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# Trends Expected in Stressed Ecosystems

Eugene P. Odum

When ecosystems are not suffering from unusual external perturbations, we observe certain well-defined developmental trends. Since disturbance tends to arrest, or even reverse, these autogenic developments, we can anticipate some ecosystem responses to stress. Trends expected in stressed ecosystems include changes in energetics, nutrient cycling, and community structure and function.

The term *stress* has been widely used for both cause and effect, stimulus and response, or input and output. Although some authors worry about this dual use of the word, I view stress as a syndrome comprising both input and output. One cannot have a response without a stimulus. One can easily identify which part of the syndrome is being singled out by using modifying adjectives, prefixes, or clauses; thus, stress as an input can be designated the *stressor* as contrasted to *stress*, the response, or output. (In referring to stress as a syndrome, I do not mean to imply a strict analogy with Selye's [1973] "general stress syndrome," although as recently noted by Rapport et al. 1985, there are interesting parallels between the physiological and community levels.)

I believe that common words in everyday language, such as *stress*, *competition*, or *community* should not be given highly technical meanings, since this only serves to confuse the general reader; as already indicated, modifiers can restrict meanings. But we must recognize that these common terms have different meanings, and often different manifestations at different levels of organization. Allen (1984), in discussing hierarchical organization, pointed out that a disturbance detrimental at one level may be beneficial at a higher level. For example, periodic fire in the fire-adapted chaparral is a stress to many organisms

that may be injured or killed, but it is not a stress at the ecosystem level; the absence of fire would be a stress at this level. Furthermore, disturbance at the same level may sometimes have a positive effect or produce both positive and

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negative responses, hence the "subsidy-stress" syndrome (see Odum et al. 1979).

In summary, I am using the term *stress* the way the dictionary defines it and the way the public understands it—to mean a detrimental or disorganizing influence. I prefer to use the term *subsidy* for an input that produces a positive response, even though it may be accompanied or followed by negative responses. In this paper I focus on negative responses to unusual external disturbances, or stressors of low probability to which a community of organisms is not preadapted.

When ecosystems are not affected by strong external perturbations, such as storms or human disturbances, we observe certain well-defined developmental trends. For example, the biomass and sizes of organisms tend to increase and net community production to decrease.

In 1969, I published a table, "Trends to be Expected in Ecosystem Development," which contrasted early and late stages of succession in terms of 24 ecosystem properties. This tabular model was subsequently revised (Odum 1971, 1983). My hypothesis is that a disordering disturbance to which a community is not adapted arrests and, in many cases, reverses these autogenic developments (Odum 1981). Accordingly, I have prepared a table, "Trends Expected in Stressed Ecosystems" (see box, page 420), whose format is similar to my model of autogenic succession.

In general, this model covers negative responses in the longer term at the ecosystem level. Many of the trends listed are well supported by observation and experiments as useful indices of stress, but others are hypothetical and require further study and testing. As already indicated, responses at the ecosystem level can be expected to be not only different but also more diffuse and longer termed than responses at the population level. Moreover, chronic stress that continues for a long time may have a different effect than an acute stress that is quickly followed by recovery and return to an unstressed state. Keeping these qualifications and boundary constraints in mind, let us now examine the 18 components in the model.

## ENERGETIC RESPONSES

Theoretically, an increase in community respiration (item 1) should be the first early-warning sign of stress since repairing damage caused by the disturbance requires diverting energy from growth and production to maintenance. Hence, the R/B ratio (the maintenance to biomass ratio, item 3) increases. Odum (1967) speaks of this response as an "energy drain," or the process of

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## Trends Expected in Stressed Ecosystems

### Energetics

1. Community respiration increases (H. T. Odum's "pumping out" of disorder [Odum 1967] or Prigogine's increase in the "dissipative structure" [Prigogine et al. 1972])
2. P/R (production/respiration) becomes unbalanced ( $<$  or  $>$  1)
3. P/B and R/B (maintenance:biomass structure) ratios increase
4. Importance of auxiliary energy increases (Margalef's [1975] exosomatic metabolism)
5. Exported or unused primary production increases

### Nutrient cycling

6. Nutrient turnover increases
7. Horizontal transport increases and vertical cycling of nutrients decreases (cycling index decreases)
8. Nutrient loss increases (system becomes more "leaky")

