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DIVERSITY AND STABILITY OF ECOLOGICAL COMMUNITIES: A COMMENT ON THE ROLE OF EMPIRICISM IN ECOLOGY

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In the Proceedings of the First International Congress of Ecology (1974), a strong theme was the relationship, if any, between species diversity and ecosystem stability. It is apparent from these proceedings that there is considerable variation in attitudes regarding what ecosystem properties diversity is supposed to stabilize. Some authors, for instance, argue that species diversity is supposed to stabilize species diversity and, further, that data contradict the hypothesis because greater species diversity in communities studied was accompanied by greater changes in diversity upon environmental variation (Larsen, p. 80, this and subsequent page references are to the Proceedings). Similar arguments have been developed elsewhere in the context of purported tests of the diversity-stability hypothesis (Hairston et al. 1968; Murdoch et al. 1972). Elsewhere in the proceedings, it was argued that a positive relationship between species diversity and stability would somehow conflict with our knowledge about the dynamics of individual populations. Goodman (p. 78), for instance, in rejecting the "validity" of the hypothesis, says that it contradicts evolutionary reasoning.

Widely varying interpretations of the hypothesis seem remarkable given its explicit and repeated presentation (Bertalanffy 1950, 1952; MacArthur 1955; Odum and Pinkerton 1955; Bray 1958; Odum 1962, 1969; Margalef 1963, 1968; McNaughton 1968; Mellinger and McNaughton 1975). Specifically, the hypothesis is: species diversity stabilizes ecosystem functional properties. Margalef explicitly stated (p. 66), "A system, highly unstable in species composition, may be stable concerning energy flow." Purported tests based on fluctuations of individual populations within an ecosystem are irrelevant, unless it is shown that outbreaks of certain species are unaccompanied by compensating declines in other species. Similarly, retrospective tests based on data collected for other purposes should be scrutinized carefully for applicability. Initial explicit empirical tests of the diversity-stability hypothesis on planktonic (Margalef 1965) and terrestrial (McNaughton 1968; Singh and Misra 1969) systems used indirect means of estimating stability and provided conflicting results. A more direct test (Hurd et al. 1971; Hurd and Wolf 1974; Mellinger and McNaughton...
1975) provided supportive evidence for the plant community, but not for the arthropod community.

The general tenor of the Congress papers is in marked contrast to those in a symposium on diversity and stability published just 5 yrs previously where most authors accepted the hypothesis (Woodwell and Smith 1969). Principal catalysts of the change in attitudes, based on Congress citations, seem to be mathematical models demonstrating that destabilization accompanies increases in number and connectance of system elements (Smith 1972; Hubbell 1972; May 1973). More recently, alternative formulations have suggested conditions under which diversity increases stability (Jeffries 1974; DeAngelis 1975). What, then, can we conclude from the mathematical modeling? Under certain constraints stability is facilitated by diversity and connectance, under other conditions it is not. Resolution of the relationship, if any, between species diversity and functional stability of ecosystems must be empirical (Mollinger and McNaughton 1975). Continued assertions of the validity of one or another conclusion about diversity-stability, in the absence of empirical tests, are acts of faith, not science.

A restatement of the traditional verbal model relating diversity and stability would seem useful at this time in demonstrating the logic of the hypothesis and that the logic is grounded in an appreciation of the adaptive properties of populations. (1) The ability of a species to invade a community is dependent upon the existence of a resource state where it can compete more effectively than present occupants (MacArthur 1965). (2) This may be one of the principal mechanisms of increasing diversity in successional ecosystems (McNaughton 1974; Mollinger and McNaughton 1975). (3) If we consider a simple resource gradient, such as nutrient concentration, different species will have different optimum physiological utilization ranges (Rorison 1969). Similarly, in a multidimensional resource field, distributions of co-occurring species will differ but overlap (Rogers and King 1972; Makarewicz and Likens 1975). (4) If resource state fluctuates in time (Haase 1970) or space (Snaydon 1962) as it does in nature, functional properties of a community consisting of species with distinct and nonoverlapping adaptive ranges will fluctuate wildly, while a community consisting of species with overlapping ranges will remain more constant as declines in one species are compensated by increases in other species (fig. 1). There is evidence to indicate that such internal compensation increases with diversity in successional vascular plant communities (McNaughton 1974; Mollinger and McNaughton 1975). (5) Therefore, the interplay between species adaptive properties and community diversity with the associated species packing (May and MacArthur 1972; Gadgil and Gadgil 1975) may stabilize aggregate community functional properties.

