To the Graduate Council:

I am submitting herewith a thesis written by S. Russell Manning entitled "The Diversity-Stability Hypothesis in Ecology." I recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Arts, with a major in Philosophy.

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THE DIVERSITY-STABILITY HYPOTHESIS

IN ECOLOGY

A Thesis

Presented for the

Master of Arts

Degree

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S. Russell Manning

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ABSTRACT

The purpose of this study was to explicate the current status of the diversity-stability hypothesis in ecology--the proposition that species diversity increases population stability. The historical and philosophical background was explored to show that the hypothesis, rather than being founded on solid scientific evidence, is more a part of our "folk science" and was readily accepted because it fit our predisposition for order and purpose in nature and satisfied our aesthetic evaluation of species diversity. But the classical argument for the diversity-stability hypothesis was shown to be inadequate; in fact, a necessary and sufficient causal relationship was shown to be false.

With diversity defined as species number, plus a measure of species interconnectedness and correct proportions, and stability defined as the ability to return to and maintain a base state, an alternative hypothesis was proposed: Diversity and stability are associated in the presence of a third factor, environmental favorability. But it was also argued that if diversity increases stability within this context, it does so only up to some level of specialization, beyond which overspecialization destabilizes the system. Support for this alternative was qualified in that it was thought that this is but one hypothesis from among many that should be put forward in order to increase the research options.

Since the alternative hypothesis stated that diversity increases stability only within a certain range of specialization and only within the context of environmental favorability, it was suggested that a universal law about diversity-stability may not be possible and that this condition is characteristic of the science of biology itself and not just diversity-stability relationships. The complexity of living organisms and their interrelationships was proposed as the factor that prevents the formulation of universal laws in biology.

It was concluded that whatever the relationship between diversity and stability, it must exist within the context of many environmental and biological factors. Because of the present ambiguity, a case was made for the exercise of caution in the management and exploitation of our natural resources along with preservation of representative ecosystems.

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INTRODUCTION

The diversity-stability hypothesis is the proposition that diverse ecosystems are more stable than simple ecosystems with the implied meaning that diversity increases stability. Such an idea is plausible since a system with many parts should more easily dissipate the force of a disturbance, or perturbation; the more trees and plants and animals and insects that inhabit a particular ecosystem, the better that system should be able to withstand an invasion of another species or a change in the physical environment without suffering drastic population fluctuations. A system with fewer constituents should not dissipate a perturbation as easily and so would be expected to exhibit fluctuations in population numbers.

This hypothesis, though readily accepted when first formulated, is in fact not supported by empirical evidence nor by mathematical models designed to test its validity. It would seem, then, that the discussion should stop here, but neither is the evidence conclusive enough to discount the idea that diversity and stability are correlated in some other way than that implied by the traditional interpretation of the hypothesis.

Purpose, Limitations, and Importance

The purpose of this study is to explicate the current status of the diversity-stability hypothesis in addition to giving a few reasons for its general acceptance when it was originally proposed.

Some alternative relationships will be explored as well to see if other, and better, hypotheses can be formulated.

There will be no effort to set up experiments or to construct mathematical models or to take biological inventories in an attempt to validate or invalidate the diversity-stability hypothesis. What is attempted is rather an evaluation and assessment of what is already known, an appraisal of our capability of resolving the issue, and a reminder of the implications of the current confusion and any forthcoming resolutions.

This reappraisal of the current status of the diversity-stability hypothesis serves as an important reminder that we do not yet have a fully formulated biology. Our resource management decisions should reflect the present uncertainty, for a belief or disbelief in the diversity-stability hypothesis will influence such issues as population control, ecosystem exploitation, species preservation, and possibly, the very survival of the human species.

Definitions

As has already been stated, the diversity-stability hypothesis is the claim that diverse ecosystems are more stable than simple systems; implied in the literature is a cause and effect relationship. But what kind of causal relationship exists between the two is part of the investigation of this study. If indeed diversity and stability occur together, this does not necessitate that they are related in a necessary and sufficient casuality. At times, for the sake of brevity, the diversity-stability hypothesis will be referred to as simply the hypothesis.

Diversity is commonly taken to mean numbers of species, but many biologists think this definition is too simplistic and prefer to use complexity--a measure of the interactions and interpdependencies between species within a community, which of course is a function of species number. Diversity will mean complexity, and the two terms may be used interchangeably depending on the author cited. This allows the more commonly used name of the hypothesis ("diversity-stability") to be retained. If only number of species is intended, it will be referred to as species number.

Constancy of population numbers is an unrealistic goal for ecological systems, so most biologists expect a stable ecosystem to at best achieve a dynamic equilibrium; stability, therefore, can be defined as resistance to fluctuations away from this equilibrium. Other scientists contend that it is more appropriate to be concerned with resilience, the ability to bounce back after a disturbance. Still others see stability as simply presistence, no extinctions. For the present, stability will be considered a measure of the resistance to population fluctuations; this definition will be modified as needed.

A perturbation, that which can potentially cause a population fluctuation, will include not only changes in the physical environment (climate and geology) but also the invasion of another species. Disturbance will connote the same meaning.

Further definitions will be presented as needed throughout the text; these will be underlined when first formulated to draw attention. It will also be necessary at times to revise or reformulate a definition as the reasoning progresses, especially for stability; in such instances, underlining will be used to indicate that a previous definition has been superseded.

Organization

The argument for the diversity-stability hypothesis will be presented in Chapter 1. Leading up to that will be a discussion of some of the factors that caused the hypothesis to be generally accepted.

Chapter 2 will show that the classical argument for the hypothesis is inadequate because mathematical models and empirical observations have not confirmed the statements and assumptions used to support the hypothesis. Each postulate of the original argument will be critically examined.

There is some disagreement over what is meant by the concepts of diversity and stability. Chapter 3 will examine the different definitions and will focus on the conflict between the concepts of resilience and stable equilibrium. Specific definitions will be formulated for use in the remainder of the discussion.

Chapter 4 will outline some of the problems inherent in doing ecological research, such as species identification, ecosystem boundaries, and temporal limitations. An approach which temporarily circumvents these problems will be presented, and the need for a new hypothesis will be explored.

An alternative hypothesis will be examined in Chapter 5--diversity increases stability only within the context of environmental favorability. Also, it will be proposed that multiple hypotheses are needed to enrich the research options.

A summary and final comments in Chapter 6 will be followed by a discussion of the implications for resource management. It will be argued in Chapter 7 that until we know more about the relationship between species diversity and ecosystem stability, it would be wise to preserve representative ecosystems and diversity of species.

CHAPTER 1

THE HYPOTHESIS

The diversity-stability hypothesis, that diverse ecosystems are more stable, was gradually formulated during the first half of this century. Early mathematical models based on the equations of Lotka and Volterra, developed in the 1920s, indicated that simple systems would continually fluctuate.[1] In 1936, Clements theorized that community stability grew stronger as the integration of community functions increased. Odum's textbook in ecology (first edition, 1953) contained the claim of a diversity-stability correlation. And in 1958, Elton gathered together evidence that was intended to confirm a diversity-stability relationship.[2]

The hypothesis was readily accepted by many because it was supported by certain assumptions, empirical observations, and mathematical models. But also, the hypothesis was supported by a predisposition for purpose and order in nature that arose out of a belief in the goodness of nature.

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[1] Charles A. Elton, The Ecology of Invasion by Animals and Plants (New York: John Wiley and Sons, Inc., 1958), p. 130.

[2] Daniel Goodman, "The Theory of Diversity-Stability Relationships in Ecology," The Quarterly Review of Biology, Vol. 50 (1975), p. 238.

Nature Is Good

In recent years we have popularized the concept of the goodness of nature. This is reflected in the back-to-nature movement, which is, at least in part, a negative reaction to the impersonality of our technological society. In response, the environmental movement has done much to improve the reputation of nature. But perhaps most importantly, a belief in the goodness of nature is based on an aesthetic appreciation of wild places and wild things.

Creation Is Good

The idea that nature is good is not new. Some people have always considered nature to be good and have found some basis for their belief in theology: God created the "grass, the herb yielding seed, and the fruit trees" and "the beast of the earth" and "every living creature that moveth," and "God saw that it was good" (Gen. 1:11,21,25).

Nature, if the product of a good and perfect creator, must also be good and perfect. Taken to an extreme, there exists a certain rightness in nature, and man does nothing but interfere.

Nature as Adversary

With the appearance of man (characterized by free will) and his subsequent fall from grace, an adversative character was introduced into nature. Although God is good, he is also righteous, and he set about to use his creation to make man's way not so easy. When man was sent out into the wild, a flaming sword was set to keep him from returning to the garden, as if "out there" was a place to be avoided. (Some people still regard forests and mountains as forbidding places.) The ground was cursed for man's sake; "in sorrow shalt thou eat of it . . . thorns also and thistles shall it bring forth to thee" (Gen. 3:17-18).

The curse served to reinforce the initial commandment to subdue the earth "and have dominion over the fish of the sea, and over the fowl of the air, and over every living thing that moveth upon the earth" (Gen. 1:28). Today, many people still consider nature a thing to be conquered and subdued to the purposes of man; no doubt this attitude in the U.S. can be attributed partly to the pioneering spirit that set out to tame a new continent. Benign neglect has not been the American way.

Back to Nature

Thoreau, Muir, Teale, and other naturalists helped to change such attitudes. Their writings emphasized a respect for natural things and a natural order. Muir, especially, portrayed nature once again as God's perfect creation, to be revered and cherished.

With the realization that the attitude of conquer and subdue had begun to threaten the very web of life on which man depends, a new respect for nature was born. The environmental movement of the 1960s and 1970s stressed the limitations of the environment and portrayed the world as the spaceship "Earth."

> The closed economy of the future might similarly be called the "spaceman" economy, in which the earth has become a single spaceship, without unlimited reservoirs of anything, either

> for extraction or for pollution, and in which, therefore, man must find his place in a cyclical ecological system . . . .[3]

Many believed that if we protect nature, if we leave it alone to "do its thing," nature will take care of us. This naive approach did not take into account that the processes of nature may have been so disrupted by man that nature can no longer be maintained under a management plan of benign neglect.

That we once again value wild places and the natural order they embody is reflected in recent legislation designed to protect and preserve natural areas. Since 1872, the U.S. has had a national park system, but to supplement this protection, the Wilderness Act of 1964 was enacted to set aside areas "where the earth and its community of life are untrammeled by man, where man himself is a visitor who does not remain." In 1980, millions of acres in Alaska were set aside for parks, refuges, and wilderness areas; the legislation had popular support. Many other countries are following the U.S. example; Israel, for instance, has set aside 5% of its land area for natural habitat. Countries in Africa and South America are beginning to see the need to save natural areas now that they are rushing into the twentieth century; many already have national park systems.

Aesthetic Appreciation

Nature is considered good not only because it is the product of God's creative act, and not only because man is inextricably linked

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[3]Kenneth E. Boulding, "The Economics of the Coming Spaceship Earth," The Environmental Handbook, ed. Garrett De Bell (New York: Ballantine, 1970), p. 96.

with his ecosystem, but also because there is an aesthetic appreciation of nature. Nature as the subject of art has inspired some of the best writing and photography that has been published in recent years. Audubon, the magazine of the birdwatcher's Audubon Society, is a highly respected publication. Hiking, canoeing, camping, and other forms of recreation that bring the participant close to nature are increasing in popularity.

For many, nature is synonymous with wild things, plants and animals. Species diversity we have valued from childhood. As children, we sat on our parents' laps while they showed us picture books of animals. The more strange and diverse the animals, the more complex and interconnected their relationships (as we grew to recognize them), the more wonder and awe we felt for them. Wandering around in our backyards, we were fascinated by any new leaf, lizard, or bug that we happened to stumble upon, a fascination that many of us carried over into adulthood as we became biologists, ecologists, or weekend backpackers.

Our literature shows that we value diversity. When describing a particular geographical area, the diversity of species is usually mentioned, and the more species the better. The Great Smoky Mountains of Tennessee and North Carolina has been designated an International Biosphere Reserve particularly because of its 130 species of trees, 1400 species of flowering plants, 49 ferns, 325 mosses and liverwarts, 200 lichen, 1200 fungi, 50 fur-bearing animals, 200 birds, 75 reptiles and amphibians, and 74 species of fish.[4] This tremendous diversity must at least in part be the reason that this is the most heavily visited national park in the U.S.

The discovery of a unique species is a particular pleasure. For biologists, the pleasure is partly professional, but there is also a degree of satisfaction in having found a new life form; its uniqueness imparts a certain beauty.

This recognition of the value of unique species encourages protection. Now that environmental consciousness and conservation are playing such large roles in management decisions, there is much interest in preserving endangered species. The Endangered Species Act of 1973 was enacted to preserve the habitat of life forms faced with extinction.

It is in wild things that we find beauty and grace. The tendency is to equate beauty with goodness. Thus, nature is good because man depends on nature for his own existence and sees beauty in its life forms and in its wild places.

Purpose in Nature

Implied in the back-to-nature approach is the idea that the processes of nature must be beneficial. That would follow logically if one accepts that nature is good, for nature is not merely the separate physical entities that make up the living world but also the

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[4] S. R. Manning, "The Great Smokies," Sierra, October 6, 1977, pp. 6-8.

activities of nature--the changes, adaptations, and processes that organisms undergo, separately and in concert. If these processes of nature are good, then it is natural to assume that they must be doing something--they must serve some useful purpose.

Teleology

Although purpose in nature is not taken seriously by biologists today, the idea was long entrenched in Western philosophical thought. Early religious teachings contained the idea of a world created by a providential God; the natural processes, begun by him and operating in the world, were fulfilling some design or plan that he had in mind.

The Greek philosophers broke with this theological emphasis and described an immanent teleology. For Aristotle, nature was "a cause that operates for a purpose," a cause "in virtue of itself and not in virtue of a concomitant attribute."[5]

This notion of an immanent teleology was not unique to Western thought. Some expositions of Taoism, a Chinese mystical philosophy, also implied a concept of everything existing and changing according to some principle possessed by the thing itself.[6]

The new science. With the scientific method, brought into focus during the Renaissance, there was a shift away from teleological

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[5]Aristotle, The Pocket Aristotle, ed. Justin D. Kaplan (New York: Washington Square Press, Inc., 1958), pp. 26, 45.

[6]Wing-tsit Chan, The Way of Lao Tzu (New York: Bobbs-Merrill Company, Inc., 1963), p. 22.

explanations. With the new science, man began to test and experiment rather than just measure and observe as the Greeks had.[7] Leonardo da Vinci:

> But first I shall test by experiment before I proceed further, because my intention is to consult experience first and then with reasoning show why such experience is found to operate in such a way.[8]

Although Francis Bacon made no direct contribution to scientific knowledge, he persuasively advocated the new scientific method, stressing an examination and observation of a collection of facts with elimination of those that did not accompany the particular phenomena being questioned.[9]

With the Renaissance, there was a shift away from Aristotle's final cause (the function or purpose) to efficient cause (who or what caused it). For Galileo, efficient cause was the necessary and sufficient condition for something to occur. So there was a change of interest away from future-oriented explanations to those originating in the past, from teleological conceptions of nature to causal explanations.[10]

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[7] Hans Reichenbach, The Rise of Scientific Philosophy (Berkeley: University of California Press, 1951), p. 97.

[8] Leonardo da Vinci in W. T. Jones, A History of Western Philosophy (New York: Harcourt, Brace and World, Inc., 1952), p. 539.

[9] Lois N. Magner, A History of the Life Sciences (New York: Marcel Dekker, Inc., 1979), pp. 130-140.

[10] Mario Bunge, Causality (New York: World Publishing Company, 1963), pp. 32-33.

Persistence of design. But it was still possible to have a teleological, or a design-oriented, view after Galileo. For many philosophers, metaphysics had not been affected by the new science; for them, the ultimate nature of reality was not empirically observable. Leibniz in particular still accepted final causes and believed them to be God directed.[11]

Though Descartes accepted only efficient cause, design was still implicit in his metaphysics for he believed God to be the first cause while nature, once created, was governed by secondary causes of inner necessity and laws of motion.[12] But Descartes' conception of nature was not necessarily teleological in character. Cartesian physics excluded all idea of animation, spontaneity, and purpose. Rather, it was mechanistic in character; it considered no other explanations other than those used in mechanics.[13]

Newton did much to reenforce the mechanistic view of nature but also believed nature to be under the control of God, the "creator-mechanic." Mechanics did not give a complete view of the universe, he thought, but suggested the existence of a creator, which Newton considered not to be mechanical in nature.[14]

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[11] Andrew Woodfield, Teleology (Cambridge: Cambridge University Press, 1976), pp. 9-14.

[12] William A. Wallace, Causality and Scientific Explanation, Vol. 2 (Ann Arbor: University of Michigan Press, 1974), pp. 6, 14-16.

[13] E. J. Dijksterhuis, The Mechanization of the World Picture (Oxford: Clarendon Press, 1961), pp. 406-414.

[14] Robert H. Hurlburt, III, Hume, Newton, and the Design Argument (Lincoln: University of Nebraska Press, 1965), pp. 3-9.

Kant argued that teleology was necessary at least as a method in biology. He developed the idea of "purposiveness without purpose" to explain the regularity found in nature. Nature was teleological, he thought, in that it functioned as if it did have purpose, as if somebody had planned it. His idea is that when we study living things, we tend not to look for their cause, but we look ahead to some end that is being served. If we are studying a part of an organism (for example, an organ or gland), we feel we understand it when we discover what it does. At this empirical level, Kant emphasized, we examine the organ or gland as if it did have purpose; this does not mean that we accept the idea that someone or something actually designed it with this purpose in mind.[15]

Opposing views. With the theory of evolution and the growing knowledge of the universe, the separation between Descartes' first and secondary causes has widened to the point that it is possible to accept the world as independent from God the creator or sustainer.[16] Marxist philosophy took the final step and totally rejected the concept of teleological explanations although it did employ Kantian views of natural explanation. Under the dielectrical materialism of Marx and Engles, the world consists of matter and energy, which do not derive their existence from a transcendent source and which are governed by dielectrical laws. Nature is characterized by spontaneous emergence,

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[15] Jones, pp. 868-889.