### Community structure

9. Proportion of r-strategists increases
10. Size of organisms decreases
11. Lifespans of organisms or parts (leaves, for example) decrease
12. Food chains shorten because of reduced energy flow at higher trophic levels and/or greater sensitivity of predators to stress
13. Species diversity decreases and dominance increases; if original diversity is low, the reverse may occur; at the ecosystem level, redundancy of parallel processes theoretically declines

### General system-level trends

14. Ecosystem becomes more open (i.e., input and output environments become more important as internal cycling is reduced)
15. Autogenic successional trends reverse (succession reverts to earlier stages)
16. Efficiency of resource use decreases
17. Parasitism and other negative interactions increase, and mutualism and other positive interactions decrease
18. Functional properties (such as community metabolism) are more robust (homeostatic-resistant to stressors) than are species composition and other structural properties

"pumping out the disorder." In the context of Prigogine's theories of open, far-from-equilibrium systems (see Prigogine et al. 1972), an increase in respiration represents an increase in activity of the "dissipative structure." In practice, respiration increase does not provide a very good early-warning distress signal because it is difficult to detect small increases in large open systems. Some indirect measure, however, might be feasible. Menzel (1980), in reviewing the results of the CEPEX (Controlled Ecosystem Pollution Experiment) mesocosm experiments, states that changes in indices of bacterial activity were detected

within hours after introducing a pollutant into floating containers. Since microorganisms respond quickly to any change, they may be the level at which we should search for early-warning signs (see Ivanovici and Wiebe 1981).

The P/R, or production/respiration, ratio (item 2) is, of course, affected by any change in the partitioning of energy between production and maintenance. Since the P/R ratio tends toward balance in undisturbed ecosystems, we can expect the ratio to become unbalanced with stress. Experience with coral reefs is a good example. The P/R ratio of an undisturbed coral reef is generally slightly

greater than one. Any input of toxic substances or silt reduces the ratio to less than one. The P/R ratio is sometimes a good indicator of stress in laboratory microcosms set up to monitor the effects of a potential pollutant. In one of our experiments with cadmium (Hendrix et al. 1982), the stressor decreased the ratio in static microcosms with no input or output of culture media but not in flow-through microcosms, where an increase in photosynthesis caused by poisoning of grazers was balanced by an increase in microbial respiration. More often than not, however, disturbance produces an increase in respiration greater than the change in the rate of production, thus altering the P/R ratio.

Margalef (1975) pointed out that the drain of productive energy in dissipating entropy "opens up" the ecosystem so auxiliary energy from the outside becomes more important in the continued survival of the system. The altered and unbalanced metabolism may result in an increase in unused resources that may then be stored within the system or exported (items 4 and 5).

To summarize, community respiration per unit of biomass tends to increase and biomass accumulation to decrease as organisms cope with the disorder created by unusual exogenous disturbance. Accordingly, stressed ecosystems will tend to exhibit unbalanced P/R ratios and increased P/B and R/B ratios—in other words, a decreased ratio of biomass to energy flow, or a low efficiency of converting energy to organic structure.

### NUTRIENT CYCLING

The three trends listed in the box are, of course, interdependent. Increased turnover and decreased cycling frequently appear in stressed ecosystems. Together they result in accumulation of nutrients which, like unused production, may be lost from the system. O'Neill et al. (1977) and Van Voris et al. (1980) have found that leaching of calcium is a good index of stress severity in terrestrial microcosms and also in the field; the more intense the stressor, the more calcium lost.

In a recent symposium edited by Mooney and Godron (1983), several authors, including M. Rapp and P. M. Vitousek, agree that leaching losses of major nutrients are normally much less than the amounts recycled within forests but that disturbance may result in increased losses.

Margalef (1975) reminds us that increasing horizontal transport (i.e., one-way flow) at the expense of internal cycling is one of the principal ways humans disturb natural ecosystems. Mining, soil erosion, stream pollution, and fertilizer runoff from croplands are familiar examples.