The idea that compensating fluctuations in the abundances of co-occurring system elements (species populations) in a variable environment can stabilize aggregate system properties is apparent in the intellectual development over the last 25 years of the hypothesis that diversity may stabilize function (Bertalanffy 1950, 1952; MacArthur 1955; Odum and Pinkerton 1955; Bray 1958; Odum 1962, 1969; Margalef 1963, 1968). The hypothesis is logical, but
Fig. 1.—Simple graphical model of how community diversity may increase temporal stability of community properties as a consequence of overlapping adaptive patterns among co-occurring species. In the upper graph, the biomasses of four species (A → D) are plotted against a soil moisture gradient. In the second graph, a hypothetical fluctuation of soil moisture with time is plotted, and in the two lower graphs the effect of diversity upon community biomass is plotted during a period of fluctuating soil moisture.

there are few empirical tests. The present paper develops further empirical data on the question, including a reevaluation of diversity changes at the primary producer level in the succession studies (Hurd et al. 1971; Melling and McNaughton 1975) and additional evidence from East African grasslands. The latter data are from a continuing study by the author on the dynamics of an old and highly coevolved ecosystem (Leakey 1965) designed to provide critical tests of the diversity-stability hypothesis.
STUDY AREAS AND METHODS

Study areas and methods in the old field studies have been described elsewhere in detail (Mellinger and McNaughton 1975) and, for present purposes, I present merely a reevaluation of species diversity data that provides additional insight into the mechanism by which plant community diversity influenced the results of these studies. The grassland studies were done in the Serengeti-Mara ecosystem in Tanzania and Kenya. This ecosystem covers an area of 25,000 km², as defined by the seasonal movements of the area's large migratory ungulates between wet season occupancy ranges on the Serengeti Plains and dry season occupancy areas near the Mara River (Talbot and Talbot 1963; Watson 1967). Green plant biomass was measured by the reflectometric technique (Tucker et al. 1974; McNaughton 1976) and contribution of individual species was estimated by a canopy interception technique based on methods of measuring leaf area index (Knight 1973). Details of both calibrations will be published elsewhere; both the reflectometric ($r^2 = .955$ for $P < .001$ with df = 18) and canopy intercept ($r^2 = .868$ for $P < .001$ with df = 18) methods were accurate for their intended purpose. Species diversity was calculated from net productivity and biomass for succession and grassland studies, respectively, by the corrected Shannon-Weaver formula. Equitability was calculated as $H'/\ln S$.

The relationship between stability and diversity of grasslands in the Serengeti-Mara ecosystem was evaluated in response to rainfall and grazing. Rainfall effects were examined during the "short rains," a period of highly variable rainfall in the ecosystem (data from Serengeti Ecological Monitoring Program). Instability was measured by fluctuations in green biomass during this period in plots protected from grazing by fencing. Grazer impact on plant communities of different diversity was evaluated in adjacent stands occupied by a resident herd of African buffalo (*Syncerus caffer*). This impact was evaluated by comparing control areas inside exclosures with grazed areas outside. Stability was defined as ability to maintain green biomass at control levels under grazing pressure.

RESULTS

As has been shown elsewhere in preliminary (Hurd et al. 1971) and more detailed (Mellinger and McNaughton 1975) analyses, the plant community of a successional shorter and less diverse ecosystem was functionally more stable than a younger and less diverse plant community upon a nutrient perturbation induced by fertilizer application. The nutrient pulse had no effect on net productivity of the older field, while the younger field had productivity increases of 40% aboveground, and 56% below ground. The difference between fields was highly significant (Mellinger and McNaughton 1975). An examination of the effect of fertilization on diversity reveals quite a different pattern (table 1). While fertilization had no effect on diversity of the younger field, there was a significant reduction in diversity on the older field. This result indicates that
fluctuations in species abundance relations were more pronounced in the more diverse plant community and that they were associated with functional stability. As reported previously (Hurd et al. 1971; Mellinger and McNaughton 1975), there were no changes in richness; the diversity change was caused by greater equitability among the same number of species. This confirms the hypothesis: compensations among co-occurring species stabilized an aggregate community functional property in the more diverse community.