[16] W. H. Thorpe, Purpose in a World of Chance (New York: Oxford University Press, 1978), p. 7.

unpredictability, and a clash of opposing forces, rather than being considered goal-directed.[17]

Louis Agassiz in the 19th century criticized both final causes and teleological explanations. As for explanations of organic structure from the perspective of purpose, ". . . there never was a more incorrect principle, leading to more injurious consequences, more generally adopted."[18] At the same time that Agassiz and others found the facts of biology to be incompatible with teleological explanations, they still could not altogether dispense with the idea of order and purpose of the universe, "a wider teleology" as Huxley called it.[19]

Darwin's theory of evolution dealt a severe blow to teleological explanations. From his studies in morphology, Darwin decided that structural similarities in a class of animals were not explained by referring to the function of the structures but by reference to a "common organization or pattern found in the ancestors of the class." Evolution, based on competition and "less-than-perfect" adaptation, excluded the idea of a purposeful design.[20]

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[17] Loren G. Graham, Science and Philosophy in the Soviet Union (New York: Alfred A. Knopf, 1972), pp. 26-52.

[18] Dov Ospovat, "Perfect Adaptation and Teleological Explanation: Approaches to the Problem of the History of Life in the Mid-Nineteenth Century," Studies in History of Biology, Vol. 2, eds. William Coleman and Camille Limoges (Baltimore: John Hopkins University Press, 1978), p. 43.

[19] Ospovat, p. 49.

[20] Ospovat, pp. 34-35.

Although evolution appeared to proceed by plan, Darwin saw that this could be explained in terms of causality alone. Natural selection reduced the apparent teleology of evolution to causality. "(C)hance in combination with selection produces order."[21]

A compromise. Carl Hempel used the concept of functional analysis as a compromise between teleological and causal explanations:

> . . . functional analysis seeks to understand a behavior pattern or a sociocultural institution in terms of the role it plays in keeping the given system in proper working order and thus maintaining it as a going concern.[22]

Functional analysis aims to show that a particular trait satisfies some need in a system by producing a certain state. But the information in a functional analysis does not give adequate grounds for expecting the appearance of a particular trait as opposed to any one of its alternatives.

Suppose we postulate, for example, that a dog can be in good health only if its blood circulates properly. If the dog is in good health, then the only conclusion we can make is that his blood is circulating properly. As a matter of fact, we know that the only way for the dog's blood to circulate is for its heart to be pumping, so we can also conclude that the dog's heart is working properly. But if we did not have this additional information, there is nothing

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[21] Reichenbach, pp. 199-200.

[22] Carl G. Hempel, "The Logic of Functional Analysis," Purpose in Nature, ed. John V. Canfield (Englewood Cliffs, N. J.: Prentice-Hall, Inc., 1966), p. 97.

in a functional analysis that requires the heart to be doing the circulating--there could have been alternative methods.
Thus functional analysis, even though it implies purpose, is not strictly teleological since it lacks a feedback mechanism that selects the particular trait that will lead to a specific state or goal.[23]

The appeal of teleology. In spite of the objections to teleology, the idea of purpose in nature persists. For instance, teleological language is still used; we talk in terms such as "purpose," "function," and "in order that." It may be that biologists have not given up such language because it is much easier to talk teleologically. For example, the purpose of the lungs is to take in oxygen, or the function of the heart is to pump blood, or animals eat in order to grow.[24]

In addition, teleology persists because people generally find a teleological nature particularly appealing; it fits a desire for order and purpose in life. Even if we are not theistic, we do not particularly like the idea of a random nature. As Einstein liked to say again and again, "God does not play dice" with the universe.[25]

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[23] Hempel, pp. 96-107.

[24] Canfield, p. 2.

[25] "The Year of Dr. Einstein," Time, February 12, 1979, p. 79.

Darwin in a letter to Asa Gray (Nov. 26, 1860) said,

> I cannot think that the world as we see it is the result of chance, and yet I cannot look at each separate thing as the result of Design. . . . I am, and shall ever remain, in a hopeless muddle.[26]

This desire for order and design in nature keeps the idea of teleology alive; nature is still generally thought of as out there doing something. This predisposition to find purpose in nature set the stage for the diversity-stability hypothesis.

Diversity-Stability

As ecological systems came under study, certain empirical observations, assumptions, and mathematical models suggested the idea that diverse systems are more stable than simple systems. The correlation between diversity and stability was supported by the lingering predisposition for purpose and order in nature.

Empirical Observations

Some observers noted that nature, if left alone, tended to increase diversity. Abandoned croplands quickly sprouted a multitude of weeds; fauna was gradually attracted to the increase in forage and shelter. If left undisturbed, specialization increased, which favored speciation.

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[26] Charles Darwin in Charles Birch, "Chance, Necessity, and Purpose," Studies in the Philosophy, eds. F. J. Ayolo and T. Dobzhansky (Los Angeles: University of California Press, 1978), p. 225.

Increasing diversity, especially increasing species number, seemed to be a natural process. With the acceptance of the idea that nature is good and that the processes of nature are also good and the predisposition for there to be purpose, it was possible to conclude that nature was doing something by increasing diversity. If nature was doing something and is not malicious, an increase in diversity must serve some useful purpose.

The diversity-stability connection began when other empirical observations found diversity and stability coincidental. Tropical rain forests, extremely diverse systems, were observed to be very stable--population numbers were not observed to fluctuate. In contrast, simple systems, for example, croplands which are typically monocultures, were noted to be especially susceptible to infestations and change in climate. The populations of simple systems were observed to fluctuate more than diverse systems. The conclusion was that diversity increased stability. For those still accepting a teleological nature, the purpose of increasing diversity was community stability.

Assumptions

Certain assumptions made the hypothesis more plausible:

1. It seemed to make sense for high diversity to buffer a system against disturbances. In a diverse ecosystem, a predator would have many food sources. If one of the prey species dropped in number, the predator could then turn to other sources of food and maintain its population. But in a simple system, where there may be only one source

of food, the predator would starve or migrate if the prey species dropped in number. The predator population would fluctuate along with the prey population in a simple system, but would remain stable in a diverse system. Likewise, if the predator population in a simple system were reduced, the prey population might reproduce uncontrollably, creating a plague. In a more diverse system, another predator could move in to check the expanding prey population.

The image is one of many parts dissipating a perturbation. High diversity buffers the system.

2. It would hardly make sense to anyone who presumed an orderly nature for a large number of species to develop if their presence resulted in instability. It seemed that instability and increasing species number could not occur simultaneously because the population fluctuations characteristic of unstable ecosystems would not provide the kind of environment that would favor speciation; shifting populations would favor generalization rather than specialization. In such unstable ecosystems, where populations fluctuate, it also seemed that extinctions of species would more likely occur.

3. It has been observed that organisms strive for survival; the struggle for existence is the cornerstone of evolutionary theory. If a single organism operates for self-preservation, it is easy to make the inference that communities, ecosystems, nature as a whole must also operate for survival. It seemed that the processes of nature, including increasing diversity, must work for self-preservation, and so stability.

Mathematical Models

Early mathematical models supported some of these assumptions. One predator/one prey systems, modeled on the equations of Lotka and Volterra, demonstrated instability. It was theorized that each member of such simple systems took turn controlling the population of the other so that the system continually fluctuated.[27]

Also, in his seminal paper on fluctuations and community stability (1955), Robert MacArthur measured foodweb diversity using a formula that Shannon and Weaver had devised to calculate information in communication. MacArthur thought this Shannon-Weaver formula would give some index of stability in a community.[28] Basically, he asserted that stability was directly related to the logarithm of the number of links in the foodweb; as the number of links increased, the stability increased. His mathematical models implied that diversity should stabilize an ecosystem because of the increased number of pathways for energy flow in the foodweb.[29]

A First Formulation

In 1958, Charles Elton accumulated the available fragmentary evidence into an argument for the basic assumption that a diverse ecosystem is more stable than a simple system:[30]

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[27] Elton, p. 130, and Paul Colinvaux, Introduction to Ecology (New York: John Wiley and Sons, Inc., 1973), p. 330.

[28] Goodman, p. 239.

[29] Robert MacArthur, "Fluctuation of Animal Populations and a Measure of Community Stability," Ecology, Vol. 36 (1955), pp. 534-535.

[30] Elton, pp. 145-149.

1. Mathematical models, specifically the Lotka-Volterra model, indicated that one predator/one prey systems fluctuate. Elton inferred that since simple systems were likely to fluctuate, complex systems would be more stable.

2. Experiments with simple systems of small organisms also exhibited fluctuating populations, a further demonstration of instability. The experiments Elton referred to were with protozoa, mites, waterfleas, and beetles, but he admitted that there was only one important set of experiments, those by the Russian ecologist G. F. Gause, and that these had not been repeated.

3. Habitats on small islands seem to be more subject to invasion than the more complex continental ecosystems. This was especially true for oceanic islands, but even very large islands exhibited susceptibility; as an example, Elton mentioned Great Britain, which had about twice as many deer and rodent species as at the time of the Norman Conquest. Elton inferred that more complex ecosystems resist invasion more strongly because the invading species face competition for food, breeding sites, and shelter.

4. Both invasions and outbreaks occur most often on cultivated land where the systems are usually monocultures. This constituted an empirical observation that simple systems are less stable.

5. The complex tropical rain forests are more stable in comparison to simple systems, such as the Artic. Less population fluctuations were observed in the tropics.

6. Orchards achieved stability when not treated with insecticide because the balanced relationship between pests and their natural

enemies would not be disturbed. The implication was that insecticides, by lowering diversity within an orchard, initiate reactions that led to instability. Elton mentioned orchards separately because he considered them communities halfway between field crops (simple) and woodlands (diverse).

This evidence and the diversity-stability hypothesis were at first accepted without much hesitation, most likely because the hypothesis fit early empirical observations and a predisposition for an orderly nature. But much more evidence was needed to actually confirm the conclusion that diversity increased stability.

Folk Science

It is not intended that the preceding argument for why the diversity-stability hypothesis was generally accepted be taken as an historical sequence of assumptions and inferences that actually led to a belief in the hypothesis. The average person that accepts the hypothesis would probably find much of this new to him. Nor is the implication intended that everyone accepted the hypothesis; there have always been those left unconvinced, and a great many people have probably not thought about it one way or the other. What is intended is a rational reconstruction, a possible scenario of how predispositions and scattered evidence could have been marshalled to make ready acceptance of the hypothesis possible.

That the hypothesis was accepted by many scientists and still remains a part of our folk science is obvious from the literature. Some current biology texts present the hypothesis without reservation (see Appendix).

It is a natural inclination to want species diversity, which many people value aesthetically, to be related to some good purpose. What better purpose than stability?[31] To believe otherwise would change the way in which the average person perceives his world. If the diversity-stability hypothesis were shown not to be true and if diversity were thought to promote instability rather than stability, increasing diversity could be portrayed as a cancerous growth upsetting the balance of nature. In that case, diversity would cease to be beautiful; it would be characterized as a malevolent phenomenon to be avoided (that is, unless we are able to stop judging diversity on the basis of stability and concentrate on other characteristics for which we also value the complexity of the living world).

Although the hypothesis was generally accepted when first formulated, several objections to the argument for the diversity-stability connection have cast serious doubt upon the hypothesis: Biologists no longer take seriously the idea of a teleological nature, so it makes no sense to ask what is the purpose of increasing diversity. That increasing diversity is a process of nature has not been proven; successionists point out that climax ecosystems possess fewer species than intermediate seral stages. Early empirical observations have been shown to be inadequate--tropical rain forests have been revealed, by man's intrusion, to be very fragile. Some counter assumptions do not

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[31]Of course, change is also good but not to the point of total instability; there must also be some degree of stability for the system to persist.

support the hypothesis; for example: (1) The interdependencies existing in complex systems could actually weaken the system rather than dissipate the force of a perturbation, (2) the overspecialization of species, which eventually occurs in a highly diverse system, makes individual species vulnerable, and (3) there is no reason to expect ecosystems to struggle for survival. Further mathematical models failed to support the earlier models upon which the hypothesis was partially based; in addition, some of the early models do not conform to reality for there actually are no extant one predator/one prey systems. Chapter 2 will deal with these objections in detail.

CHAPTER 2

CHALLENGING THE EVIDENCE

The evidence for the diversity-stability hypothesis consisted of mathematical models and experimental studies of simple ecosystems and observations of islands, croplands, tropical forests, and orchards. Charles Elton assembled this fragmentary evidence into an argument for the proposition that diverse systems are more stable. This conclusion was supported by certain assumptions and predispositions as outlined in the previous chapter. But Elton's classic formulation of the hypothesis argument has been seriously questioned during the last decade.

Mathematical Models

Elton's first assertion was that mathematical models of one predator/one prey systems exhibited population fluctuations, implying that such systems are unstable. But this conclusion is evidence for the diversity-stability hypothesis only if mathematical models of many prey/many predator systems show less fluctuation.

MacArthur's paper on fluctuations and community stability had been an attempt to show that these complex systems would be more stable by demonstrating that stability was directly related to the number of links in a foodweb. The assertion was that stability increased as the number of links increased.

As late as 1973, Colinvaux claimed that MacArthur had proved the hypothesis to be mathematically sound:

> That complex systems should be more stable than similar simple systems is susceptible to formal mathematical proof using information theory and may be accepted as true.[1]

Contradictory Models

Robert M. May, writing about the same time as Colinvaux, was not able to verify this conclusion. By constructing his own models and testing them using progressively larger numbers of species, May found that "(s)tability is not a general mathematical consequence of multispecies diversity per se."[2] Although in studying very simple systems he found vegetation-herbivore-carnivore systems to be more stable than vegetation-herbivore alone,[3] he also observed that in more diverse systems, increased complexity tended to cause systems to be, in general, less stable and never more stable than simple systems.[4]

A possible conclusion from this evidence is that instability in multispecies communities results from high foodweb connection and interaction, a direct contradiction to MacArthur.[5] This also contradicts

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[1] Paul Colinvaux, Introduction to Ecology (New York: John Wiley and Sons, Inc., 1973), pp. 237-238.

[2] R. M. May, "Stability in Multispecies Community Models," Mathematical Biosciences, Vol. 12 (1971), p. 74.

[3] R. M. May, Stability and Complexity in Model Ecosystems (Princeton: Princeton University Press, 1973), pp. 4, 107-108.

[4] May, "Stability," pp. 61-62.

[5] R. M. May, "Will a Large Complex System Be Stable?" Nature, Vol. 238 (1972), p. 414.

the assumption attributing a buffering quality to diversity; rather than a perturbation dissipating among the parts of a diverse system, the interconnedtedness could actually exaggerate the perturbation effects.

Inconsistencies

Although May's mathematical models do not support the hypothesis, neither are they conclusive for rejecting a diversity-stability connection--May concedes that empirical evidence points to a tendency for diversity and stability to occur together.[6] A possible reason for the inconsistency may be that diversity and stability are not directly related as many mathematical models assume but are associated through some other factor not represented in the models. (This idea is explored in more detail in Chapter 5.) McNaughton states that more recent mathematical studies are beginning to show that under certain conditions diversity does increase stability. He reasons that empirical studies must be the basis for resolving the inconsistencies.[7]

Probably the fundamental reason for the inconsistency between mathematical models and empirical evidence is that mathematical models do not accurately copy reality. May points out this problem:

> That stability may usually go with complexity in the natural world, but not necessarily in mathematical models is not really paradoxical. In nature we deal not with

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[6]May, Stability and Complexity, p. 75.

[7]S. J. McNaughton, "Diversity and Stability of Ecological Communities: A Comment on the role of Empiricism in Ecology," The American Naturalist, Vol. 111 (1977), p. 516.

> arbitrary complex systems, but rather with ones selected by a long and intricate process; mathematical theorems tend to deal with general complex systems, which are quite another matter.[8]

Austin and Cook recognized the same problem. In reporting their work on ecosystem stability using an abstract simulation they state, "The model is essentially a biologically rational abstract and makes no clain to represent a real world system."[9]

This criticism is also relevant for the one prey/one predator models upon which Elton based his confirmation of the hypothesis. Systems so simple are not actually found in nature, so it is appropriate to question their practical value.

Caution Recommended

Rosenzweig recommends caution in either accepting or rejecting the results of mathematical models. Since many of these models show instability following enriched diversity, discretion should be exercised when increasing the diversity of the natural environment, at least, he says, until such mathematical models are shown to be false.[10]

Goodman also recommends caution in accepting mathematical proofs either in favor of or opposed to the hypothesis for he says that all mathematical models are simplified abstractions and so always depart

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[8] May, "Stability," p. 74.

[9] M. P. Austin and B. G. Cook, "Ecosystem Stability: A Result from an Abstract Simulation," Journal of Theoretical Biology, Vol. 45 (1974), p. 437.

[10] Michael L. Rosenzweig, "Paradox of Enrichment: Destabilization of Exploitation Ecosystems in Ecological Time," Science, Vol. 171 (1971), pp. 385,387.

from reality. Mathematical models of ecosystems, he recommends, should be considered "an interesting branch of recreational mathematics, which, by coincidence, has appropriated some language which also appears in biology."[11]

Models Are Heuristic

Lawler sees some value in discovering the differences between mathematical models and reality. The question is not whether May's randomly constructed systems are more or less stable with changes in diversity, he says, but rather in how these systems differ from real ecosystems and how these differences affect stability.[12]

May thinks that mathematical models have practical value though they may not be able to confirm or deny the diversity-stability hypothesis. Although models cannot claim to be producing general ecological principles, he says, those which try for detail and specific descriptions are useful in individual projects of resource management and in making manageable a mass of experimental data. General mathematical models, May says, though they do not conform to reality, serve a heuristic function by raising general issues for discussion.[13]

The minimum that recent mathematical models have accomplished is to show that the implication of Elton's first argument in support of

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[11] Daniel Goodman, "The Theory of Diversity-Stability Relationships in Ecology," The Quarterly Review of Biology, Vol. 50 (1975), p. 257.

[12] L. R. Lawlor, "A Comment on Randomly Constructed Model Ecosystems," The American Naturalist, Vol. 112 (1978), p. 446.

[13] May, Stability and Complexity, pp. 10-12.

the hypothesis is unsubstantiated--many prey/many predator models do not possess more stability than one prey/one predator models.

Experiments

Further empirical tests seem to refute the inference of Elton's second statement (that experiments with simple systems demonstrate instability). Again, the implication is that complex systems would be more stable, but that inference is valid only if experiments with complex systems exhibit a greater degree of stability. But many experiments do not show this.

For example, in their perturbation experiments with old fields, Hurd et al. found that increased diversity at the primary producer levels (plant and herbivore) caused decreased stability at the next higher level.[14] In their studies of the introduction of exotic species for biological control of pests, Turnbull and Chant concluded that ecosystems may adjust more quickly and with fewer effects if only one species is introduced rather than several;[15] the conclusion could be that an increase in diversity (with the introduction of other species) causes instability.

