3.5 Ecosystems under stress[1]

Introduction

Ecosystems, complex entities that they are, undergo manifold changes in response to external perturbations, such as rapid temperature change, sudden nutrient addition, osmotic pulses, etc. There appears to exist no clear consensus as to how to quantify the effects of stress under all circumstances (Thorp and Gibbons, 1978).

Nevertheless, any rational discussion of the topic of systems response to stress must proceed under an assumption as to how to quantify system change. Now, throughout this book we have chosen to place heavy emphasis upon the measurement of flows in ecosystems. In fact, in Section 2.2.2 the hypothesis was considered that the optimization of a state variable (the community ascendancy) synthesized from the network of flows provides the criterion for ecosystems development.

Ascendancy was taken to be the product of two trends: growth and development. The development, or integrity, of a network is a measure of how well the flows within the system relate one to another. If Q_i is the fraction of the aggregate network flow passing through compartment i, and f_{ij} is the fraction of throughput i which flows directly to sustain throughput j, then the average mutual sustenance of the system can be measured as

$$D = \sum_j \sum_k f_{kj} Q_k \ln\left(f_{kj} \Big/ \left[\sum_i f_{ij} Q_i \right] \right). \qquad (138)$$

Other things being equal, this index is enhanced by increases in cycling, positive feedback and specialization of contributions—in short, those elements which characterize a 'developed' community (Margalef, 1968; Odum, 1969).

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As a working postulate, we choose to describe the effects of stress upon a community in terms of the change induced in the development index, D. It should be made clear that this measure is intrinsic to the system and is not meant to convey a sense of benefit to man. For example, less-developed systems can be more productive (Margalef, 1968), and the upwelling and estuarine zones of the marine habitat are 'arrested' communities which yield a greater abundance, in a direct sense, to man than the more developed open-sea systems.

The usual perception is that external perturbations act to decrease ecosystem development. This is almost always the outcome of high-intensity stochastic stress. The response to lower-level or more predictable stresses, however, can be qualitatively quite different. Atlan (1974), for example, resolves the apparent paradox that low levels of stress are necessary for a system to undergo self-organization. In the biological realm, then, stress can sometimes give rise to more organized configurations.

Although the development index defined here gives some semblance of rigour to the discussion of community response to stress, it has the disadvantage that the data required to calculate the state variable are extremely costly to obtain. The ecosystem manager, like the engineer, often wishes to make a sound decision based on the quickest, most inexpensive data collection possible. The only requirement is that the variable computed from measurements should correlate well with the development index. In contrast, the ecosystems researcher is more concerned with the dynamic character of the community and would require data enabling a closer approximation to the actual response.

Simple correlates of development

Perhaps the simplest indicators of ecosystem stage are ratios of extensive system variables. For example, more developed communities appear to support more biomass, B, for each unit of energy throughput, E. The ratio B/E might, therefore, serve as an approximation to community development (Margalef, 1968). Likewise, the ratio of standing crop to gross productivity increases in relatively undisturbed systems. Odum (1969) lists twenty-two other similar ecosystem attributes which appear to correlate with increasing community development.

Well-developed pelagic communities have roughly the same volume concentration of various-sized particles (Sheldon *et al.*, 1972). Stressed communities tend to become depauperate in larger-sized organisms (Kerr, 1974*b*). The relative ease with which particle size distributions may be automatically measured makes this assay most attractive (see also Section 2.2.3).

Probably the most widely measured index of system response to stress is species diversity. It is likely that species diversity reflects underlying flow diversity, which in turn is necessary (but not sufficient) to allow greater network development. Species diversities are thus seen to be indicators of the upper bound to ecosystem community development. Any significant decline in the limits to development is likely to impact upon development itself.

Sanders (1968), for example, showed clearly that benthic communities which had been subjected to physically stable conditions for long periods of time had greater numbers of species than communities in environments which were physically unstable, particularly if the physical variability was irregular and unpredictable. Johnson (1970) extended Sanders's ideas and showed that stresses such as storms, salinity changes, or sudden temperature changes cause regression of benthic communities towards earlier stages of development. Conversely, periods of environmental stability led to further community development with higher species numbers. In 1978 Sanders showed that oil pollution was a stress that produced changes analogous to those seen under the influence of natural stresses, i.e. reduction in species diversity and population instability.

A note of caution must be sounded here. The theoretical development index is a property of the whole ecosystem, and it might be expected that a species diversity index would correlate well with the development index if it, too, related to the whole biological community in the system. In practice it has been possible to derive species diversity indices only for rather restricted subsets of a biological community, e.g. a few groups of benthic invertebrates, or the zooplankton retained in a standard net. Diversity indices representing the whole community from bacteria to vertebrates have not been obtained and would be almost impossible in practice, since the scales of spatial distribution of the various components of the biota are so different. Hence, we must remember that the literature on diversity indices refers only to small subsystems, which may or may not behave in the same way as the total system.