The examination of the impact of African buffalo on grasslands indicated that the more diverse plant community was subject to a greater diversity modification by grazing (table 2). Once again, however, a greater diversity impact was translated into a reduced effect on a functional property, green biomass of the community. Although the actual amounts eaten were identical
in the two stands, growth of uneaten species in the more diverse stand compensated for grazer consumption. This could be traced primarily to growth of *Themeda triandra*, which made up 6.2% of the biomass in the control area and 23.1% of the biomass in the grazed area. Compensation by the community for grazer offtake was 83% in the more diverse community, only 9% in the less diverse community. The compensation effect could be traced clearly to the adaptive properties of the compensating species: *Themeda triandra* is an understory species in this tall grassland, and opening up of the canopy by buffalo grazing released it from competition. Its increased growth compensated for consumption of taller species by buffalo.

Rainfall effects were evaluated during a 5-wk period when the study area (Musabi Plains) was subject to periodic showers. There were five replicates in each of four adjacent stands which differed in plant community diversity, as measured here by maximum diversity recorded during the study period. This study revealed that the ability of a stand to maintain its photosynthetic biomass during a period of variable rainfall was significantly associated with its species diversity (fig. 2). Once again, this greater stability was mediated by fluctuations in species abundance of the type suggested by figure 1: Some species traded, in the adaptive sense, greater growth rate after a shower for rapid drying between showers; others traded less rapid growth rate after a shower for a less rapid drying between showers. The consequence, for the community, of a reservoir of species with different adaptive modes was a stabilization of community functional properties.

Finally, the impact of a single species on community function, unconfounded by diversity effects, was evaluated by isolating two stands of identical diversity in which the sedge, *Kyllinga nervosa*, varied in abundance. *Kyllinga* is a dominant species in the driest part of the ecosystem (Anderson and Talbot 1965), and its adaptive strategy is apparent: It has an extremely rapid growth rate as soon as it rains, but it dries out extremely rapidly without sustained rainfall.
TABLE 3

RELATIONSHIP BETWEEN ABUNDANCE OF Kyllinga nervosa AND RELATIVE INSTABILITY
OF GREEN BIOMASS DURING A PERIOD OF ERRATIC SCATTERED SHOWERS IN
THE SERENGETI PLAINS

<table>
<thead>
<tr>
<th>Property</th>
<th>Kyllinga-dominant</th>
<th>Kyllinga-subordinate</th>
<th>t</th>
<th>df</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Kyllinga (%)</td>
<td>40.4</td>
<td>6.2</td>
<td>3.232</td>
<td>7</td>
<td>&lt; .01</td>
</tr>
<tr>
<td>Diversity ($H'$)</td>
<td>0.947</td>
<td>1.051</td>
<td>0.686</td>
<td>4</td>
<td>NS</td>
</tr>
<tr>
<td>Instability ($V$)</td>
<td>171.4</td>
<td>91.4</td>
<td>28.179</td>
<td>7</td>
<td>&lt; .005</td>
</tr>
</tbody>
</table>

Note.—Kyllinga nervosa is an ephemeral, drought-resistant species. Instability is measured by the coefficient of variation of green biomass during a 5-wk study period with four replicates in each stand measured every 6 days.

It is an ephemeral species, drought adapted by virtue of this strategy. A stand dominated by Kyllinga was found near the southern boundary of Serengeti National Park, in an area of short grassland where the bulk of the region is dominated by Sporobolus verdcourtii, a less rapidly growing but more persistent species. The results indicated that the Kyllinga-dominated stand was much less stable than the surrounding plant community, with the fluctuation in green biomass over a 5-wk period almost twice as great as in the control stand (table 3). This fluctuation resulted from alternate periods when Kyllinga was rapidly growing, others when it was rapidly drying out. This demonstrates that it is possible to uncouple the diversity-stability relationship in exceptional stands where the adaptive properties of community members may uncouple the general stabilizing effect of diversity. An ecological community, of course, is not a completely deterministic system, but it is subject to considerable local variation. Within the Sporobolus-dominated vegetation, the Kyllinga-dominated stand represents such variation. But this local pattern, by contributing to overall vegetation diversity, may stabilize ecosystem response to longer-term environmental fluctuations. The Kyllinga-dominated stand, for instance, might provide an invasion locus for a more drought-adapted species should the climate become progressively drier.