Paine conducted a study in which one species was removed from a complex intertidal community. He concluded that complexity had very

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[14] L. E. Hurd et al., "Stability and Diversity at Three Trophic Levels in Terrestrial Succession Ecosystems," Science, Vol. 173 (1971), p. 1136.

[15] A. L. Turnbull and D. A. Chant, "The Practice and Theory of Biological Control of Insects in Canada," Canadian Journal of Zoology, Vol. 39 (1961), p. 733.

little influence in correcting short-term changes, thus contributing very little to stability.[16]

Paine was obviously expecting this complex community to withstand the loss of a species if the hypothesis is true, but to use a perturbation such as the removal of a species prejudices the experiment against the hypothesis so that the results are questionable--the diversity has been lowered artifically so a decrease in stability should have been expected. An environmental perturbation may have been a better condition under which to study the effect on stability rather than an artificial change in diversity.

Further evidence against the hypothesis was provided by Luckinbill who concluded in experiments using three ciliate protozoans as prey for Didinium that increasing prey diversity destabilizes but also the individual characteristics of prey have more influence than simply the number of species. Didinium coexisted with the smallest protozoan alone, but when one or both of the larger prey were added to the system, stability decreased. It appeared that the Didinium and the smallest prey were able to coexist alone because the prey was a small target and so was not depleted. When larger prey were introduced, the Didinium thrived, producing larger densities and more vigorous individuals, which depleted the first prey as well as the introduced prey.[17]

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[16] R. T. Paine, "A Note on Trophic Complexity and Community Stability," The American Naturalist, Vol. 103 (1969), p. 1136.

[17] Leo S. Luckinbill, "Regulation, Stability, and Diversity in a Model Experimental Microcosm," Ecology, Vol. 60 (1979), pp. 1098-1102.

Problems in Experimental Design

The studies of Turnbull and Chant, Luckinbill, and Paine raise particular problems about experimental design. In the case of Turnbull and Chant and Luckinbill, the artificial introduction of a new species should be considered a perturbation rather than an increase in diversity, for an invasion of a species is an external impact to a system. If introduction of a species is considered a perturbation, then the conclusion of Turnbull and Chant reduces to the statement that ecosystems adjust more quickly with a single disturbance rather than with many disturbances, an obvious occurrence. For Luckinbill, the introduction of larger prey for the *Didinium* is a perturbation which allows the predator to expand beyond the balance of the system; the introduction was not simply an increase in diversity. For both studies, the correlation between diversity and stability is too vague to make any definite conclusions.

In Paine's experiment, the removal of a species was intended to be a perturbation, and although that is an appropriate disturbance, it appears that the results have been weighed against the diversity-stability hypothesis. By removing a species from an ecosystem, the diversity has been artificially lowered, and according to the hypothesis, instability *should* be more likely. It should not have been particularly surprising that instability ensued in Paine's study. The decrease in diversity due to the removal of a species should make a system more fragile if the hypothesis is true. Any conclusion from Paine's study would then be confused by the fact that the diversity was artifically lowered at the time of trying to determine its effect on stability.

Observations of Complex Systems

Empirical observations also contradict Elton's implication that complex systems would be more stable. May gives several examples of the invasion and disruption of complex communities: Japanese bettle, European gypsy moth, and the Oriental chestnut blight.[18] Murdoch et al. found in a study of three old fields in southeast Michigan that rearrangement of species and species abundances occurred more in highly diverse fields than in simple ones.[19]

Watt concluded in his statistical studies of insect populations that the more a species' environment is filled with acceptable food sources (high diversity) the more likely the species is to increase in number and become unstable. He speculated that a species which has a wider variety of food sources wastes less energy in searching for food and has more energy for reproduction and thus can expand more rapidly up to some natural limit past which it becomes unstable. On the other hand, he admits that there may be no connection between the expanding population and available food sources; secondary food species may be used only when there is a population fluctuation in the predator species

[18] May, Stability and Complexity, p. 39.

[19] William W. Murdoch, Francis C. Evans, and Charles H. Peterson, "Diversity and Pattern in Plants and Insects," Ecology, Vol. 53 (1972), p. 825.

for other reasons. Under normal conditions these secondary food sources may exist sympatrically with the predator and not be utilized.[20]

Yet Not Conclusive

Though the empirical evidence does not support Elton's second argument, still the evidence is not conclusive for completely rejecting the diversity-stability hypothesis either, for there is evidence supporting it as well. In successional studies in a temperate ecosystem and grassland studies in a tropical ecosystem, McNaughton found evidence that diversity stabilizes the functional properties of the communities. But he also recognizes the inconclusiveness of all evidence gathered to date for he facetiously adds, "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."[21]

Islands

Elton's third argument, that simple island systems are more subject to invasion than more complex continental ones does not deal with the issue that islands may simply be more vulnerable. Islands may be susceptible to invasion because of geographical limitations

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[20] K. E. F. Watt, "Comments on Fluctuations of Animal Populations and Measures of Community Stability," The Canadian Entomologist, Vol. 96 (1964), pp. 1436-1440.

[21] McNaughton, pp. 521-522.

and/or genetic weaknesses in inbred populations, rather than because of low diversity.[22]

Croplands

Goodman questions Elton's fourth proposition that croplands (mostly monocultures) are susceptible to invasions and outbreaks. He argues that croplands may well achieve equilibrium if allowed to do so; crop rotation and insect control may be preventing equilibrium from occurring.[23] It may also be that agricultural lands are part of a larger system including man, which taken as a whole exhibits stability.

May claims that Elton's fourth point is irrelevant in that it is actually a comparison of artificial systems to natural, not simple to complex. But to counter Elton's argument anyway, May mentions the east coast marsh grass, a natural stable monoculture.[24]

Tropical Forests

Elton's fifth argument, that complex tropical forests exhibit more stability than simple ecosystems in the north, is not supported by the factual evidence. Though research has been inadequate, enough has recently been done in the tropical rain forests to raise doubts that this extremely complex system is really stable.

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[22] Goodman, p. 238.

[23] Goodman, p. 238.

[24] May, Stability and Complexity, p. 173.

Some writers argue that the tropical forests only appear to be stable--due to the forests' great complexity and manpower limitations in doing research, it may be that many populations fluctuate and become extinct without our even knowing of them.[25] The difference in numbers of species observed between northern and southern latitudes may simply be due to a lack of information caused by too little empirical research.[26]

The Amazon

Evidence being gathered from the Amazon indicates that the tropical forests are actually very fragile systems. The tropical rain forest of the Amazon is the world's most complex system with 5000 plants for every animal and a forest diversity of 100-250 species of trees on 5 acres, compared to 10 species per 5 acres for a U.S. woodland. It took 60 million years for this forest to develop to a steady state equilibrium, yet it is an equilibrium that is precariously balanced.

The forest is very susceptible to collapse because the layer of litter humus, which nourises the vegetation, is only 3 inches thick; the land has been described as a forest on top of a desert. Nutrients are not in the soil but in the foliage, as much as 70%. This precarious balance is also a result of the forest's participation in creating its own climate; rainfall is directly cycled through the forest. As trees are cut during exploitation, not only are the nutrients removed but

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[25] Goodman, p. 239.

[26] Colinvaux, p. 238.

the climate as well. Rainfall is reduced, water sources dry up, and the ground is baked hard and dry. For large clearings it is estimated that it will take 100-500 years for the forest to recover, if it ever does.[27]

Fragile Tropical Species

Gomez-Pompa et al. say that tropical forests, such as the Amazon, are unable to regenerate under current abuse. In contrast, more temperate forests are more likely to survive because they contain tree species that are represented by a large number of individuals scattered over a large area and that have developed seeds adapted to long periods of inactivity. As a result, individual tress in the temperate areas are more likely to survive than in the tropics. An isolated tree in the tropics stands little chance of survival because of the "complex and delicate net of relationsips of each individual with the environment."[28]

Holling supports the idea of a stable environment producing a fragile species. It appears to him that species taken from a stable climate, such as the tropics, would not easily survive if faced with severe climatic changes even though in their natural habitat they appear quite stable.[29]

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[27] Anne LaBastille, "Heaven or Hell," Audubon, November 1979, pp. 68-97.

[28] A. Gomez-Pompa, C. Vizquez-Yanes, and S. Guevara, "The Tropical Rain Forest: A Nonrenewable Resource," Science, Vol. 177 (1972), pp. 764-765.

[29] C. S. Holling, "Resilience and Stability of Ecological Systems," Annual Review of Ecology and Systematics, Vol. 4 (1973), p. 18.

It may be that the tropical rain forests, in spite of their fragility, have exhibited great stability for so long because of the greater environmental constancy of the tropics. Now faced with the artificial disturbances caused by man, the forests face extinction, and we must reevaluate our preconception that these forests are stable complex systems.

Orchards

Finally, Elton's sixth argument, that a reduction of diversity in orchards through the use of insecticides causes instability, meets the same criticisms as his fourth proposition. Orchards are artificial monocultures and thus not comparable to natural systems but, if left alone, may achieve stability within the larger ecosystem.

Succession

As stated in the previous chapter, part of the argument for the diversity-stability hypothesis is the observation that nature tends to increase diversity as a normal process. But Ehrenfeld points out that diversity is not always found to increase with succession. Assuming that natural systems move toward stability and organization, it should follow from the diversity-stability hypothesis that each seral stage would be more diverse than the preceeding one. Empirical evidence does not always support this idea; a climax forest is not a more diverse system compared to earlier stages of forest succession. A wider variety of trees, undergrowth, and fauna are present in the intermediate stages of forest development because successional stages increase in diversity up to some saturation point at which certain species become dominant and begin to exclude other species.[30] Goodman says that if there is something that increases diversity, then there must also be an opposing force which balances things at this point of saturation.[31]

Others argue that the end decrease in diversity is purely observational. In the process of succession, as a new niche opens, immigration of potential inhabitants occurs. This is followed by a takeover of the most successful. What is observed, then, is an increase in diversity followed by a drop in species number due to competition, not the result of diversity-stability interactions. The successful organisms must be given time to sort themselves out by competitive exclusion.[32]

Although this scenario is probably like what happens in nature, it does not serve to counter the argument that diversity does not always increase with succession. What is being referred to here is the immediate reaction to a new niche and not the long gradual process of succession.

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[30] David M. Ehrenfeld, "The Conservation of Non-Resources," American Scientist, Vol. 64 (1976), p. 651.

[31] Goodman, p. 247.

[32] Joseph H. Connell and Eduardo Orias, "The Ecological Regulation of Species Diversity," The American Naturalist, Vol. 98 (1964), p. 408.

Counter Assumptions

One assumption that added to the believability of the diversity-stability hypothesis was the idea that diversity buffers a system, many parts dissipate an impact. But many scientists argue that interconnectedness also means interdependencies, which actually weaken a system.

In their work with mathematical linear models, Gardner and Ashby noted that complex systems exhibit stability up to some critical degree of connection, after which an increase in diversity suddenly causes instability.[33] This could be because a perturbation in an overly dependent system may cause a rash of population fluctuations.

Futuyma stresses that interdependencies weaken a system. He argues that with increasing complexity there will be many interdependent relationships; the population of one species will determine the population of several others. This creates instability, at least on a local level. A perturbation in a simple community of independent species might cause the extinction of an inflexible one, but a perturbation in a complex system, with its greater interconnectedness, might cause the extinction of an inflexible species plus some other species associated with it.[34]

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[33] Mark G. Gardner and W. Ross Ashby, "Connectance of Large Dynamic (Cybernetic) Systems: Critical Values for Stability," Nature, Vol. 228 (1970), p. 784.

[34] Douglas Futuyma, "Community Structure and Stability in Constant Environments," The American Naturalist, Vol. 107 (1973), p. 444.

If interconnectedness is a weakening factor, this could explain why a final drop in diversity is observed when a system approaches climax. The point at which interconnectedness becomes a liability could be the saturation point at which any beneficial effects of diversity are counterbalanced.

A second assumption was that it was not possible for diversity to be increasing at the same time that it caused instability. It seemed that instability and increasing species number could not occur simultaneously because the population fluctuations characteristic of unstable ecosystems would not provide the kind of environment that would favor speciation; shifting populations would favor generalization rather than specialization. The first objection to this is that even if it were shown that diversity did not occur with instability, it would not follow that the hypothesis is true--it would not follow that diversity causes stability. There may be no correlation between diversity and stability at all; stability might occur without diversity.

A second objection to this assumption is that it is possible to conceive of an increase in diversity causing instability not only because of the weakening effects of the increasing internal dependencies of intermediate systems but also because of the overspecialization of more mature systems. Edwin O. Willis, an American zoologist working in Brazil, concluded from bird population studies that extinction depends upon both scarcity and specialization. An environmentally stable system allows specialization to occur along with a smaller number of individuals within a species. Yet it is the habitat of the specialized species that is most easily destroyed. With the demise of these species, he says, instability ensues because the accompanying specialized predators may be left with too little prey. Specialization, a characteristic of increased diversity, seems to destabilize the system.[35]

The third assumption was that since individual organisms strive for survival it can be inferred that communities and ecosystems also strive for survival, and increased diversity may be a way to do that. The problem here is that the inference does not hold. What may be true for a single organism does not necessarily hold true for higher biotic groupings. Although it is true that single organisms struggle for survival, an ecosystem could likewise struggle for survival only if there were some group consciousness within which each organism somehow recognized its link with other organisms and helped to preserve the ecosystem.

In short, the assumptions used to support the hypothesis can be argued against using counter assumptions which are equally plausible. I do not claim the original assumptions are necessarily wrong, only that they do not give sufficient reason for accepting the hypothesis.

Inconclusive Evidence

The diversity-stability hypothesis is based on fragmentary evidence consisting of certain mathematical models, assumptions, and

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[35] "The Ark is Sinking," Win, February 1979, p. 10.

empirical observations. It was readily accepted partly because of a desire for order and purpose in nature based on a belief in the goodness of nature.

But a teleological nature is no longer considered seriously by many scientists--the theory of evolution based on competition and selective adaptation showed that the natural world does not function according to some end purpose. For a future goal to determine current events is opposed to the direction of time; therefore, causality is the only practical method of scientific explanation. Within that context, the only way purpose can work is for there to be a plan; the organism must possess anticipation. That appears to happen in some cases; for example, many animals store food for the coming winter; they act as if they had a plan. To say that they actually have a plan is an analogy to human behavior, but other organisms are not conscious. Such an analogy is a pseudo-explanation, so it would be false to say that an organism or nature has some purpose in mind.[36]

The predisposition for finding purpose in nature, which made the diversity-stability hypothesis attractive to many, has no scientific basis. Therefore, it makes no sense to ask what is the purpose of diversity. But more fundamentally, that increasing diversity is a function, or a process, of nature has not been demonstrated; successional observations have shown that diversity does not always increase with succession.

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[36] Hans Reichenbach, The Rise of Scientific Philosophy (Berkeley: University of California Press, 1951), pp. 194-195.

Neither does Elton's classical argument provide adequate proof for the hypothesis: The instability shown by mathematical models of simple ecosystems is inconclusive because models of complex systems do not exhibit any greater stability. Empirical evidence, gathered from both simple and complex systems, is relatively inconclusive. Islands may exhibit vulnerability not because of low diversity but because of geographical and genetic limitations. Tropical rain forests with their greater complexity are no longer thought to be very stable. And Elton's examples of orchards and croplands (simple, unstable systems) seem irrelevant, for they are artificial communities.

Although the argument for the hypothesis has been shown to be inadequate, the evidence does not refute the idea that diversity and stability are somehow related: Some mathematical models and empirical tests and observations do show diversity and stability occurring together. Mathematical models and theoretical arguments to the contrary do not refute some kind of correlation, for everyone is willing to accept exceptions. Empirical evidence cannot refute or confirm a correlation unless tests and observations can be consistently repeated and anomalies explained. That has not yet been achieved.

Until a more complete biology has been structured, within which a correlation can or cannot be incorporated, the diversity-stability hypothesis will at least continue to serve a heuristic function. One function it has served is to provide the basis for a discussion of what is meant by the concepts of diversity and stability.

CHAPTER 3

DIVERSITY AND STABILITY CONCEPTS

The concepts of diversity and stability have been explored in the debate over the diversity-stability hypothesis. There seems to be a consensus on what is meant by diversity, but there is much incongruity and contradiction in the different definitions for stability. It is generally agreed that more research is needed about diversity-stability relationships, but it would be helpful to have clearly defined concepts within which to evaluate the research.

Diversity

For a time, diversity was regarded as simply numbers of species. But as more research was done, ecologists realized that this was too simplistic a definition, and concepts such as evenness and complexity were introduced into the meaning of diversity.

Evenness

Hurlburt defined diversity as a function of the number of species, which he called "species richness" or "species abundance," and the evenness with which the individuals are distributed among the species present, "species evenness" or "species equitability.[1] For Hurlbert,

[1]Stuart H. Hurlbert, "The Nonconcept of Species Diversity: A Critique and Alternative Parameters," Ecology, Vol. 52 (1965), pp. 577-578.

then, diversity was, not simply the number of species present, but it was also a function of how uniformly the entire population was distributed among the species.

Support for this definition was provided by Nybakken. In his studies of nudibranch mollusks in an intertidal community, he found that high diversity usually indicated high evenness of numbers among the various species. Both diversity and evenness he mathematically defined as functions of total number of individuals and numbers of individuals of each species.[2]

Conceptual implications. Whether evenness is considered a partial measure of diversity will affect the classification and evaluation of empirical evidence. Take for example a community whose starting point is several dominant species with large numbers and several rare species. Because of competition, some of the rare species may succumb leaving behind a greater resource base for the remaining rare species, which then have a better opportunity to grow and reproduce, given other right conditions. Eventually the numbers of the predominant species and those that have been scarce may tend to be equalized.

In such an example, the number of species would decrease while species evenness increased. An observer who defines diversity simply as species number would classify this latter state as less diverse,

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[2] J. Nybakken, "Abundance, Diversity, and Temporal Variability in a California Intertidal Nudibranch Assemblage," Marine Biology, Vol. 45 (1978), p. 137.

while someone who defines diversity as a function of both species number and species evenness might classify the end state as possessing the same or a higher diversity. The complications when trying to equate diversity with stability are obvious.

Correct proportions. If the concept of evenness is integrated into a definition of diversity, some modification of evenness is necessary since evenness of species populations is not practical for real ecosystems. Possibly species within a single trophic level could have equal populations, but higher trophic levels must have smaller numbers. If prey and predator populations had the same number of individuals, the system would not persist for very long. Rather than evenness, correct proportions is the more practical concept.