However, species diversities calculated from net tows or bottom counts and size diversities derived from particle counts (Parsons, 1969) are readily obtainable and may well be important correlates to the theoretical development index. Spatial, or pattern, diversity is rarely mentioned in connection with stress, but should also play an analogous role in assessing environmental impact.

Dynamic indicators of a stressed community

The impingement of a stress upon a community and the subsequent system response are both dynamic processes. It is unlikely that any of the aforementioned snapshot indices are likely to be the sole descriptors of time-dependent behaviour. The information necessary to address the more philosophical question of *how* ecosystems cope with stress is sure to be more extensive and costly to obtain. It may be that the satisfactory exposition of ecosystem stress response will take the form of a mathematical model (e.g. Odum, 1971; Austin and Cook, 1974), but it appears more likely that an explanation at the systems level will require the use of variables which characterize the composite community.

The reader's attention, therefore, is directed to the second section of this book on holistic methods in ecology. There the point was emphasized over and again that answers to questions of community dynamics will most probably result from data on ecosystems processes. Thus, the measurement of the ecosystems flows should be given research priority over the measurement of compartmental contents. In particular, just knowing the weighted digraph of community exchange rates will allow for a number of alternative assessments of the response to stress.

Odum, for example, indicated that cycling accounts for a greater percentage of total system flow in more developed communities. Finn (1976) showed how input–output analysis can be used to derive a cycling index for the entire assemblage. Hypothetically, excessive stress should cause a decrease in Finn's cycling index. In principle, cycled flows can be aggregated according to the trophic length of their loops. In the absence of inordinate stress, cyclic controls develop involving loops of greater length. Control response time diminishes (Golley, 1974). The effect of inordinate stress would presumably be to diminish the magnitude of higher-order cycles. Trophic flow spectra of impacted systems should, therefore, show diminished magnitude of cycling at all levels and particular decline in the higher-order control loops.

Kerr (1974*b*) has remarked that stressed pelagic communities tend to possess a smaller proportion of larger-sized organisms. In pelagic systems larger-sized animals also tend to feed higher on the trophic chain. One would expect, then, that stress would reduce the ranks of organisms feeding at higher levels. Ulanowicz and Kemp (1979) present an algorithm for apportioning populations into trophic aggregates. Homer and Kemp (1977) provide data from a thermally stressed marsh community showing that the lower trophic aggregations remain practically unperturbed, whereas the higher trophic compartments are drastically impacted. Interestingly, the species list in the two communities did not differ significantly. Many animals normally feeding high in the trophic chain were subsisting on lower forms, and their trophic index (Levine, ~~1979~~) had fallen. (1977)

If a full description of all ecosystems flows were available, then the development index, D, could be directly calculated and its response to various stresses observed. In practice this ensemble of data is formidable and almost impossible to collect in its entirety. An alternative to knowing all the flows is a cross-correlation of all the changes of the various compartments of the ecosystem. In the parlance of information theory, each compartment would constitute a channel and the *changes* in compartmental content (of mass or energy) would comprise a signal within that channel. The average mutual information among the various channels should reflect the intrasystem control in a manner similar to Mulholland's (1975) index for flow structures. Unlike the flow analysis, however, the residual uncertainty cannot be attributed to system overhead. This does not detract from the utility of the information measure as an index of system response to stress, i.e. average mutual information would decline under damaging perturbation. The subsection on particle-size spectra describes how measurement of particle size might be employed to estimate the dynamic information of a pelagic ecosystem.

Characterization of stress

This section would be incomplete without a few words on characterizing the causal perturbations. Exogenous stresses acting on a system are described by their magnitude, duration and physical extent. While stresses are often conveniently approximated by step functions or impulse functions, other perturbations are temporally and spatially more complex. More often than not, disturbances are stochastic in time and space, and such functions are often described as temporal and spatial spectra (Fasham, 1978*b*; Platt and Denman, 1975). Spectral descriptions of ecosystems are growing in popularity. In addition to the temporal and spatial classifications of ecosystem changes, particle size spectra and 'trophic' spectra (Ulanowicz and Kemp, 1979) are finding use in holistic description of systems.

The implications of the trend towards spectral description of ecosystems are straightforward. The dynamics of community behaviour can be effectively summarized by spectra. One strives to describe stress and systems response in the same general terms. Therefore, the chance discovery of a stressed community by any of the previously described methods is an impetus to describe *both* the system dynamics and the abiotic forcing functions in terms of appropriate spectra. Comparison of the two sets of data is very likely to result in a more enlightened view of the dynamics of stress upon ecosystems.