DISCUSSION

The successional studies were done in a temperate successional ecosystem that is nonpersistent in time, while the grassland studies were done in a tropical ecosystem that is the culmination of a long evolutionary and successional history. Both studies provide confirmation of the hypothesis that plant community diversity stabilizes functional properties of the community to environmental perturbations, whether experimentally induced or intrinsic to the ecosystem. These data further indicate that adjustments in species abundances in the more diverse community, resulting in greater diversity changes, mediate
functional stability. Changes in the diversities of more diverse communities result from compensating homeostatic interactions among co-occurring species that stabilize community processes. These changes are a direct result of the interacting effects of adaptive characteristics of a population resulting from evolution, and niche overlap and competition that result from community diversity. This in no way implies an emergent property for ecosystems; the stability of community functional properties is a consequence of adaptive properties of constituent individuals. Diversity stabilizes function, not diversity. On an isolated basis, as the *Kyllinga*-dominated stand documented, the relationship can be uncoupled. Community development is a much less orderly process than development of the individual or, perhaps, the evolution of a population. It seems obvious that the degree of determination in “developmental” processes is a negative function of the level of biological organization.

The weight of evidence resulting from explicit tests of the diversity-stability hypothesis (Margalef 1965; McNaughton 1968; Hurd et al. 1971; Melliger and McNaughton 1975) suggests, not that the hypothesis is invalid, but that it is correct. The one empirical exception, in which stability was measured directly, is the marked instability of arthropods in the older and more diverse successional community (Hurd et al. 1971; Hurd and Wolf 1974). Two alternative explanations suggest themselves, one methodological, one ecological. First, because the entire consumer fauna was not sampled, it is possible that declines in other consumers may have compensated for arthropod increases. Frankly, this seems implausible because arthropods were clearly the major consumers on these fields. Second, this outcome may have been a direct result of compensatory adjustments at the primary producer level. Higher diversity at the producer level in the older field is probably translated into an arthropod community consisting of species specialized for finding rarer prey in a more complex physical and olfactory environment (Pinentel 1961; Tahvanainen and Root 1972; Root 1973). Therefore, diversity reduction at the primary producer level accompanying fertilization would result in a significantly increased probability of the arthropods finding food plants (McNaughton 1974; Melliger and McNaughton 1975). The fertilizer-induced reduction of equitability at the producer level, therefore, would tend to have a destabilizing effect on higher trophic levels. This suggests that plant-plant interactions are more significant than plant-herbivore interactions in these old fields, and this is supported by the relatively low energy flow through the arthropods compared with the plants. Further, in an agricultural area such as the northeastern United States, much of the flora and fauna may consist of introduced alien species which have not become well integrated into a coevolved system. We might expect the plant-herbivore relationship to be quite different in the Serengeti-Mara ecosystem, where herbivore load is intense (McNaughton, in preparation) and the period of coevolution is long (Leakey 1965). The studies these are abstracted from are designed to provide additional insight into the operation of such an ecosystem.

Finally, how can we account for the marked instability of attitudes regarding the diversity-stability hypothesis, exemplified by a comparative reading of papers in Woodwell and Smith (1969) and *Proceedings of the First International Congress of Ecology* (1974)? The explanation seems to be the appearance in the
interim of a plethora of more rigorous models suggesting alternative conclusions (Smith 1972; Hubbell 1972; May 1973). It is fascinating that there has been so much modeling and so little empirical testing during this period. The data reported here indicate that the “less rigorous” traditional verbal model suggests more reliable generalizations about how diversity mediates function in plant communities than most of the “more elegant” mathematical analyses produced to date. I think the marked instability of attitudes regarding diversity-stability relationships in ecosystems arises primarily from a low diversity of empirical tests of the hypothesis.

SUMMARY

The diversity-stability hypothesis developed over the past 25 years appears widely misunderstood by ecologists, although it simply states that species diversity mediates community functional stability through compensating interactions to environmental fluctuations among co-occurring species. Fluctuations in the abundances of species with different adaptive modes may be a mechanism stabilizing community function in a varying environment. The available empirical evidence, including data from an experimental perturbation of successional old fields and data on the impact of environmental fluctuations on properties of grasslands in the Serengeti-Mara ecosystem of Tanzania and Kenya, suggests that the hypothesis is true at the primary producer level. As components of natural science, models are true only insofar as they are verified as accurate descriptions of the systems they purportedly characterize. The data on diversity-stability relationships in plant communities indicate that the traditional verbal model is considerably more robust in application than recent “more rigorous” mathematical models.

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