MacArthur implied that diversity is partially a function of correct proportions. He included in his paper on stability and complexity that a simple increase in the number of species will increase stability only if the number of prey species for each predator species remains constant.[3]

Of course the correct species proportions for an ecosystem would not be specific ratios; the numbers of both prey and predator would vary over a range. The number of prey would possibly range between a low, in which the prey are threatened with extinction (because the predators would consume the few that are left) and the predator would

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[3]Robert MacArthur, "Fluctuations of Animal Populations and a Measure of Community Stability," Ecology, Vol. 36 (1955), p. 535.

then starve or migrate, and a high, in which the predator population would not be able to control the prey and the prey would begin to deplete the resources on which it subsists. The number of the predator would probably range between a low, in which it could not check the expansion of the prey, and a high, in which it would deplete the prey population. There is probably some optimal proportion within that range, but I see no simple way to arrive at that ratio.

It is obvious that proportions of numbers needs to be a part of the measure of the diversity of an ecosystem, at least to give an indication of the degree of participation of a particular species. But this implies that there must also be a measure of the interactions of species.

Complexity

Since ecology includes the study of interactions of organisms with each other and their environment, many scientists find that diversity as simply numbers of species and their population proportions was still too simplistic for studying real ecosystems. Most ecologists now think that diversity should include some measure of the complexity of the interactions between species.

May defines complexity as the number and nature of individual links in the foodweb.[4] Since most foodweb dependencies are between different species, this implies that complexity is inextricably related to species number.

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[4] R. M. May, Stability and Complexity in Model Ecosystems (Princeton: Princeton University Press, 1973), p. 3.

Significance of complexity. An example will show the significance of defining diversity as a function of complexity. Some studies indicate that the average number of trophic levels in an ecosystem is approximately three. One reason for so few trophic levels may be that long food chains result in severe population fluctuations that do not allow the highest predators to persist. A predator in a long linear food chain with few parallel dependencies must be fairly specialized and have few interactions other than with a primary food source.[5] If this primary food source becomes scarce, the predator population will fluctuate drastically. This then would be an example of an unstable system with a large number of species. But a system with a few trophic levels, where the predators have several food sources and where there are many interactions between parallel species, would be a more complex system of possibly the same number of species exhibiting a greater stability. In this example with two systems of equal numbers of species, it seems that complexity (specifically interconnectedness) is the determining factor for stability.

The diversity-stability hypothesis would not be supported by this example if diversity is defined as merely numbers of species, for the comparison demonstrates the possibility of having equal numbers but different levels of stability. There must be something else increasing the stability of the latter system besides numbers of

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[5] R. M. May, "The Evolution of Ecological Systems," Scientific American, Vol. 239 (1978), pp. 172,175.

species. If diversity includes the concept of complexity, then a system with fewer trophic levels and more parallel interactions would be considered more diverse while a long linear system would be considered more simple. If diversity is considered to be species number only, then it would have no correlation with stability in this particular example.

An unresolved contradiction. This example and MacArthur's paper, in which he claimed stability increased with the number of links in the foodweb, contradict Futuyma's argument against the diversity-stability hypothesis (Chapter 2). Futuyma claimed that interdependencies and interconnections actually create an unstable situation; such complex systems, he thought, would have the potential for quickly spreading disruption, for the fluctuation of a single species would cause others to be disturbed.

This is the same contradiction of assumptions mentioned in Chapter 2. On the one hand, it seems true that a complex system of many dependencies would be less stable, for if one species fluctuates, several others would also be affected. But on the other hand, it seems equally true that interdependencies and interconnections could serve to buffer the impact of a perturbation, assisting the fluctuating species to regain its equilibrium. This remains an unresolved issue.

A Consensus

Goodman agrees that there is a range of definitions for the concept of diversity. Diversity is the number of species and their relative abundances, but, he adds, in order for diversity to affect stability, the definition must also take into account the interactions between species.[6]

It seems to be a consensus that diversity is a function of interactions, species number, and correct proportions. Possibly the hypothesis should be referred to as the complexity-stability hypothesis instead, but if diversity is considered to include complexity, then the more traditional name, diversity-stability, can be maintained. It is clear that when speaking of diversity-stability relationships, a simple counting of species is inadequate.

Stability

Definitions for stability range from "constant numbers" to "the ability to bounce back after a disturbance" to simply "no extinctions." There is much disagreement over what is meant by stability, and so although a consensus has been reached on diversity, there has been none for the concept of stability.

Population Fluctuations

For Colinvaux, stability is rather inflexible: The number of individual living things remains constant from year to year.[7] A lack of population fluctuations then is a sign of stability.

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[6]Daniel Goodman, "The Theory of Diversity-Stability Relationships in Ecology," The Quarterly Review of Biology, Vol. 50 (1975), p. 240.

[7]Paul Colinvaux, Introduction to Ecology (New York: John Wiley and Sons, Inc., 1973), p. 237.

But like the first definitions for diversity, this first definition of stability is too simplistic when dealing with real ecosystems. Even without perturbations to an ecosystem, fluctuations in populations would be expected as a natural consequence of internal dynamics.

Stable Equilibrium

Others define stability, not as maintaining constant numbers, but rather as returning to an equilibrium state. May says a system is stable if "when . . . disturbed it returns to its equilibrium state after a temporary disturbance."[8] For Holling, stability is "the ability of a system to return to an equilibrium state after a temporary disturbance."[9]

The equilibrium that the system returns to is a dynamic balance of opposing forces. Herbert Spencer described this biological equilibrium in the 19th century:

> Every species of plant and animal is perpetually undergoing a rhythmical variation in number--now from abundance of food and absence of enemies rising above its average, and then by a consequent scarcity of food and abundance of enemies being depressed below its average . . . amid these oscillations produced by their conflict, lies the average number of species at which its expansive tendency is in equilibrium with the surrounding repressive tendencies.[10]

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[8]May, Stability and Complexity, p. 13.

[9]C. S. Holling, "Resilience and Stability of Ecological Systems," Annual Review of Ecology and Systematics, Vol. 4 (1973), p. 14.

[10]Herbert Spencer in C. B. Huffaker and P. S. Messenger, "Population Ecology--Historical Development," Biological Control of Insect Pests and Weeds, ed. Paul DeBack (New York: Reinhold Publishing Corporation, 1964), p. 54.

Hurd et al. add another factor to the definition of stable equilibrium: maintaining a base state. Stability they say is "the ability to return to and maintain a base state after a disturbance." The degree of stability is, therefore, based on the amplitude of fluctuations, the quickness of response, and the rate at which a population fluctuation is dampened.[11]

Although Hurd et al. do not describe their base state as an equilibrium, I assume that what they have in mind for the base state is the same kind of equilibrium referred to by May and Holling. It is this more complete definition that I will use for stable equilibrium.

Westman refers to this definition of stability as "resilience," for he defines resilience as a measure of "the degree, manner, and pace of restoration of initial structure and function" after a disturbance.[12] In fact, a stable equilibrium does fit the commonly accepted definition for resilience (the ability to recover from change). But I prefer to continue to call this definition of stability "stable equilibrium" to more easily distinguish it from Holling's resilience, which I discuss in the next section.

Westman restricts his definition of stability to "the pattern of fluctuations in a relatively unimpacted ecosystem."[13] But Westman

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[11] L. E. Hurd et al., "Stability and Diversity at Three Trophic Levels in Terrestrial Successional Ecosystems," Science, Vol. 173 (1971), p. 1134.

[12] Walter E. Westman, "Measuring the Inertia and Resilience of Ecosystems," Bioscience, Vol. 28 (1978), p. 705.

[13] Westman, p. 705.

cannot be right, for stability is an attribute, not a pattern of fluctuations. I propose to use "the pattern of fluctuations while unimpacted" as the base state of a stable equilibrium. The base state would be determined by empirical observation. Whether a system has returned to a base state after a disturbance could then be determined by whether it is again exhibiting the former pattern of fluctuations while unimpacted.

The definitions for stable equilibrium say that a system is stable if it returns to the base state after a disturbance. This does not preclude the idea that a system may be so stable that it recovers after the onset of a disturbance yet before the disturbance has ended, but a system would not have to possess that ability to be classified as a stable equilibrium. In the case of a permanent change that the system is unable to recover from, we could say that the system itself has changed so that now a new system exists with a different base state. Persistence based on more than one base state is the kind of behavior Holling refers to as "resilience."

Resilience

Holling defines resilience as the ability of systems "to absorb change and disturbance and still maintain the same relationships between populations or state variables."[14] Although Holling says that resilience is a measure of persistence, he does not mean to equate

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[14]Holling, p. 14.

the two, for later he says that resilience is the property of a system, and persistence, the result.[15]

The difference between stable equilibrium and resilience is that stable equilibrium includes the concept of returning to a specific base state, and since it also includes the concept of maintaining the base state, it also designates systems that have few fluctuations. Holling specifically relates stable equilibrium to a lack of fluctuations, which admittedly fits the commonly accepted meaning of "stability." He says of a stable equilibrium, "the more rapidly it returns, and with the least fluctuation, the more stable it is."[16]

Holling's resilience, on the other hand, does not include the idea of returning to a specific base state, but rather describes systems which continually fluctuate with large amplitude and which persist by moving between, what Holling calls, domains of attraction (regions within which stability occurs).[17]

Examples of Resilience

Holling gives examples of highly unstable fluctuating systems (budworm-spruce forest community, Pacific salmon) which because of their population fluctuations produce stable cycles in which members

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[15]Holling, p. 17.

[16]Holling, p. 17.

[17]Holling, pp. 3, 19.

of the community are maintained short of extinction. In the budworm-forest community, periodic drops in numbers of budworm allow the forest to regenerate.[18] On the other hand, during population expansion, say Turnbull and Chant who also cite the example, the spruce budworm attacks trees which otherwise would dominate the forest. Without the disturbance by the spruce budworm, the community would reach a climax stage in which many tree species would be eliminated.[19]

Both Holling and Preston use the example of the Pacific salmon to show that fluctuations are sometimes necessary for survival.[20] The salmon occur in "salmon runs," which have wide fluctuations. From the standpoint of canneries, the population is unstable, but this instability may be necessary for the salmon's survival, they say. During years in which big runs occur, predators (bear and trout) cannot consume all the salmon, so some get through to spawn and eggs are allowed to hatch. If this level of population were kept at a constant equilibrium, the predator species would expand to meet the food supply and the salmon population would collapse from overexploitation. But lean years alternate in which small salmon runs cause predators to starve or migrate in search of food, preventing the predator populations from expanding. In this way a prey species with a shorter life

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[18] Holling, p. 15.

[19] A. L. Turnbull and D. A. Chant, "The Practice and Theory of Biological Control of Insects in Canada," Canadian Journal of Zoology, Vol. 39 (1961), p. 733.

[20] Frank W. Preston, "Diversity and Stability in the Biological World," Brookhaven Symposium in Biology, Vol. 22 (1969), p. 6.

span can, through regular cyclic fluctuations, restrict its predator populations to levels that allow the prey species to survive.

Preston also uses the example of the cicada 17-year cycle to show that fluctuations are necessary for survival. With the cicada's appearance, the predators become saturated and would expand to eventually decimate the cicada population if the cicada did not disappear for much of the time.[21]

There is an implication, in especially the salmon and the cicada examples, that the prey are controlling the predator populations by fluctuating. But it could be that the cycle is caused by the predator populations. For example, in years when the salmon population is large, the predator populations expand, reducing the salmon population for the next year. Until in years when the salmon population is very low, the predators starve or leave the area in search of food. The salmon are then once more able to expand to a large population. So we could just as well say that predator populations control the prey population fluctuations. But also, the salmon control the predator populations in turn, though not through periodically lowering its own population, but rather the salmon expand when allowed to by the absence of predators, thus causing the predator populations to expand once again, preventing the predator populations from completely disappearing.

So there are no grounds for saying simply that the prey population controls the predator population, or vice versa; rather, both

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[21]Preston, p. 7.

populations fluctuate in balance with each other. Such systems, Holling defines as resilient, for they persist; they are not stable equilibriums, he says, because they do not return to and maintain specific base states.

Stable Equilibrium vs. Resilience

Holling sees equilibrium stability and resiliency as opposed to each other. He says, for instance, that to achieve a stable equilibrium might actually cause extinction and that instability may introduce resilience and thus the capacity to persist.[22]

In an attempt to relate diversity to what he considers to be two different concepts, Holling goes on to say that diversity does not reduce the fluctuations of a stable equilibrium but does increase the resilience of a system. So he concludes that May's mathematical models correctly show that diverse systems fluctuate no less than simple systems. But, Holling says, even though diverse systems fluctuate just as much, or more than, simple systems, diverse systems may have greater persistence because they possess resilience.[23]

But upon closer examination of May, it is not clear that his equilibrium definition of stability is extremely different from Holling's definition of resilience. May defines a stable system as one in which a disturbed population returns to its equilibrium value. If the disturbance amplifies itself, the system is unstable. If the

[22]Holling, p. 15.

[23]Holling, p. 19.

system is stationary or oscillates in a constant amplitude set by the disturbance, then the system possesses neutral stability. Equilibrium, he maintains, is not the constancy of the physical scientist but an average around which the system fluctuates because of environmental changes.[24]

It appears that there is room in May's definition of stability to include the kinds of fluctuations that Holling attributes to a resilient system. Holling admits that the kind of behavior he is reserving for resilience "could be viewed as a stable limit cycle with large amplitude . . . ."[25] My argument is exactly that--the kind of behavior Holling describes as resilience is a stable equilibrium with large amplitude.

Holling has simply defined equilibrium stability too narrowly. He wants to describe a resilient system as one that fluctuates without bouncing back to some stable equilibrium after a disturbance, but May seems to be claiming that such fluctuations would be contained within the amplitude of an equilibrium state.

The kinds of examples Holling uses to describe resilience (spruce budworm, Pacific salmon, etc.) lead me to the conclusion that they are actually "stable limit cycles with large amplitudes." His domains of attraction ("determined by the interaction between budworm and its associated natural enemies (and) periodically exceeded through the

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[24]May, <u>Stability and Complexity</u>, pp. 13, 109.

[25]Holling, p. 14.

chance consequences of climatic conditions"[26]) are actually the equilibrium states of stable equilibriums. The constantly fluctuating systems that Holling describes are base states.

Fluctuation Parameters

Wu sets the parameters for fluctuating populations which can yet be called stable: The lower limit would be the point below which the species would become extinct, and the upper limit would be the carrying capacity of the system, the point above which the species faces hunger or threatens the survival of other species.[27] (The parameters must necessarily be defined separately for each species.) Preston similarly defines the boundaries for stable fluctuations.[28]

These parameters cause the distinction between stable equilibrium and resilience to blur. If Wu's parameters for fluctuations are accepted for a stable equilibrium, the fluctuations Holling attributes to a resilient system would be included.

The Remaining Difference

With such an interpretation, the only difference between resilient systems and stable equilibrium is that resilient systems may have many base states--Holling says that there are many domains of attraction within which a system can be stable. Doult and DeBach say

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[26] Holling, p. 14.

[27] Lilian Shiao-Yen Wu, "The Stability of Ecosystems--A Finite-Time Approach," Journal of Theoretical Biology, Vol. 66 (1977), pp. 347-348.

[28] Preston, p. 7.

that there may be different equilibrium points for different localities; equilibrium points may also undergo permanent change, either through a change in the habitat or by the introduction of new species.[29]

The problem is: Can a system be classified as a stable equilibrium if it settles into a different base state after a disturbance or in the case of a permanent environmental change? Surely an ecosystem can do that; but do we call it stable?

If a system settles into a different base state as a result of a disturbance, it seems to me to be appropriate to say that we no longer have the same system (at least the population numbers would be different). This seems especially appropriate for systems being maintained for exploitation; a farmer would not say that a cornfield with a few weeds is the same system as a field of weeds with a few withered corn stalks.

If a system changes base states, then we can say that the former system was not stable since it did not return to its base state. There is now a new system with a new base state; life has persisted but maybe not in the particular proportions we would have liked. The questions to be answered then are: Does a concentration on maintaining a single base state and reducing fluctuations invite disaster? And, does diversity help a system return to its base state or does it allow

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[29]Richard L. Doult and Paul DeBach, "Some Biological Control Concepts and Questions," Biological Control of Insects, pp. 119-120.

the system to shift to different base states as Holling would claim? At present, there are no definite answers to these questions.

Uniform Equilibrium States

Previously, I defined the base state of stable equilibrium as the pattern of fluctuations while unimpacted. If this is to be empirically determined for each system through observation, then the equilibrium must exhibit some uniform fluctuation to be observed and recorded. But even though Holling's examples are those of large, uniform fluctuations, there is nothing that requires the fluctuations while unimpacted to be in some uniform pattern; if graphed, the fluctuations might wander all over the page. The problem is: How would one define the base state of such a system?

The answer might be that, holding strictly to the definition for a base state (the pattern while unimpacted), the base state parameters of such a system must be set very wide to include its meanderings. For such a system, it is possible that the fluctuation parameters for the base state would be so wide that anything short of extinction would be included in a base state. A system that happens to have a base state with parameters just short of extinction could only maintain the base state; there would be no room for fluctuating and returning.

Resilience and Resistance

The fact that a system may only be able to maintain a base state suggests that the two components of the definition for stable equilibrium can be separated:

1. The ability to return to a base state

2. The ability to maintain a base state

The first is the ability to bounce back; this is what I shall refer to as resilience rather than using Holling's definition. The second is the ability to withstand a disturbance without fluctuating; Harrison calls this resistance.[30]

Resilience, Harrison says, is made stronger in a given population by a strong feedback mechanism--a drop in population through predation or disease is counterbalanced by increased birth and survival due to increased food resources and less competition for space. Of two species, if one has an especially strong feedback, it will possess the greater resilience. But if the other species happens to be less sensitive to environmental changes than the first, then this one will have a higher resistance. Both species may be equally persistent, able to maintain population levels within reasonable limits, even in an unpredictable environment.[31]

A highly resistant system would rarely fluctuate beyond its equilibrium base state. A highly resilient system might fluctuate frequently but would always return to its base state. Both kinds of systems (and those possessing degrees of both properties) may be equally stable. In my last chapter I emphasize that what we are most

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[30] Gary W. Harrison, "Stability under Environmental Stress: Resistance, Resilience, Persistence, and Variability," The American Naturalist, Vol. 113 (1979), p. 668.

[31] Harrison, pp. 600, 664-665.

concerned with in managing croplands, forests, etc., is stability based on resistance.

For the remainder of this paper, I will mean by stability the ability of a system to return to and maintain a base state. The base state will be the pattern of fluctuations while unimpacted but broadly defined to include the kind of dynamics Holling had in mind for his definition of resilience. Resilience will refer to the ability to return to a base state, and resistance, to the ability to maintain a base state--both are components of stability.