## COMMUNITY STRUCTURE

As long as conditions remain favorable for a variety of organisms, competition for resources will tend to favor K-selected species as nutrients and energy become fully used, especially in the mature system. Accordingly, with stress we would expect a decrease in such species and an increase in opportunistic, or r-selected, species (item 9); this frequently happens when forests are clear-cut or subjected to ionizing radiation, or in just about any case of severe disruption. Woodwell (1983) points out that generally, "disturbance favors communities dominated by small-bodied, rapidly reproducing, hardy species." The "weedy type plants" and "pest-type animals," as it were, take over. In the CEPEX experiments, organism size decreased (item 10) no matter what kind of pollutant was added to the mesocosms. In the plankton, for example, large diatoms were replaced by small green algae, which, in turn, could reduce the number and size of organisms in higher trophic levels. A good example of the reduction in lifespan (item 11) is the response of pine forests to air pollution. We often see the first sign of stress when needles, which normally remain on the branches for two years, fall off after the first year (Williams 1980). If pollution stress continues, the lifespan of the trees themselves is reduced.

The impact of stress on the food web is not clear-cut. A shortening of food chains with a reduction in top predators (item 12) frequently follows eutrophication and toxic waste pollution in lakes. The reasons for this are not understood, although two different explanations have been suggested: (1) Small organisms out-compete large organisms, both under conditions of enrichment and toxic stress. (2) Although large organisms are often more efficient feeders when resources are scarce (the size-efficiency hypothesis; see Dodson 1974), they are subject to bioaccumulation of toxins, have vulnerable life history stages, or are otherwise more sensitive to disturbance than are small organisms. The demise of

predatory birds resulting from DDT pollution is an example.

The effect of stress on diversity is also complex and not well understood, partly because responses may be different at different levels. Species diversity, for example, may be affected differently from food chain diversity or nutrient diversity. Species diversity is almost always reduced (item 13) by toxic inputs (insecticides, for example) unless the diversity is very low to begin with (Barrett 1969). But a decrease in species diversity is not a reliable index of stress in general because a disturbance affecting the

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structure of the system (e.g., patch cutting in a forest) often increases the diversity of species of both plants and animals. In theory, redundancy of parallel processes (or what Hill and Wiegert 1980 call "congeneric homeotaxis") should be reduced by stress at the ecosystem level (item 13), but I know of nothing documenting this possibility.

Interestingly, human settlement at first tends to make the landscape more diverse (patchy), but with increasing urbanization and monoculture in agriculture, the landscape becomes less diverse, unless parks, open space, and nature reserves are planned during development.

## GENERAL SYSTEM-LEVEL TRENDS

The last five items (14 through 18) summarize the overall trends that might be expected in stressed ecosystems. Items 14–16 follow logically from the discussion of trends 1–13, but the last two statements are hypothetical and require discussion.

Cooperation and mutualism seem to develop when resources become scarce, and working together for mutual benefit has a high selective value (see Axelrod 1984, Axelrod and Hamilton 1981). Accordingly, we find that mutualism is important in mature ecosystems, such as

large biomass forests, and also in ecosystems adapted to nutrient-poor conditions. My hypothesis is that, in either case, a disordering input should disrupt these intricate homeostatic positive interactions and increase the likelihood that parasitism, overgrazing, and other negative interactions will develop, as when forests are subjected to air pollution or ionizing radiation. I realize one can argue instead that stressful environments tend to promote mutualism as a strategy for survival, as for example, lichens on rock outcrops or mycorrhizal pine trees on poor soils. My view is that such mutualistic systems are the adapted, or normal, state, which is especially vulnerable to additional or unusual exogenous stress. Indeed, lichens are sensitive to air pollution. One can cite numerous examples of increased parasitism and predation resulting from stress. For example, game managers find that an increase in stomach worms in deer is a good indicator of an overbrowsed range (Eve and Kellogg 1977).

That functional properties may be more robust than structural properties (item 18) is an intriguing and important possible trend. Schindler's whole-lake experiments certainly support this hypothesis (Schindler 1974, Schindler and Turner 1982). When large amounts of acid or nutrients were introduced into lakes, primary productivity and other aspects of community metabolism were remarkably homeostatic, but species composition of the plankton and fish were greatly altered. We are reminded here of Margalef's statement (1981) that: "Stress is something that puts into action the mechanism of homeostasis." In this case, species replacement and other adjustments keep the overall function of the system steady. Accordingly, early warning of stress will be more easily seen at the species level, although shifts here should be accompanied by changes in the rate of respiration and/or decomposition, which are more difficult to detect in large systems. When stress is detectable at the ecosystem level, there is real cause for alarm, for it may signal a breakdown in homeostasis.

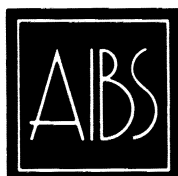
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