming very simple decay rates for C and R . Following May's suggestion that more complex assemblages are vulnerable to quicker decline, one may choose $dC/dt = -a$. Furthermore, assume the system can reduce its redundancy at a rate b , i.e., $dR/dt = -bR$. In isolation, the decay of complexity and redundancy will be described by the function $C_0 e^{-at}$ and $R_0 e^{-bt}$, where the subscript 0 denotes initial values of C and R . Substitution of these negative exponentials into (6) gives

$$\frac{dI}{dt} = C_0 [R_0(a + b) e^{-(a+b)t} - a e^{-at}] \quad (7)$$

which will vanish when

$$t = t_m = 1/b \ln [R_0(1 + b/a)]. \quad (8)$$

In other words, provided there is sufficient initial redundancy ($R_0 > a/[a + b]$), the information content of the system will increase over a period t_m , after which it will begin to decay (die). The amount of increase will be modulated by the initial complexity. Therefore, adequately high values of complexity and redundancy are seen to be necessary (but not sufficient) conditions for self-organization to occur.

But a mere increase in I will not lead to self-organization if the duration of the increase is too short. Equation (8) says that the duration of increase in system information will be abetted by slow decay rates. The system must possess some degree of resistance to and resilience from disturbances.

The preferred form of stability that allows for self-organization is best conjectured by regarding a physical system possessing high complexity and redundancy, but not exhibiting self-organization behavior. For example, a crystal of macromolecules at low temperature (disturbance level) is in stable oscillation about its configuration at absolute zero. Stability is so rigid, however, that the process of self-organization cannot begin. In contrast, the same crystal exposed to high levels of disturbance (temperature) possesses practically no stability of structure, and the decays of C and R are so rapid that any increase in I would be of infinitesimally short duration.

Hence, the perturbation level and the stability strength need be appropriately matched. Furthermore, the stability would best exhibit some “plasticity,” that is, the best strategy in the face of disruption may not be a return to the previous form, but rather to a nearby state, which new configuration will better enable the system to persist in the face of a repeat of the perturbation. Such

"buffered stability" is portrayed in the model of Austin and Cook (1974) where a many-specied abstract ecosystem returns to a stationary point near, but not identical to, the undisturbed state. It is interesting to note that such behavior is possible only when stationary points proliferate, i.e., where complexity is sufficiently high.

In summary, if one is willing to attribute the capability for self-organization to entire ecosystems, a new framework for the description of structure and function in ecological communities becomes possible. The dependent variable describing system function is identified as the (yet unspecified) capacity for self-organization (see also Odum et al., 1960). The ability of the system to increase its informational content in the face of disturbance is viewed as a necessary prerequisite for advantageous restructuring. Increasing information, in turn, is seen to depend on at least three *independent* variables – two structural (complexity and redundancy of flows) and one functional (buffered stability). Diversity and stability are likely correlated, in that the most advantageous type of stability requires a modicum of complexity. There is no reason, however, to assume *a priori* a one-to-one functional relationship between them. Finally, the decay of complexity in response to noise is viewed as necessary to initiate the organization process.

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