CHAPTER 4

PROBLEMS OF EMPIRICAL RESEARCH

It is generally agreed that more research is needed in order to better understand diversity-stability relationships. Hopefully, arising out of empirical studies will be some conclusions as to why diversity and stability are correlated at some times and some locations but not at others. But there are some difficulties in studying living systems which impede the research.

Determining Ecosystem Stability and Diversity

There are difficulties in trying to determine the diversity and stability of ecosystems and in attempting to make a correlation which will serve as a general law. Problems exist with ecosystem boundary designation, temporal limitations, and untested systems.

Boundary Identification

In an effort to quantify population fluctuations, species, and their interactions, it is necessary to first identify the boundaries of an ecological system in order to know what is to be included in a count and what is not. But when we draw boundaries to delineate ecosystems, we are forcing an artificial partitioning on the real world, a partitioning not respected by nature--ecosystems are constantly invaded.

Since stability is the ability of a system to return to and maintain a base state, then the only way to judge whether a system possesses stability is to observe the population fluctuations to see if the population numbers return to the base state after a disturbance and/or resist fluctuating during a disturbance. But population fluctuations due to perturbations are obscured by fluctuations due to migration in and out of the system. To make a judgement of stability, there would have to be some way to distinguish between fluctuations due to perturbations and fluctuations due to natural migration patterns. It is debatable whether such a distinction can be made.

Migration poses an equal problem for counting species when getting a measure of diversity. The number of species is never constant for very long.

A way to avoid the problem of migration across artificial boundaries may be to try to establish only a temporary diversity-stability correlation. Such a correlation would be true only for a certain time while a system is closed or approximately closed. These correlations would be similar to intermittent laws, which are discussed later in this chapter.

Temporal Restrictions

Empirical research into the diversity and stability of ecosystems is further restricted by having only present ecosystems for study. Deevey maintains that the time-rates of change needed for studying stability require time intervals which are only found in the fossil record.[1] But Simpson states that there is no fossil record complete enough to reach any empirical conclusions; ecosystems that existed in the past can never be adequately known.[2]

Because of the lack of information from past ages, we have no way of developing a perspective beyond our present time. If it could be determined that the behavior of present ecosystems does in fact support a diversity-stability correlation, we have no way of determining whether the present circumstances are representative of ecosystems of the past or, by extension, of the future. It could be that the current state of ecosystems might be seen to be a rare occurrence if we could study all past ecosystems. If past ecosystems have behaved differently, then the greater number of past ecosystems would weight the evidence against any diversity-stability correlation existing in current ecosystems. As a result, all we could know for certain is that any discovered correlation would be true for current ecosystems; it may not be true for past or future ecosystems.

Untested Systems

To judge the stability of an ecosystem, it is necessary that the system be perturbed in order to observe whether the system fluctuates in response to perturbations and whether the system returns to its

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[1] Edward S. Deevey, Jr., "Species Diversity in Fossil Assemblages," Brookhaven Symposia in Biology, Vol. 22 (1969), p. 225.

[2] G. G. Simpson, "The First Three Billion Years of Community Evolution," Brookhaven Symposia in Biology, Vol. 22 (1969), p. 163.

base state if it does fluctuate. But if an ecosystem exists in a very stable environment and so is not tested, we have no way of judging its stability.

The Amazon is the prime example. Once thought to be very stable, the tropical rain forest has been found to be quite fragile when faced with man's disruption--the forest is unable to regenerate (return to its base state) at least in the foreseeable future. Since the Amazon was never tested, it was considered stable and so was accepted by many, including Elton, as an example of a stable diverse ecosystem.

The problem of untested systems is how to recognize the stability or instability of the ecosystem while it is unimpacted. Again, intermittent laws (discussed below) may be all that are possible when studying untested systems.

Local and Global Stability

An additional problem in judging the stability of a system is the distinction between local and global stability. Confusion may arise because local instability can exist within a globally stable system, or local stability can exist within a globally unstable system.

Krebs defines local, or neighborhood, stability as returning to an original position after slight disturbances. Global stability is returning to this same position after large perturbations.[3] May states that a locally stable system is also globally stable when,

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[3]Charles J. Krebs, Ecology (New York: Harper and Row, Publishers, 1972), p. 544.

after pouplation fluctuations caused by large perturbations, the population numbers return to the base state. A locally stable system is not also globally stable when large perturbations cause the population numbers not to return to the base state.[4] With this definition, it is possible to have local stability exhibited by a globally unstable system.

But many scientists mean much more by global stability than Krebs' limited definition. Global stability can also mean that a system is stable everywhere, or over the whole range. In that case, local instability could exist within a globally stable system--a system may remain globally stable by shifting to different base states, as Holling suggests, but it would not be locally stable since the system does not return to an original base state. Unstable croplands, for example, may exist within a globally stable system.

If we combine Kreb's definition of local stability with the more broadly defined global stability, then another interpretation is possible. A system could be locally stable with respect to each base state (in that it returns to the base state with small disturbances) but also globally stable (even though the system may not return to the same base state) if it maintains persistence by shifting to another base state.

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[4]R. M. May, Stability and Complexity Model in Ecosystems (Princeton: Princeton University Press, 1973), pp. 13-15.

Most of the work being done in this area is highly mathematical in nature. A meaningful discussion of the topic would be beyond the scope of this paper.

Intermittent Laws

A partial solution to the problems of boundary designation, temporal restrictions, and untested systems is to simply work within the limitations and not expect any conclusion to be all encompassing. We would like to do better than this, for what is needed is a universal theory about the relationship of diversity and stability. But it seems that the state of the art of biology and ecology does not permit the formulation of such universal statements.

Rather than being forestalled by the fact that ecosystems are not closed, that we only have current ecosystems for comparative studies, and that at times a judgement of stability may not be possible because a system is untested, research can continue on a limited number of ecosystems in an attempt to study correlations of diversity and stability, even though the formulation of a theory may not now be possible. With such an approach we may be able to formulate laws or rules which would hold true for as long as a system is closed; such laws would be true for only current ecosystems and under the given physical environments of the ecosystems.

The kinds of laws that might be derived would be similar to the intermittent laws proposed by Hull. We can develop laws for intermittent periods, he says, even though biological systems do not remain closed for very long. Such biological laws would be applied only under special circimstances, such as the ecosystem remaining closed to migration. We would not expect these laws to be true all the time, nor would we expect them to be true for the entire life of the community.[5]

We must ask the question though: Are intermittent laws really scientific laws? Are they not simply "rules of thumb" for particular circumstances? Laws are usually thought to be universal in form--true without exception. But Hempel gives examples of laws that are not so strictly true: Galileo's and Kepler's laws are only approximate according to current physical theories, and light does not travel in a straight line under certain conditions. Hempel applies the term "law" also to these kinds of statements, "known to hold only approximately and with certain qualifications."[6] This certainly seems similar to Hull's intermittent laws.

Intermittent laws about diversity-stability, although not universal, have meaning since we have an interest in knowing the effect of diversity on stability, even if it is only for a limited period of time, under certain conditions, and in a limited area. Even though croplands, for example, may exist within a globally stable system and even though their degree of stability may not be relevant for global stability, we are interested in maintaining croplands for production

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[5] David L. Hull, Philosophy of Biological Science (Englewood Cliffs, N.J.: Prentice-Hall, Inc., 1974), pp. 49,71.

[6] Carl G. Hempell, Philosophy of Natural Science (Englewood Cliffs, N.J.: Prentice-Hall, Inc., 1966), p. 55.

purposes during a given length of time and with certain physical factors. Whether diversity affects stability at this local level will influence management decisions.

But also, once intermittent laws are established, they should begin to suggest more general laws that would give us some indication about diversity-stability relationships in other systems. These suggestions of more general laws would pose puzzles for ecologists to answer, such as why a certain diversity-stability correlation exists in one system but not in another when it was predicted for both.

If intermittent laws and suggestions of more general laws are all that are possible for diversity-stability relationships, then all that can be done is to correlate diversity with stability for certain times, places, and physical circumstances. Therefore, it does not seem possible to develop and confirm a universal law for diversity-stability--one to be applied in all situations.

Species Identification

An additional empirical problem in establishing a diversity-stability correlation is that in order to take a measure of diversity and to observe population fluctuations and extinctions, it would be necessary to identify and count species. But the distinction between species it not so obvious. Some scientists go so far as to say that nature produces only individuals and that designating species is an artificial way of grouping organisms. Although some methods are surely artifical, to say that there is no natural way to distinguish species is to deny any biological distinction that allows grouping, which many biologists do not accept.

In the past, the physical form and structure of plants and animals had been a way of defining species, but as classification continued, morphology presented problems, such as whether every physical variant should be considered a species. More recently, biological criteria have been used to distinguish species, especially interbreeding populations. But all criteria have particular problems of application.

Criteria for Classification

Many different criteria for species identification have been suggested by biologists. But each has specific limitations.

Crowson's criteria. Crowson lists eight criteria that can be used for species classification: (1) structure, (2) distribution, (3) behavior, (4) mating, (5) physiology, (6) breeding, (7) genetics, and (8) temporal limitations. Not all of these, he says can be applied in any one particular case to define species, because they all have limitations:[7]

Morphology is limited because species tend to grade into each other, particularly when viewed over evolutionary time--evolution describes species as gradually emerging through natural selection. But also, a species can exhibit polymorphism (two or more distinct

[7] R. A. Crowson, *Classification and Biology* (New York: Atherton Press, Inc., 1970), pp. 28-36.

phenotypes) and alternation of generations, in which they appear different. Also, what are very distinct species may appear very similar.

Distribution as a criterion is also not adequate because some species do have natural discontinuous populations, and especially now, species are being artifically divided by man's impact on the ecosystem. Behavioral patterns, including mating, are useful criteria, but only for limited areas since the same species may exhibit different behaviors in different environments, especially environments with different climates. Also, groups of organisms may not be mating because they are physically separated and have no opportunity. Physiological or biochemical differences may prove to be useful criteria, but as yet there is insufficient knowledge to make them applicable.

Interbreeding and genetic differences, Crowson says, are the most truly fundamental. But genetics as a criterion is inadequate because of a lack of knowledge of chromosomes for individual organisms, and breeding criteria cannot be applied to those organisms which do not exhibit sexual reproduction.

Species are limited and continuous in time, but to use this fact as a criterion is difficult since the fossil record is inadequate. In the rare cases where entire lineages have been reconstructed, there is a gradual change, not distinct species.

Numerical taxonomy. Since no one criterion is sufficient for defining species, Sneath and Sokal advocate classification according to a total degree of difference and similarity, a numerical taxonomy; organisms will be of the same species if they have a certain number of characteristics in common. Some scientists criticize this approach as impractical because organisms are not so well known that all of their characteristics can be enumerated. Sneath and Sokal suggest that a sufficiently large number of characteristics would be adequate--as more and more characteristics are noted, each new characteristic would have less influence on the classification--there would be less and less reason to change a particular classification. But given the complexity of living organisms, a sufficient number of characteristics seems still too large to be practically measured. The virtually infinite numbers of organisms would also be a barrier--every organism would have to be studied since any a priori way of grouping them for study would be a recourse to other forms of classification, such as morphology, and so it would not be a true numerical taxonomy. The future of numerical taxonomy, Crowson says, rests in the advancement of computer technology.[8]

Phylogeny. Phylogenetic classification is often mentioned as a main approach to species identification--a natural group is one in which all members have a common ancestor that is not ancestral to any organism outside the group. But phylogeny also seems inadequate, for the fossil record is not sufficient to establish very many complete

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[8] Crowson, pp. 196-197.

lineages; ancestors would have to be deduced from other factors, such as comparative morphology and geographical distribution.[9]

Anyway, a literal interpretation of classification based on phylogeny would be vague and relatively meaningless. A dendritic scheme of evolution would allow no objective way of deciding the ancestor of a species, since most organisms are related at some point in the past; many different phylogenies could be constructed.

Biological species concept. Mayr claims that all attempts at species classification arise from three species concepts: (1) typological (morphological differences), (2) nondimensional (studied in a single locality, species appear very distinct in genetics and behavior, usually expressed as interbreeding populations), and (3) multidimensional (species are interbreeding populations but not just for one locality--they interbreed potentially as well as actually).

With a classification built on morphology, Mayr says, every variant would be considered a species, and so most species definitions now avoid solely morphological distinctions. A nondimensional species concept is too limited, in that groups of organisms may not interbreed simply because they are geographically isolated. So Mayr uses the multidimensional concept for a biological species definition consisting of reproductive isolation (biologically caused) and a common gene pool. Of course this would imply a phylogenetic scheme as well, because the species would then be an evolutionary unit.

[9]Crowson, p. 95.

But there are problems with this biological species definition as well: (1) there is a lack of information since it is impractical to check actual and potential interbreeding possibilities, (2) speciation may not be evolutionarily complete, so that what may eventually be distinct terminal species may at present be represented by interbreeding populations, and (3) perhaps most seriously, the biological definition can be applied only to organisms which exhibit sexual reproduction.[10]

A Compromise

As far as the counting of diversity is concerned, the problem of species identification can be partially resolved by limiting ourselves to certain localities. This should be adequate for studying diversity-stability relationships, since we are only concerned with establishing, intermittent laws--those limited in time to a certain ecosystem. In a single locality, species are relatively distinct, and for the purpose of judging the diversity, there is no need to distinguish species from others that have existed at different times and in different places.

The use of Mayr's biological definition of species for measuring diversity is the most practical since the inherent problems can be partially resolved:

1. The lack of information about breeding practices can be alleviated by examining other evidence; by considering morphological,

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[10] Ernst Mayr, Animal Species and Evolution (Cambridge, Mass.: Harvard University Press, 1963), pp. 16-27.

ecological, and distributional characteristics, we can infer whether organisms are of the same species.

2. Since we will be concerned with only an intermittent law about diversity and stability, whether speciation is complete is irrelevant; we are only concerned with the current number of species.[11]

3. Asexual organisms can be classified by morphology. Dobzhansky could think of no better way than grouping together those that resemble each other.[12]

The first and third solutions are appropriate since the phenotype, which includes morphology, behavior, and physiology, is determined by the genotype. Morphology is an indication of genetic makeup.

Using Mahr's biological species concept of actual and potential interbreeding as the criterion for species identification simplifies the process of classification. When not possible, as with asexual organisms, other criteria, even morphology, are adequate since when counting species, we are limiting ourselves to a single locality in which species are relatively distinct; the problems of ancestors, which are not distinctly different, and other phenotypes of the same species (which have developed in different environments) do not have to be resolved.

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[11]Mayr, p. 23.

[12]T. Dobzhansky et al., Evolution (San Francisco: W. H. Freeman and Co., 1977), p. 232.

Such a mix of classification criteria is not inappropriate for counting species in an attempt to get a measure of diversity. Hull says that all classifications are mixed; a numerical taxonomy, for instance, would include the biological species concept since interbreeding would be one common characteristic when gauging similarity, but also numerical taxonomy would be valuable in helping to judge the potential interbreeding within the biological species concept--a lack of similarity would be an indication of reproductive isolation.[13]

Interactions and Proportions

But although we may be able to count species for a locality, numbers of species alone is not a measure of diversity; a simple counting of species is not adequate since it would not reflect the ecological impact of individual species. There must also be a measure of interconnectedness and proportions. For instance, three insect species would surely not contribute the same diversity as two insect species and a herbivore, and neither group would contribute the same measure of diversity as an insect species, a herbivore, and a predator. A measure of interactions, interconnectedness, and interdependencies is necessary.

Interconnectedness and correct proportions pose greater problems of quantification than simply the counting of species. How do we

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[13] David Hull, "Contemporary Systematic Philosophies," Topics in the Philosophy of Biology, eds. Marjorie Grene and Everett Mendelsohn (Boston: D. Reidel Publishing Company, 1976), pp. 418, 425.

take a measure of interconnectedness or arrive at an optimal ratio? Frankly, the problem seems presently insurmountable; I cannot visualize counting and giving appropriate weight to all of the interdependencies in a single ecosystem. But I qualify my pessimism with the word presently because in principle there is nothing to prevent such a measure. Possibly at some future time, our techniques and capabilities will have developed so that the complexity of living systems does not seem so formidable.

In the meantime, it may not be necessary to have a precise, quantitative definition of diversity. Although the biological species concept is not completely adequate, it should do, in alliance with other criteria, to give a general idea of species number. Species number combined with efforts to judge interdependencies and proportions should give a general impression of high, medium, or low diversity. (Mathematical models are already capable of constructing scales of even greater precision.) A relative difference in diversity may be all that is needed to begin to relate diversity and stability.

A New Hypothesis Needed

In spite of the problems encountered in doing empirical research into the relationship of diversity and stability, science need not be forestalled by the problems involved. By limiting ourselves to specific localities in time, place, and physical circumstance and counting species based on specifically (and maybe subjectively) selected criteria, we can continue to study stability and diversity in an attempt to draw some correlation, at least for selected systems that are to be managed. This would give us the starting point for attempting to establish a theory about diversity-stability relationships. But the way to do this is not through confirmation or falsification of various hypotheses but rather through formulating hypotheses which help to solve the puzzles posed by the original diversity-stability hypothesis.

Confirmation

Let us say, for example, that several systems were studied and a correlation between diversity and stability were found. Could we then begin to prove a hypothesis about this correlation?

The cases where the correlation existed would provide evidential support for the hypothesis, but would hardly be considered proof. Hempel says that a favorable outcome of even extensive testing cannot prove a hypothesis but only confirm it.[14] The only way that confirmation could actually prove a hypothesis would be for every system to be studied and found to support the hypothesis, but the infinite number of ecosystems in nature would not allow such a process.

Falsification

Popper proposed that since a hypothesis cannot be proven but only confirmed and since confirmations are fairly easy to come by, a hypothesis can only be falsified. Falsifiability is his criterion for

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[14] Hempel, p. 33.

the scientific status of a theory or hypothesis. A hypothesis must at least imply a test which would falsify it; hypotheses which are not falsifiable are not scientific.[15]

With the diversity-stability hypothesis, as traditionally stated (implying a direct cause and effect relationship), it appears that it has already been falsified by experiments and empirical observations which have not supported the idea that diverse systems are more stable. Yet what has been falsified is not the hypothesis itself but just a specific interpretation. If the hypothesis is taken to mean that all diverse systems are more stable, then clearly it has been falsified. But even the most ardent supporters of the hypothesis recognize that some simple systems are also stable and that occasionally diverse systems are unstable. In that case, the causal relationship is not necessary and sufficient so as to cause all diverse systems to be more stable and all simple systems to be less stable; there are exceptions.

Then it may be that the causal relationship implied by the original hypothesis is neither necessary nor sufficient in the same sense that we say smoking causes lung cancer. That interpretation of the relationship between diversity and stability cannot be falsified with a few exceptions. It seems then that some degree of falsification must be decided upon before the hypothesis can be said to be falsified and then other hypotheses formulated.

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[15] John R. Platt, "Strong Inference," Science, Vol. 146 (1964), p. 350.

Puzzle Solving

But Kuhn argues that this is not the way in which science progresses. Kuhn says that in the actual practice of science (what he calls "normal science"), scientists are not occupied in attempting to falsify hypotheses; rather, they are involved in solving the puzzles that the hypotheses have created and the puzzles that particular failures create. He says, "To rely on testing as the mark of a science is to miss what scientists mostly do and, with it, the most characteristic feature of their enterprise." A hypothesis is replaced not when it is falsified, but when it has "ceased adequately to support a puzzle-solving tradition," either in not posing puzzles to be solved or in not providing the proper context for solving the puzzles.[16]

The diversity-stability hypothesis (simply stated as "diversity increases stability") needs to be replaced or modified not because it has been falsified, but because it has proved to be inadequate for puzzle solving. The hypothesis has not provided the framework for solving the puzzle of why some simple systems are stable and why some diverse systems are unstable, or the puzzle of why successional stages are not increasingly diverse, or why some models and experiments with diverse systems show no more stability than models of simple systems.

The very least that has been shown is that the relationship between diversity and stability is not as simple and direct as originally thought. It seems then that we are ready for a new hypothesis.

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[16]Thomas S. Kuhn, The Essential Tension (Chicago: The University of Chicago Press, 1977), p. 277.

CHAPTER 5

AN ALTERNATIVE HYPOTHESIS

Since the traditional conception of the diversity-stability hypothesis, that diverse systems are more stable, has been shown to have exceptions, then it is obvious that something other than a necessary and sufficient causal relationship is at work. But even if it is assumed that the causal relationship is neither necessary nor sufficient in order to circumvent the exceptions, the hypothesis as originally conceived is inadequate for explaining the exceptions. Some modification or alternative hypothesis is needed.

The diversity-stability hypothesis, as it is traditionally proposed, is but one of the possible relationships between diversity and stability. It has served a heuristic function, providing a framework within which to evaluate work and direct research, but alternative hypotheses can serve an equally valuable function in providing other perspectives which may lead to discoveries that can not otherwise be achieved.

Association Through Other Factors

One such alternative found in the literature is that stability and diversity are not causally related apart from any context, but associated through the effects of other factors. Margalef says that empirical studies seem to show that diversity and stability both increase with succession and coincide in other situations, but he sees no simple way to connect the two directly.[1] May conjectures that diversity and stability are associated and not directly related as cause and effect.[2]

Odum thinks that diversity and stability are correlated to some extent, but he also is not certain whether it is a cause and effect relationship.[3] Goodman thinks that it is possible that diversity and stability are both the result of the same environmental factors.[4]

Hastings speculates that stability and diversity are the result of the mobility of predator and prey. If the mobility of a predator is low, the possibility of extinction of the predator is increased, especially in a one predator/one prey system. If predator mobility is high and prey mobility low, no equilibrium can result. But if the mobility of both is high, he says, stability and constancy result.[5]

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[1]Ramon Margalef, "Diversity and Stability: A Practical Proposal and a Model of Interdependence," Brookhaven Symposia in Biology, Vol. 22 (1965), p. 32.

[2]R. M. May, Stability and Complexity in Model Ecosystems (Princeton: Princeton University Press, 1973), p. 76.

[3]E. P. Odum, Fundamentals of Ecology (Philadelphia: Saunders, 1953), p. 148.

[4]Daniel Goodman, "The Theory of Diversity-Stability Relationships in Ecology," The Quarterly Review of Biology, Vol. 50 (1975), p. 248.

[5]Alan Hastings, "Spatial Heterogeneity and the Stability of Predator-Prey Systems," Theoretical Population Biology, Vol. 12 (1977), p. 37.

Yoon and Blanch think that diversity is not a major factor in stability. In their studies with a mixed microbiological system as a model, they conclude that the interacting structure of the community is what determines stability, and they list four factors which have an effect: spatial heterogeneity, seasonal events, population movements, and presence of refuges for prey.[6] King lists three other factors which may affect stability: length of life cycle, duration and frequency of reproduction, and relative constancy of environmental conditions.[7]

Leigh seems to think that stability is some function of productivity and biomass. With a fixed biomass, he says, increased productivity would cause population turnover, an unstable situation; thus, stability would increase with a decrease in productivity. But if the biomass is increased as well, then an increase in the number of species would increase stability.[8]

Environmental Stability

Implicit in much of the literature is the idea that there is a relationship between environmental stability and diversity-stability.

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[6] H. Yoon and H. W. Blanch, "The Stability of Predator-Prey Interactions in Microbial Ecosystems," Mathematical Biosciences, Vol. 35 (1977), p. 85.

[7] Charles E. King, "Relative Abundance of Species and MacArthur's Mode," Ecology, Vol. 54 (1973), p. 716.

[8] Egbert G. Leigh, Jr., "On the Relation Between the Productivity, Biomass, Diversity, and Stability of a Community," National Academy of Sciences Proceedings, Vol. 53 (1965), p. 777.

It may be that a stable environment is the factor needed for diversity and stability to occur together.

May suggests this idea. Since nature tends to become more organized if left undisturbed (a view supported by Colinvaux[9]), May says that a stable environment would then select for more complex systems because highly organized systems are able to exploit their community resources more efficiently than simple systems. If the environment becomes unstable, then fluctuations occur, which, if drastic enough, cause complex systems to collapse, leaving behind simple systems with unstable populations.[10]

May goes on to say in a later work that one of the determining factors of diversity is the age and climatic stability of a region; such areas have more intricate species relations and more numbers of species.[11] In his earlier work, he suggests that complexity is actually precarious and permitted by environmental stability.[12]

Other Views

Many others have supported similar views. Ehrenfeld implied that diversity is dependent upon environmental stability, for he

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[9] Paul Colinvaux, Introduction to Ecology (New York: John Wiley and Sons, Inc., 1973), pp. 564-565.

[10] May, Stability and Complexity, p. 76.

[11] R. M. May, "The Evolution of Ecological Systems," Scientific American, Vol. 239 (1978), p. 168.

[12] May, Stability and Complexity, p. 172.

stated that more diverse communities exist in those environments which have been stable for the longest times.[13]

Margalef says that a diverse system uses energy more efficiently and will naturally replace a previous, more simple state. But the limit to such succession is disruption from the outside; succession builds diversity only when the environmental is stable, he says.[14]

Slobodkin and Sanders point out that low diversity occurs in three environments: New, severe, and unpredictable. In a predictable environment, species may specialize, leading to the eventual development of new species and an increase in diversity. In an unpredictable environment, they say, there is greater competition due to a lack of specialization--the populations demand a broader base of food resources. The increased competition may reduce stability.[15]

Futuyma states that the coevolution of specialized relationships among species, another factor in diversity, occurs most in constant environments.[16] MacArthur makes the same point that if the environment is constant, then a large number of species can coexist; a more

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[13]David M. Ehrenfeld, "The Conservation of Non-Resources," <u>American Scientist</u>, Vol. 64 (1976), p. 652.

[14]Margalef, p. 362.

[15]Lawrence B. Slobodkin and Howard L. Sanders, "On the Contribution of Environmental Predictability to Species Diversity," <u>Brookhaven Symposia in Biology</u>, Vol. 22 (1969), pp. 83,89.

[16]Douglas Futuyma, "Community Structures and Stability in Environments," <u>The American Naturalist</u>, Vol. 107 (1973), p. 444.

variable environment will hold less species.[17] Colinvaux admits that "it seems possible to conclude that diversity varies from place to place because the stability of the environment varies from place to place."[18]

Two Kinds of Stability

Two kinds of stability are now being referred to: stability of population numbers and stability of environmental factors. To keep the two separate, I will continue to use stability to refer to the ability to return to and maintain a base state, while environmental stability will refer to maintaining a certain base state in the physical environment (climate, geology, etc.).

Since the literature refers to two kinds of stability, it should not be construed that this alternative hypothesis is a reverse formulation of the traditional hypothesis. The statement "diverse systems are more stable" refers to stable populations, whereas something like "stability increases diversity" usually refers to stable environments, which might include some measure of population fluctuations, but more appropriately are measures of physical factors not biological rhythms.

Objections to Environmental Stability

There are objections to the idea that environmental stability increases species diversity. For example, it is not always true that

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[17] Robert MacArthur, "Species Packing and Competitive Equilibrium for Many Species," Theoretical Population Biology, Vol. 1 (1970), p. 11.

[18] Colinvaux, p. 547.

diversity increases with natural succession--unless environmental instability disrupts succession, climax stages occur in which diversity is less than in intermediate stages.

Slobodkin and Sanders state that a stable environment is not the only alternative. They argue that a predictably fluctuating environment would allow adaptation about as well as a constant environment.[19]

The idea that environmental stability favors diversity is complicated further by the fact that at times diversity can influence the environment. For example, trees being cut and cattle allowed to overgraze along the southern Sahara (a lowering of diversity) must at least contribute to the fact that the desert environment is slowly moving south. In other areas, deserts are being reclaimed by planting trees and other vegetation; whether this is a permanent reclamation has yet to be shown. And, as already mentioned, the tropical rain forests participate in their own favorable climate. Connell and Orias state, "The presence of populations of plants or animals almost always decreases the amplitude of fluctuations in physical factors."[20]

Environmental Favorability

Another objection to the idea of diversity increasing in the presence of environmental stability is that some environmentally stable

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[19] Slobodkin and Sanders, p. 85.

[20] Joseph H. Connell and Eduardo Orias, "The Ecological Regulation of Species Diversity," The American Naturalist, Vol. 98 (1964), p. 406.

ecosystems do not possess a diversity of species. Deserts and frozen mountaintops are as environmentally stable as the tropics (in that the physical factors are constant) but do not have as much diversity. Obviously something else must be at work.

Colinvaux provides a partial resolution by introducing temporal and frequency factors. He says that few species grow in most rigorous places, not because of the extreme conditions, but because such environments are rare and short-lived. (Rigor is used to mean extremes of environmental factors.) There simply has not been enough time nor enough rigorous places for many adaptable species to evolve.[21] But this is only a partial explanation because there are rigorous environments with low diversity which have existed for long periods of time and in large areas, such as the poles and the deserts.

In actuality, environmental stability does not appear to have a good correlation with diversity. Diversity increases from the north to the tropics, but environmental stability does not necessarily change latitudinally.

Available Energy

In arguing against the idea that environmental stability increases diversity, Connell and Orias are not willing to attribute the high diversity of the tropics to environmental stability because there is no fossil evidence, they claim, to indicate that the more temperate regions have been any less subject to disruption than the

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[21] Colinvaux, p. 535.

north. Nor are they willing to attribute low diversity to rigor per se, because if some species can adapt, others should be able to also. They answer the problem of differences in diversity from north to south by saying that diversity is directly related to the amount of energy flowing through the foodweb and to how it is used. They give two uses of energy: maintenance and productivity. In colder climates more of the available energy must go for maintenance.[22]

Slobodkin and Sanders point out that in colder environments species frequently face changes which sometime exceed their tolerance, and that they constantly face competition because of the characteristically large niche size required for such environments. Both factors work to establish low diversity.[23]

In more productive habitats, say Connell and Orias, where the temperatures are higher, not only is there more energy but more of the energy can go for reproduction. Also, since there is less need for mobility in search of food, small isolated pockets develop, which favor speciation. So it follows that the more available the energy and the less needed for maintenance, the greater the diversity.[24] The implication is that high diversity is more due to the available energy present and its use in reproduction (rather than maintenance), than in the stability of the environment or the lack of rigor per se.

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[22]Connell and Orias, pp. 400-401.

[23]Slobodkin and Sanders, p. 89.

[24]Connell and Orias, pp. 402-405.

Why it takes a particular level of available energy for reproduction and speciation to be favored over maintenance is a singular puzzle. Since the colder regions have been in existence for as long as the warmer regions, one could expect that species should have evolved that are just as well adapted to the cold and function as well as species in warmer climates. It may be that the reactive chemistry of biological processes is such that a certain range of energy is required for optimal functioning of organisms. But there is no room in this paper for a thorough discussion of the possible reasons.

Favorability

A problem with Connell and Orias' theory is that it does not explain great permanent areas where high energy and low diversity do occur together. They have not explained why the Sahara has not done as well as the Amazon basin. Probably the determining factor is moisture level, considering the fact that the Amazon has a massive river in its center maintained by a high level of rainfall.

So more is involved in increasing diversity than just available energy; other factors are involved, such as moisture levels and also degrees of environmental stability, lack of rigor, and sufficient time spans. All of these considerations, which contribute to an efficient energy use, make up what I term environmental favorability. Within the context of this discussion, it is the favorable environment that is needed for diversity to increase, not simply a stable environment nor just available energy for reproduction and speciation.

A Limitation

If Connell and Orias are right, then diversity should continue to increase within a favorable environment because efficient energy use would serve as a positive feedback; diversity should increase, which will then help to buffer the system and increase population stability. This is related to MacArthur's view that stability is a function of the number of paths that energy has to travel through the foodweb[25] and Leigh's view that stability is maximized by maximizing the number of links in the trophic web.[26]

But at some point, say Connell and Orias, there will be a negative feedback which will lower the stability of the system. Within a favorable environment, speciation will increase with a greater and greater degree of specialization; species will tend toward linear food chains where each will depend on few food sources rather than being dependent upon several. An environmental perturbation, if severe enough, might cause extinction of a species which will then severely disrupt the entire food chain in which the species existed. Diversity and stability would continue to increase only if new species could remain flexible, they say.[27]

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[25] Robert MacArthur, "Fluctuations of Animal Populations and a Measure of Community Stability," Ecology, Vol. 36 (1955), p. 534.

[26] Leigh, p. 777.

[27] Connell and Orias, pp. 405-406,409,411.

Association

According to this viewpoint, diversity and stability are associated under certain circumstances and not linked in a sufficient cause and effect relationship. It may be that it is environmental favorability that tends to increase both diversity of species and population stability, at least up to some level at which there is a negative feedback.

But without environmental favorability, diversity and stability may not occur together. Gomez-Pompa et al. have made the point that unfavorable environments produce more resilient species. They found that the drier tropics, which undergo a more frequent disturbance because of drought and fire, are able to regenerate more easily and quickly than the more moist tropics.[28] This seems to be supported by Slobodkin and Sanders who say that organisms respond to irregular and unpredictable environments by developing a broad physiological tolerance.[29]

What is implied is that systems existing in unfavorable environments evolve species that are more tolerant, and thus these systems can also be stable because the indigenous species are hardier, although the system is probably less diverse because the conditions for speciation are not present. So stability would not correlate with diversity in such cases.

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[28] A. Gomez-Pompa, C. Vizquez-Yanes, and S. Guevara, "The Tropical Rain Forest: A Nonrenewable Resource," Science, Vol. 177 (1972), p. 765.

[29] Slobodkin and Sanders, p. 85.

It seems then that a favorable environment increases reproduction and speciation and thus diversity increases, while a less favorable environment, although characterized by low diversity, increases physiological tolerance. It may be that ecosystems in both environments are equally stable over real time intervals, but it is only in favorable environments that diversity and stability occur together.

That stability can be associated with both high and low diversity is supported by Goodman who states that any susceptibility to extinction possessed by the small numbers within simple systems may be counterbalanced by the less competition present in the simple systems.[30]

An Alternative Hypothesis

A possible alternative hypothesis based on the above discussion would read as follows: Environmental favorability is needed for natural succession to increase an ecosystem's diversity, which then increases population stability by using the resources of the system more efficiently and serving as a buffering effect against perturbations. Population stability would then be associated with diversity under the influence of environmental favorability. As diversity increased it would raise the resistance level of the system to perturbations so that it would take a greater and greater perturbation to disrupt the process until (1) a climax stage is reached, determined

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[30] Goodman, p. 259. Although,this contradicts Slobodkin and Sanders who say that species of simple systems do face greater competition because they are characteristically in rigorous environments, which require large niche size. Slobodkin and Sanders, pp. 83,89.

by the resources of the system and accompanied by a drop in diversity as certain species dominate, (2) a chance perturbation exceeds the resistance and resilience of the system and causes a disruption in which a new base state is established, and/or (3) diversity increases to a level of overspecialization that causes the system to be precariously balanced and more easily disrupted by environmental impacts than earlier stages.

This alternative hypothesis is seen to be a weakened version when compared to the traditional interpretation with its implied sufficient cause and effect relationship. The alternative would be much more difficult to apply in a managerial plan if it were adopted as the manner in which diversity and stability are correlated, for the environmental factors involved would have to be adequately considered before determining what level of diversity to preserve in order to maintain stability (if that were the goal). Whether that could be practically done is questionable.

Multiple Hypotheses

This alternative is but one possible hypothesis about the relationship of diversity and stability. I do not claim that this is the best alternative, only that this is an example of a reinterpretation of the traditional hypothesis that is implicit in the literature. Other alternatives need to be proposed to enrich the research possibilities.

Science progresses by using various hypothesis, discarding those which do not support a "puzzle solving tradition." Multiple hypotheses are therefore necessary to begin to organize the research which has been done and to designate some areas in which future work should be carried out. Chamberlain urged the method of multiple working hypotheses:

> It differs from the simple working hypothesis in that it distributes the effort and divides the affections. . . . if a group of hypotheses encompass the subject on all sides, the total outcome of means and of methods is full and rich.[31]

Feyerabend takes this idea to an extreme:

> Knowledge so conceived is not a series of self-consistent theories that converges towards an ideal view; it is not a gradual approach to the truth. It is rather an ever increasing ocean of mutually incompatible (and perhaps even incommensurable) alternatives, each single theory, each fairy tale, each myth that is part of the collection forcing the others into greater articulation and all of them contributing, via this process of competition, to the development of our consciousness. Nothing is ever settled, no view can ever be omitted from a comprehensive account.[32]

Ad hoc hypotheses, he says, "give new theories a breathing space, and they indicate the direction of future research."[33]

The traditional hypothesis that diversity causes stability clearly needs to be modified or replaced with an alternative hypothesis.[34] The alternative that diversity and stability are associated through

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[31] T. C. Chamterlain in John R. Platt, "Strong Inference," Science, Vol. 146 (1964), p. 350.

[32] Paul Feyerabend, Against Method (London: Verso, 1975), p. 30.

[33] Feyerabend, p. 93.

[34] It may be that no hypothesis should be discarded; the evidence against the traditional diversity-stability hypothesis, for example, may have been misinterpreted or experiments designed incorrectly.

entironmental favorability is but one alternative. Since hypotheses serve a heuristic function by providing a framework within which to do research, many others should be postulated in an effort to explore other possibilities of diversity-stability correlations and to provide alternative pathways that researchers can follow.

CHAPTER 6

SUMMARY AND CONCLUSION

This discussion has proceeded by first presenting the evidence supporting the diversity-stability hypothesis (that diverse systems are more stable). Starting with the concept that nature is good, I suggested that there is a predisposition for order and purpose in nature which led to what proved to be an unsubstantiated belief in the hypothesis. Since some observations supported the idea that diversity increases with succession, then it was thought that increasing diversity was a process of nature--nature must be doing something. Again relying on a belief in the goodness of nature, I claimed that the inclination was to expect the purpose of increasing diversity to be, at least in part, the stability of the ecosystem; otherwise, nature would appear to be malicious in intent. This teleological conception of nature contributed to the ready acceptance of the hypothesis that diversity increases stability.

I also presented the more concrete evidence used to support the hypothesis: (1) certain empirical observations showed a coincidence of diversity and stability (simple croplands are unstable; diverse tropical forests were considered stable), (2) islands, which possess less diversity, are more easily invaded, (3) experiments with simple systems demonstrated instability, and (4) mathematical models showed simple systems to be unstable.

Also, some basic assumptions supported the hypothesis: (1) A diverse system, one with many parts, should be able to dissipate the force of a perturbation more easily than a simple system; (2) instability and speciation could not occur together, for the fluctuating populations of an unstable community would favor adaptation rather than specialization; and (3) an ecosystem must be struggling to survive just as an individual organism, so a possible conclusion was that ecosystems become stable in order to persist.

But each of these pieces of evidence has been countered by other arguments: (1) Biologists no longer take seriously the idea of a teleological nature, so it makes no sense to ask what is the purpose of diversity; (2) that increasing diversity is a process of nature is not so obvious, for climax stages are usually less diverse than intermediate stages; (3) unstable croplands are considered artificial by many scientists and so irrelevant for examining diversity-stability relationships; (4) the diverse tropical forests, once thought to be very stable, have been found to be quite fragile when confronted with man's exploitation; (5) mathematical models and experiments with more diverse systems show no more stability than those with simple systems; and (6) islands may be invaded for other reasons than their low diversity.

The basic assumptions used to support the hypothesis are not so obvious either: (1) The interconnectedness of diverse systems could just as easily spread and multiply the impact of a perturbation as it could dissipate the force; (2) increasing diversity and instability can occur together, for overspecialization would result in a system vulnerable to perturbations; and (3) there is no logical reason for making the leap from individual organisms struggle to survive to ecosystems as a whole struggle to survive. (Although through natural selection the fittest ecosystems survive, an individual ecosystem as a whole does not consciously try to persist.) Eventually, I argued that the original statement of the hypothesis with its implied sufficient cause and effect relationship is inadequate for explaining all of the exceptions, and so a modification or an alternative hypothesis is needed.

In an effort to contribute more exactness to the discussion, I formulated more precise definitions of diversity and stability. There seems to be a consensus in the literature that diversity includes not only numbers of species but also a measure of the interconnectedness of the species and their optimal proportions. But there seemed to be no consensus on stability, so I choose to let stability refer to the ability of a system to return to and maintain its base state, with the base state as the empirically determined pattern of fluctuations while unimpacted. Although I have passed lightly over base state, I do not mean to imply that defining a base state would be a simple task. Long and extensive observations would be needed, and then only an approximation would be likely because ecosystems are continually confronted with perturbations.

From among the multiple hypotheses that are needed to enrich the research into diversity-stability relationships, I presented one which is implied in the literature--that diversity and stability are associated through one or more other factors rather than being causally related apart from any context. I postulated that a third factor might be environmental favorability. If an environment is favorable, diversity is able to increase; the diversity then increases population stability by more efficiently using the energy of a system and by serving to buffer external impacts.

I presented this alternative hypothesis as merely an example. I do not support it as the correct alternative because the question of whether the interconnectedness of a diverse system could just as easily spread and multiply an impact as it could buffer the impact of a perturbation is still unanswered.

An additional problem is that even in a favorable environment, diversity-increasing-stability would work only up to some level of specialization, beyond which overspecialization would act as a negative feedback to weaken the system. It would be very difficult to determine this level of overspecialization, and without such a determination, this alternative hypothesis is unfalsifiable, for if a diverse system exhibits instability, then the conclusion could just as easily be that the system is overspecialized as it could be that the hypothesis is false. Possibly a relative measure of specialization (beyond which the system is weakened) could be established by examining a number of systems and determining a range of diversity within which systems are stable. If no such ranges are found, then the hypothesis would be considered false or at least would lack any experimental value.

Implied in this discussion is the idea that universal laws relating diversity and stability may not be possible. If it is true that diversity increases stability only during certain levels of specialization and only within the context of environmental favorability, then all we are capable of are intermittent laws--laws which are true only for a given time, place, and circumstance; in which case, they would not be universal in their application.

Cause and Effect

One reason a universal law may not be possible for diversity-stability relationships is that diversity and stability do not conform to the kind of cause and effect relationships which are the basis for universal generalizations. Typically, causal relationships are thought of as one event causing another event, but diversity and stability are not events; they are properties of an ecosystem. Properties, rather than causing events to happen, produce the right circumstances for events to occur. If a perturbation caused a population fluctuation, then the internal dynamics (the biological and chemical events performed by individual organisms) would cause the population numbers to return to the base state. These are the events that would be involved in a causal relationship. Diversity and stability are the properties that determine the relative probability of whether these events will occur.

But if we do speak in terms of diversity causing stability, it is apparent that the causality only works some of the time; there are exceptions. This is not the kind of causality on which universal laws are based.

Hull identifies three types of causal relationships: (1) sufficient but not necessary, as in the explosion of the sun destroying all life on earth, (2) necessary but not sufficient, as in a bacterium causing tuberculosis, or (3) neither necessary nor sufficient, as in smoking causing lung cancer.[1] If there is a cause and effect relationship between diversity and stability, it seems that it is like the relationship between smoking and lung cancer, neither necessary nor sufficient. Other factors may have to be present before diversity increases stability, possibly environmental favorability.

Hull says that cause can be context dependent.[2] Hempel, also, says that "a cause must be allowed to consist in a more or less complex set of particular circumstances."[3]

Yet, Hull says that this type of causality is not universal in nature; cause must be both sufficient and necessary for it to be universal.[4] So if diversity and stability are only related in a causal relationship that is neither necessary nor sufficient but only contributory, then there can be no universal laws about diversity-stability

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[1] David L. Hull, Philosophy of Biological Science (Englewood Cliffs, N.J.: Prentice-Hall, Inc., 1974), p. 73.

[2] Hull, p. 74.

[3] Carl G. Hempel, "Explanation in Science and History," Ideas of History, Vol. 2, ed. Ronald H. Nash (New York: E. P. Dutton and Co., Ind., 1969), p. 83.

[4] Hull, p. 73.

relationships; only intermittent laws which many think are not laws at all. But intermittent laws do have value, as pointed out in Chapter 4.

Reducibility

If intermittent laws are all that are possible, then this may be an indication that what Hull calls "upward reductionism"--the reduction of observed facts and specific laws to more general universal laws--may not be possible for biological systems.[5]

The current paradigm of a scientific law, Hull says, is a process law, "a generalization that permits an inference about the state of a system at any time whatsoever." Process laws are only possible for systems which are closed, but biological systems are rarely closed long enough to establish a process law.[6] That is why Hull suggests that laws be derived for intermittent periods.

Some argue that the same is not true for the physical sciences. More accurate predications can be made, they say, for planets and balls rolling down inclined planes; the descriptions of such systems are "short and simple, permit numerous repetitions, and are universal in form."[7] Many scientists have thought the disparity between the biological and physical sciences is because living things are different

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[5]Hull, pp. 9,134.

[6]Hull, p. 49.

[7]Hull, p. 99.

from nonliving things, and so biology must be done differently. Arguments for this position claim either that living systems are too complex or that living organisms contain some vital element beyond the actual physical makeup of the organism.

Vitalism

The vitalists have believed that biological systems contain a "vital force" that places life processes beyond the range of interpretation available to the physical sciences; this vital force directs the activities of living organisms. Aristotle called it "entelechia," a purposive force underlying the development of living things.[8] For Bergson, it was élan vital, a vital impulse which produced variations and directed evolution toward higher levels of organization.[9]

But in more recent years, molecular biology and genetics with the discovery of DNA have made all processes, before explained by vital functions, open to experimentation. Now the possibility exists for describing the formation of organisms in physicochemical terms.[10]

Even though vitalist doctrines are now held in disrepute by most scientists, there are still difficulties in reducing biology to the

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[8]Bernard Rensch, Biophilosophy (New York: Columbia University Press, 1971), p. 284.

[9]Thomas A. Goudge, "Introduction," to Henri Bergson, An Introduction to Metaphysics (New York: The Bobbs-Merrill Company, Inc., 1955), p. 17.

[10]Elizabeth Gasking, The Rise of Experimental Biology (New York: Random House, 1970), p. 164.

kinds of universal laws more characteristic of the physical sciences. For example, some argue that a mechanistic approach--that life processes can be explained exclusively in physicochemical terms--has been hindered by the fact that the origin of life has not been explained, or that the consciousness and adaptiveness of the higher organisms influence evolution, or that organisms exhibit a wholeness which allows explanation only in terms of the usefulness of a structure or process to the whole system.

But to explain these kinds of problems in terms of vitalist doctrines is inadequate because such doctrines have no explanatory power. No vitalist doctrine explains how vital forces work nor allows any better prediction than other hypotheses. From Kuhn's viewpoint, vitalist doctrines do not support a puzzle-solving tradition.

Hempel says that vitalist doctrines have failed to produce a theory from which implications can be derived as to how or when vitalist forces take over and direct biological processes. Although a more mechanistic approach has not been completely successful in reducing biology to physicochemical terms, he says, we may expect that the reduction will one day be accomplished, but he also warns that as research continues the line between biology and the physical sciences may lose its distinction.[11]

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[11]Carl G. Hempel, Philosophy of Natural Science (Englewood Cliffs, N.J.: Prentice-Hall, Inc., 1966), pp. 71-72, 101-106.

Complexity

Although vital forces are not taken seriously by many scientists any longer, some argue that universal laws for biology are still not possible. The likely reason, they say, is the greater complexity of living matter.

Hull says that the genetic makeup of an organism is so complex that very precise descriptions are necessary to explain the behavior of living systems, and it may be that the degree of specification is too great for universal laws to be developed, and so at best, only intermittent laws are possible. Perhaps the upward reduction of specific to universal laws is more difficult for biology than the physical sciences, he says, but this is a difference of degree, not of kind.[12]

The difference in complexity between living and nonliving matter is not sufficient grounds for accepting any vitalist doctrine. It may be that only the methodology of the sciences need be different.

Rensch also believes that the complexity of biological systems places us in the predicament of only being able to establish rules about certain life processes. These processes, he says, are subject to superimposition, interrelationships, and mutual interference, plus living systems have only a relative constancy, so we cannot establish biological laws, only rules of thumb.[13]

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[12] Hull, pp. 99, 134-135.

[13] Rensch, pp. 18, 283.

New Hypotheses

At least for the present, any kind of a reduction of biology to universal laws is stalemated by the complexity of life processes. This problem of reducibility has direct implications for the diversity-stability hypothesis.

If a reduction to universal laws is not possible, it means that the empirical evidence gathered from the study of living systems will never be able to make of any interpretation of the diversity-stability hypothesis any more than what it is, a hypothesis. Without universal laws, either because we cannot get to them or simply because they do not exist, we will never be able to accurately predict the behavior and character of living systems and thus will never be able to predict the effect of diversity.

Although complexity is clearly a block to establishing universal laws, no one has presented a reason in principle why the reduction to universal laws cannot at some time be made. Most scientists still expect that universal biological laws will be established as the science progresses.

If a relationship between diversity and stability is discovered, it is safe to say that it will not be simple. Empirical research may eventually establish a correlation between stability and diversity, but it is clear that the correlation must exist in a context of several other biological and environmental factors.

The traditional conception of the diversity-stability hypothesis--that diverse systems are more stable with an implied sufficient causal relationship--is inadequate for explaining real ecosystems. Perhaps we have not completely discarded this interpretation of the hypothesis because we have yet to propose anything better. Kuhn says that

> the act of judgment that leads scientists to reject a previously accepted theory is always based upon more than a comparison of that theory with the world. The decision to reject one paradigm is always simultaneously the decision to accept another, and the judgment leading to that decision involves the comparison of both paradigms with nature <u>and</u> with each other.[14]

The diversity-stability hypothesis has served a useful purpose. It has been the paradigm that has guided research and provided a context within which to study the concepts of diversity and stability. And it has been the paradigm that has given form to the questions and puzzles which now point out its own inadequacy. "Anomaly appears only against the background provided by the paradigm."[15]

It is the anomalies which now require a new formulation of the hypothesis (or several) in order to solve the puzzles and to keep the research vital. Popper says that the hypotheses should be put forward as bold conjectures, that we should jump to conclusions. We can arrive at a good hypothesis, he says,

> by jumping first to <u>any</u> theory and then testing it, to find whether it is good or not; i.e., by repeatedly applying the critical method, eliminating many bad theories, and inventing many new ones. Not everybody is able to do this; but there is no other way.[16]

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[14] Thomas S. Kuhn, <u>The Structure of Scientific Revolutions</u> (Chicago: The University of Chicago Press, 1962), p. 77.

[15] Kuhn, p. 65.

[16] Karl R. Popper, <u>Conjectures and Refutations</u> (New York: Harper and Row, Publishers, 1963), pp. 55-56.

CHAPTER 7

IMPLICATIONS FOR RESOURCE MANAGEMENT AND PRESERVATION

The implications of the diversity-stability debate pertain to such problems as exploitation of resources, preservation of species, and human population control. A belief or disbelief in a diversity-stability correlation will affect management decisions in these areas and others.

Resource Exploitation

One goal of management policies for forests and croplands is long-term exploitation; a constant and consistent source of food and wood products is needed by the economy. Those ecosystems which are stable (able to return to and maintain a base state) provide the most consistent exploitation, so we are interested in factors which stabilize a system.

From this perspective, we are only interested in a system which does return to and maintain a specific base state. Although a system may persist by shifting to different base states, it would not provide a consistent source of products unless it maintained specific population numbers; a particular base state is what is needed for a specific crop or a specific tree harvest.

But also, if consistency is our goal, we will need to concentrate on the second half of the definition for stability--the ability to maintain a base state. In reality, methods of achieving stability exist on a continuum--ecosystems remain stable with degrees of both resilience and resistance. But for resource exploitation, we are mostly concerned with stability based on resistance, for an ecosystem possessing that kind of stability will fluctuate less and so permit the most consistent exploitation.

For management, therefore, we are concerned with (1) whether diversity is correlated with stability characterized by resistance, (2) whether a concentration on resistance alone actually weakens a system in the long-term, and even (3) whether a concentration on stability (characterized by a single base state) actually threatens the persistence of a system. As yet, these questions have no definite answers; more research is needed. But preconceptions about diversity-stability relationships have been formed and will influence decisions and actions as ecosystems are managed for exploitation.

Forest Management

Forest management options are prime examples of the differing views on resource exploitation. If we want a stable forest community that will guarantee a consistent and continuing supply of wood products, we need to know whether to maintain a diverse community or to establish a monoculture. If those who manage the forest community accept a correlation between diversity and stability, then they will value the natural diversity of wilderness and will manage for it. This might include allowing some natural perturbations since there is some evidence that fluctuation is necessary to maintain diversity--fire, for example, causes a climax forest to revert to a more diverse successional stage.

Louchs says that the natural perturbations which our forests experience cause recycling and maintain diversity. Any modification precluding this disturbance would be detrimental to the system. To achieve a high level of species diversity and a high level of productivity, he says, we should restore the natural mechanisms which cause recycling and rejuvenation.[1]

If the managers of our forests do not accept a correlation between diversity and stability, they will most likely manage for monocultures, such as pine forests. Fast-growing, hybrid pines would give the maximum yield and would probably be sustainable if diversity is not needed for stability.

It appears that both views are at work in the management of our National Forest System. In the National Forest Management Act of 1976, Congress directed the Forest Service to "provide for the diversity of tree species."[2] Though there are other reasons for maintaining diversity, it is probable that more than a few Congressmen

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[1] Orie L. Louchs, "Evolution of Diversity, Efficiency, and Community Stability," American Zoologist, Vol. 10 (1970), pp. 17,25.

[2] "National Forest Management Act of 1976," U.S. Code Congressional and Administration News (St. Paul, Minn.: West Publishing Co., 1976), pp. 2953-2954.

approved of this language based on some vague belief that diversity increases stability.

On the other hand, alternatives currently considered by the Forest Service for management of the National Forests include a policy of reforestation with genetically improved growing stock in areas that have been logged or destroyed by fire. Replacing forests with genetically improved stock would lower diversity through what would tend to be a monocultural substitution.

A policy of converting complex systems to simple systems is widespread. For example, Jari Forestry and Agricultural Enterprises, owned by an American industrialist, is clearing 10,000 acres of Amazon forest per year for wood pulp production and cultivation of the land. Most of the land is recovered in monocultures, and some conservationists predict that there will be no intact forest left in 30 years except for possibly a few mountainous areas.[3]

If there is a correlation between diversity and stability, we are inviting diaster with practices which tend toward monocultural substitution, for it will then also be true that monocultures are more susceptible to infestation and disease, which seems to be born out by the evidence. If there is no correlation, then monocultural substitution is acceptable, and other justifications must be found to preserve the diversity of woodlands.

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[3] Anna LaBastille, "Heaven or Hell," Audubon, November 1979, pp. 87,97.

But at times the guiding factor cannot be a general management plan based on diversity per se; there are times when monocultures are necessary, such as tree farms and croplands. At such times the choice is not whether to preserve diversity but how best to maintain a monoculture. A management plan must then take into consideration which monocultures are best (one particular tree species may be more resistant than another) and what environments are present (a less resistant species may survive adequately in a relatively stable environment).

Croplands

Even if there is a correlation between diversity and stability, there will still be this need to manage some simple systems for temporary maximum exploitation, e.g., croplands. In such cases, stability per se is not the goal; rather, the goal is resource production.

But Colinvaux warns that if there is a correlation, the planting of crops (a transition from natural diversity to simple systems) invites disaster. Agriculture with more diversity than is now practiced would be at least moderately stable and would make outbreaks of pests less likely. Colinvaux recommends several crops interspersed with shelter-belt woods and hedgerows.[4]

If diversity and stability do not occur together, then the low diversity of croplands does not contribute to making them any more

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[4]Paul Colinvaux, Introduction to Ecology (New York: John Wiley and Sons, Inc., 1973), p. 240.

susceptible to collapse than natural, diverse ecosystems. In that case, we would need to look for other reasons for the apparent susceptibility of croplands.

Wilderness Preservation

If we are to manage simple systems for resource production in spite of the possibility that there is a correlation between diversity and stability, it is all the more important that separate diverse systems be maintained. A variety of species must be preserved, at least in isolated pockets, in order to provide stock for replenishing areas where perturbations may destroy the simple systems that are doing the production. Setting aside wilderness areas is the most natural way to do this.

Natural diverse systems are valuable, not only for restocking, but also for maintaining our potentiality. Plants and animals contain the entire stock of genetic material in the world, and once this gene pool is depleted, it cannot be replaced. The genetic material stored in the diversity of nature is the source of change and development in our attempt to utilize our natural resources; in the future, new strains of corn, wheat, and trees may be needed. Conserving diversity is inextricably linked with preserving a range of choices for individual life styles.[5]

Wilderness preservation is, therefore, justified even if there is no correlation between diversity and stability--diversity has value

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[5] Jeremy Swift, The Other Eden (London; J. M. Dent and Sons Ltd., 1974), pp. 141,147.

apart from whether it is linked with stability. If diverse natural systems prove to be unstable, they must still be preserved to maintain our genetic resources. Other reasons for preserving diversity apart from its influence on stability are discussed later in this chapter.

Endangered Species

If stability is desirable and there is a correlation with diversity, then the protection of endangered species takes on new importance--they will be needed to maintain diversity. There is the possibility that the natural extinction of species at one time was balanced by the evolution of new species so that diversity was maintained in spite of natural extinction. But if such a balance ever existed, it does no longer because of man's impact on the environment. Many species are driven to extinction each year; clearly the balance has been pushed in favor of extinction.

The case of TVA's Tellico Dam Project provides an example of the concern over preservation of endangered species. Completion of the dam on the Little Tennessee River in eastern Tennessee has destroyed the habitat of a unique life form, the snail darter. Conservationists fought unsuccessfully for years to stop the dam but lost the battle when the U.S. Congress passed a law requiring completion. This incident is unique in that a species was for the first time intentionally placed in danger of extinction.[6] (Some of the fish have been transplanted to

[6] Russ Manning, "The Damning of the Little T: TVA's Tellico Dam," Appalachia Journal, December 1980, pp. 40-53.

other locations and may be establishing viable populations. Also, recent sightings of the fish in other locations have raised the possibility that it was not actually endangered.)

One of the arguments used by those opposed to the dam was that unique forms of life need to be preserved not only for their own worth but also because the extinction of species indicates a deterioration of the environment. For the environmentalists, then, a lowering of diversity signifies an unstable ecosystem. Clearly they were using a diversity-stability correlation as part of the justification for saving the snail darter. In actuality, the environmentalists were arguing that a lowering of diversity indicated that the environment was becoming unfavorable. By extension, they argued, it is becoming unfavorable for humans as well.

The Endangered Species Committee, originally empowered to decide the fate of the Tellico dam, also favored species diversity. They implied that ecological diversity is beneficial and argued that

> the snail darter may contribute to ecological diversity by virtue of its specialized habits. It may also contribute to genetic or evolutionary diversity because it represents a unique store of genetic information.[7]

If diversity does increase stability, then there is more than adequate justification for the preservation of endangered species--extinctions would lower diversity and consequently, further reduce

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[7] U.S. Department of Interior, Tellico Dam and Reservoir, Staff Report to the Endangered Species Committee, Washington, D.C., January 19, 1979, p. 4.5.

the stability of ecosystems. If diversity does not increase stability, then other reasons must be found for preserving endangered species.

Population Control

For human population management, a correlation between diversity and stability would mean that the continuing expansion of the human race produces a vulnerable system as other species of both plant and animal life are forced out of existence. Preston says that the steady growth of the human population is destabilizing because it displaces and causes the extinction of other species.[8]

The ubiquitousness of man has an adverse effect on diversity, not only because we have become a dominant species, contributing uniformity by our very pervasiveness, but also because we attract other species which contribute an additional degree of uniformity, for example, cows, dogs, cats, rats, and sparrows. But Swift adds that man's interaction with the environment is what has had the greatest effect on diversity. Some of the actions of man have increased diversity, such as roadside clearings and the opening of fields where mature forest once stood. These actions originally diversified and enriched the landscape. But with the advent of technology and its accompanying pollution, diversity began to decrease.[9] The world

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[8] Frank W. Preston, "Diversity and Stability in the Biological World," Brookhaven Symposia in Biology, Vol. 22 (1969), p. 8.

[9] At least temporarily; it is possible that technology is also creating new niches not yet filled so that at some point diversity will increase once again. Improved irrigation techniques have already increased the diversity of arid regions.

has gravitated toward uniformity in the face of high-yield agriculture, weather control, land development, and other facets of our technological society. Technology tends to universalize; it simplifies structure and destroys diversity.[10]

Alternative Approaches

Whether a diversity-stability correlation is accepted by those in management positions will affect management policy. Those who accept the original statement of the hypothesis will manage for diversity; those who do not will see no danger in establishing monocultures and may or may not preserve diversity for reasons other than stability.

For those holding the opinion that the original hypothesis has been disproved but that some alternative correlation may still be at work in the real world, a more cautious approach will probably be adopted which will include a recognition that we as yet do not fully understand the dynamics of diversity and stability. If, for example, it is believed that diversity increases stability only up to a certain level of specialization, then a much more complicated management plan must be initiated. Such a plan would favor diversity, but diversity managed so as to avoid overspecialization, which would weaken the system.

[10] Swift, pp. 138-139.

This cautious approach must include the acknowledgement that our ability to control the environment (the physical sciences) has gotten ahead of our ability to decide what direction that control should take (the biological sciences).[11] We are capable of changing the diversity of nature but as yet do not know how our actions affect the stability of nature. If man makes the wrong choices as he exploits the world's natural resources (either increasing or decreasing diversity with a concurrent stability or instability--if there is a correlation), then the collapse of our entire ecosystem and the demise of the human race is possible, probably not in our time, but not too many generations into the future.

But since no decision is possible, at least for the present, on the relationship of diversity and stability, then a diversity-stability correlation cannot be used as a guide for managing ecosystems; some other guiding principle must be found. Whatever management plan emerges, it must contain a view of nature as the origin of our resources and the repository of our wastes. Working with such a view, our options will be left open. Without such a perspective, it is most likely that we will make the wrong decisions.

Other Reasons for Preserving Diversity

If diversity is to be preserved for its own sake, then a different management plan will be adopted to protect species diversity

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[11] Swift, p. 149.

even beyond the level of overspecialization. Cantlon gives various reasons for maintaining the diversity of species:[12]

1. As man becomes more responsible in his exploitation and coexistence with nature, a gene pool of diverse species will be needed for ecosystem design changes.

2. Complex systems with large diversities are needed for the reprocessing and recycling of air, water, and inorganic nutrients. (Actually, it is questionable whether diversity is needed--a large number of organisms of few species might do as well for reprocessing and recycling.)

3. Species and ecosystems should be preserved purely for aesthetic reasons, for man's enjoyment. (Of course, this would be a subjective judgement and raises the question of who would decide which species and systems to preserve.)

If indeed there is no correlation between diversity and stability, Goodman says, that is not necessarily a loss for environmentalists, for it is clear that the disruption of ecosystems and the loss of species cause other negative consequences and so can be argued against on other grounds.[13] A diversity-stability correlation can no longer be used to argue for preservation of species and

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[12]John E. Cantlon, "The Stability of Natural Populations and Their Sensitivity to Technology," Brookhaven Symposia in Biology, Vol. 22 (1969), p. 201.

[13]Daniel Goodman, "The Theory of Diversity-Stability Relationships in Ecology," The Quarterly Review of Biology, Vol. 50 (1975), p. 261.

natural ecosystems, but the above reasons should prove to be the adequate basis for an alternative justification.

Ehrenfeld agrees that if the correlation does not exist, then environmentalists have made an error in using it to advocate climax systems; in many instances it has been shown that such environments are very fragile. But, he argues, it may be because of this very fragility, among other values, that climax environments need to be protected.[14]

Education

With the implications (outlined above) of whether or not a diversity-stability correlation is accepted by the public, what is being taught in our public schools takes on a greater importance. In a survey of eight high school biology texts (see Appendix), seven texts did not mention the hypothesis at all, while one, which dealt specifically with environmental issues, accepted the original statement of the hypothesis as true. In a similar survey of sixteen college texts, seven did not discuss the hypothesis, one accepted it without reservation, three recommended acceptance with caution, and five expressed doubts, saying that the relationship between diversity and stability is not a simple one but is probably a complicated interrelationship with other factors. More interest was expressed at the college level with a trend toward an expression of caution in

[14] David M. Ehrenfeld, "The Conservation of Non-Resources," American Scientist, Vol. 64 (1976), p. 652.

accepting the hypothesis without reservation. This survey is not intended to be comprehensive but is given here to merely demonstrate the general stance taken toward the hypothesis in the classroom.

The importance of a belief or disbelief in the diversity-stability hypothesis places a responsibility upon the classroom teacher to present the controversy in a proper perspective. If textbooks happen not to mention the issue, then supplemental material is needed, taken from sources which do adequately address the hypothesis. The works of May and Goodman cited in this paper are good sources.

If a textbook accepts the hypothesis as fact, then it is the responsibility of the teacher to present opposing views and to show that a belief in the hypothesis is as much culturally based as it is scientifically based. In the selection of a textbook, the discussion of the diversity-stability hypothesis can be used as a check of the book's comprehensiveness and the author's ability to present difficult, thought-provoking issues.

What should come out of such an educational process is (1) the awareness that there is as yet no definite conclusion to be drawn about diversity-stability correlations, (2) that the hypothesis is similar to other scientific theories and hypotheses in that it serves a heuristic function but may change or be discarded as we learn more, and (3) that this development and modification of hypotheses and the eventual substitution of a new hypothesis when the old has become inadequate for solving puzzles is descriptive of how science progresses.

Arising out of this portrayal of science is the implication that science is not as definite and precise as is commonly thought. Hypotheses and theories continually become outdated and need to be modified or replaced--what was once considered true may later appear to be inadequate, if not incorrect. A cautious approach in the application of scientific hypotheses is necessary. Especially in managing and exploiting our natural resources a great deal of caution is needed, for we do not yet fully understand, nor are we now able to predict, the effects of our actions.

Caution Recommended

The empirical evidence in hand does not permit a decision on the diversity-stability hypothesis other than to say that as traditionally stated it is inadequate. Due to the complexity and virtually infinite number of ecosystems, it may prove to be impossible to arrive at any firm position. Goodman states that it is not even clear whether high diversity is order or disorder. "Clearly, the belief that more diverse communities are more stable is without support," he says, but the hypothesis is attractive and will continue to be believed as "folk science."[15] McNaughton says that "continued assertions of validity of one or another conclusion about

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[15]Goodman, pp. 245, 261.

diversity-stability, in the absence of empirical tests, are acts of faith, not science."[16]

In light of this uncertainty and the vast implications, many scientists recommend caution. Preston cites the case of DDT (which destroys both pest and predator and then allows the pest to bounce back first) as evidence that study should precede man's intrusion to see if a population fluctuation will be good or bad. He adds that stability may not even be an ultimate goal, for he thinks that to get rid of all instability would be to destroy all of life.[17]

But in the midst of recommendations for caution are also heard calls for action. For example, in a paper dealing with the world energy problem, Häfele argued that efficiency, productivity, and capital investment can be substituted for energy. So what is needed is

> more general progress, not less. . . . . An almost exclusive concentration on energy conservation measures and related changes of lifestyles could very easily result in reduced productivities.
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> Once labor and energy productivities are sufficiently high there is no sufficient reason why the world's energy problem should not be solved. Nature has endowed us with enough resources provided we use them in a sophisticated manner.[18]

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[16] S. J. McNaughton, "Diversity and Stability of Ecological Communities: A Comment on the Role of Empiricism in Ecology," The American Naturalist, Vol. 111 (1977), p. 516.

[17] Preston, pp. 7,12.

[18] Wolf Häfele, "World Energy Productivity and Production: The Nature of the Problem," paper read at the International Energy Symposium I, October 15, 1980, Knoxville, Tennessee, mimeographed, pp. 14,18.

Though Swift denounces the mindless exploitation of resources which has gone on in the past, he also recognizes that there is not much purpose in preserving resources since they will eventually be exhausted regardless of what conservation measures are taken. Rather, our resources should be used to develop a different economy, one, he implies, which would exist in harmony with the environment.[19]

Possibly too much caution might doom our efforts to failure. If we are to stabilize and preserve ecosystems already impacted by man, it is probably better to proceed with a course of action incorporating the various views of management, possibly experimenting with different diversity-stability hypotheses in different ecosystems. Even if we make some wrong choices, we hopefully will learn to manage ecosystems and may find ways to correct the mistakes that we make.

But I would limit such experimentation to those ecosystems already substantially disrupted by man, because this more active approach does not discount the need or the desire for preservation of representative ecosystems and species diversity. As has already been pointed out, even if the diversity-stability hypothesis is wrong, there are other reasons for preserving diversity, not the least of which is our aesthetic enjoyment. But also, the preservation of diversity keeps our options open, for the solutions to problems that arise may lie in the diversity we have preserved.

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[19] Swift, p. 55.

May cautions,

> Until such time as we better understand the principles which govern natural associations of plants and animals, we would do well to preserve large chunks of pristine ecosystems.[20]

But of course we must preserve large chunks of pristine ecosystems even after we better understand the principles which govern the natural associations of plants and animals, even if we find that diversity is not needed for stability. A world devoid of natural places would lack much of the adventure and beauty that enriches our lives.

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[20]R. M. May, Stability and Complexity in Model Ecosystems (Princeton: Princeton University Press, 1973), p. 174.

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APPENDIX

APPENDIX

SURVEY OF SELECTED HIGH SCHOOL AND COLLEGE TEXTS

Diversity-Stability Hypothesis

Not Mentioned

High School

Haynes, Nancy Lehmann, ed. Biological Science, An Ecological Approach. Chicago: Rand McNally and Co., 1973.

Liebhen, Harold G., et al. Biological Science: Patterns and Processes. New York: Holt, Rinehart and Winston, Inc., 1970.

Moore, John A., et al. Biological Science, An Inquiry into Life. New York: Harcourt Brace Jovanovich, Inc., 1973.

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Smallwood, William L., and Edna R. Green. Biology. Atlanta: Silver Burdett Co., 1968.

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College

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Hylander, Clarence J. Wildlife Communities. Boston: Houghton Mifflin Co., 1966.

Kucera, Clair L. The Challenge of Ecology. St. Louis: C. V. Mosby Company, 1973.

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Wagner, Richard H. Environment and Man. New York: W. W. Norton and Company, Inc., 1974.

Whitton, B. A., ed. River Ecology. Berkeley: University of California Press, 1975.

Hypothesis Accepted

High School

Troost, Cornelius J., and Harold Altman, eds. Environmental Education: A Sourcebook. New York: John Wiley and Sons, Inc., 1972, pp. 34-35.

College

Clark, Mary E. Contemporary Biology, Concepts and Implications. Philadelphia: W. B. Saunders, 1973, p. 454.

Cautious Acceptance

College

Colinvaux, Paul. Introduction to Ecology. New York: John Wiley and Sons, Inc., 1973, pp. 237-238.

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College

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Odum, Eugene P. Fundamentals of Ecology. Philadelphia: W. B. Saunders Company, 1959, p. 148.

Pianka, Eric R. Evolutionary Ecology. New York: Harper and Row, Publishers, 1974, p. 242.

Pielou, E. C. Ecological Diversity. New York: John Wiley and Sons, 1975, pp. 129-130.

VITA

Stephen Russell Manning was born in Selma, Alabama on September 22, 1946. He spent his early years in Monroeville, Alabama and attended public school there, graduating from Monroe County High School in 1964. He attended Samford University in Birmingham, Alabama and in 1968 received a Bachelor of Science degree in chemistry with a minor in English. During his latter years of undergraduate school, he worked as a lab technician for hospitals in the Birmingham area.

Moving to Knoxville, Tennessee, he began teaching in public schools, first with Harriman City Schools and then with Knoxville City Schools. His teaching duties included math, reading, and science. From 1974 to 1976 he was employed as a senior research technician with Oak Ridge National Laboratory where he had spent the summer of 1969 on a special project to develop a tantalum-hafinum alloy. This time he worked in reactor safety studies and in his spare time conducted an independent project to determine the funding feasibility of a solar water pump that had application for arid Third World regions.

Leaving ORNL in 1976, he pursued a writing and editing career and has since published science, conservation, environmental, and travel articles in such periodicals as Sierra, The Tennessee Conservationist, Country Journal, Environmental Ethics, EnviroSouth, and Appalachia. He has also published photographs in Road Notes, Young World, and Esquire and reported on assignment for the U.S. International Communication Agency.

His editing experience has been with technical groups in such areas as ecology, energy conservation, reactor safety, radiopharmaceuticals, and textile instrumentation. He is presently acting as writer and editor for Spinlab, Inc. of Knoxville and as senior information analyst for Franklin Research Center in Oak Ridge, Tennessee. During the years since ORNL, he has also conducted adult education classes for Knox County Schools, homebound instruction for Knoxville City Schools, and classical guitar classes for Anderson County Schools along with private instruction in folk and classical guitar.

During his years of public school teaching, the author entered The University of Tennessee, Knoxville, first in Education C & I receiving a Tennessee Teaching Certificate and then in the Department of Philosophy, first completing the equivalent of an undergraduate major and then receiving a Master of Arts degree in philosophy in August 1981. The author is a member of the American Chemical Society, the National Association for Public Continuing and Adult Education, the Society for Technical Communication, the Tennessee Outdoor Writer's Association, and the American Association for the Advancement of Science. Following graduation Russ Manning will continue as a writer and editor.