coherent framework for viewing the ecological world. It is possible the metaphysic could pertain as well to the broader biological and social sciences.

It is appropriate to note in closing that the indefinite article appears in the title of this essay modifying the word *metaphysic.* No one is pretending to have developed "the" metaphysic for ecology, much less for all higher-level phenomena. Other combinations may be possible; however, the encouraging feature of the perspective just formulated is that it appears to reconcile disparate schools of ecological thought into one overarching, coherent structure. As a unified vision, it offers the promise for a fecund, new outlook that, it is hoped, will elicit more penetrating insights into ecosystem behaviors.

PART 2

Community, Niche, Diversity, and Stability

There is a popular saying that ecology has few, if any, principles, but many concepts. Frequently ecologists find hunting for exceptions to generalizations to be good sport, but equally frequently the quarry escapes the hunter because the argument often hinges on a definition of terms. Since ecology has a complex history of being formed from several sciences, its language can be ambiguous and confusing. Concepts are loose enough to be the subject of this type of sniping, but, of course, they are exceedingly useful because they bridge many observations and link interpretations.

The relationship between a concept and a principle is not a matter of either/or; rather, these two forms of generalization represent a continuum. A principle has withstood tests and is widely recognized as certain in an empirical sense. The areas of application of the principle usually are well understood. In contrast, a concept is a generalization based on fewer cases than a principle, and seldom are concepts tested through experimentation or formal observation. A concept represents the usual circumstances and may be weak in certain applications. We are less sure of a concept, although it represents a useful generalization that can guide research and application. Well-established concepts may even be recognized and used outside the field, although with qualifications.

For part 2, we have chosen four concepts that are central to ecological science, being generalizations of long standing or answers to fundamental definitional problems of ecology. These concepts are community, niche, diversity, and stability. They represent only a few of the many generalizations used in the science.

The Community Concept

The word *community* means "entities having interests or characteristics in common." In human terms *community* often refers to those who live together in a village or city and share a common space. The study of human communities has always been a central theme in human ecology, just as the study of plant and animal communities has been a recurring feature of the ecology of nature.

Early ecologists automatically adopted the term *community* for assemblages of plants and animals. For example, Anton Kerner von Marilaun, professor of botany at the University of Vienna, reported on his travels through the Danube Basin in 1863: "Wherever the reign of nature is not disturbed by human interference the different plant-species join together in communities, each of which has a characteristic form, and constitutes a feature in the landscape of which it is part" (1951). In the late nineteenth century, Karl Möbius, professor of zoology at Kiel, invented the word *biocœnosis* (meaning "biota living together") for the living organisms on an oyster reef in the Baltic Sea. In "An Oyster Bank Is a Biocönose, or a Social Community" (1881), reprinted here as chapter 6, Möbius describes plants and animals in terms of a single biotic community, recognizing the interconnections between taxa representing different trophic groups.

These two examples illustrate the two main options in community analysis. One might focus on the taxa, as Kerner did, or on the area shared by the taxa, as Möbius did. These different foci yield different approaches to community ecology because they lead toward problems of identification and quantification of taxa, or toward questions of the ways species and individuals share space, their trophic relationships, and so on.

Initially ecologists in their description of diversity merely listed the plants or animals observed within a habitat. But the invention of numerical methods of sampling meant that quantitative representation of species and the abundance of individuals could be in statistical form. Standardized sampling led toward theories of abundance.

Robert McIntosh, in *The Background of Ecology* (1985), traces the development of the numerical theme in community studies. As far back as 1789, Gilbert White, the naturalist parson of Selborne, England, recognized that the larger the area examined, the more species would be found (White 1981). The relationship describes a curvilinear pattern in which new species are encountered rapidly early in the sampling, but as the sample becomes larger, fewer new species appear (figure 7). Eventually all the species present in the community appear in the sample and the curve levels off. There are exceptions. Tropical rain forests' species-area curves sometimes continue to increase. Highly polluted habitats may exhibit declining diversity since fewer species can live in the inhospitable conditions.

August Thienemann (1939), director of the German Limnological Station at Plon, observed that the longer conditions at a site remained the same, the more species were present and the more stable the community. Thus there is a connection between stability and biological diversity.

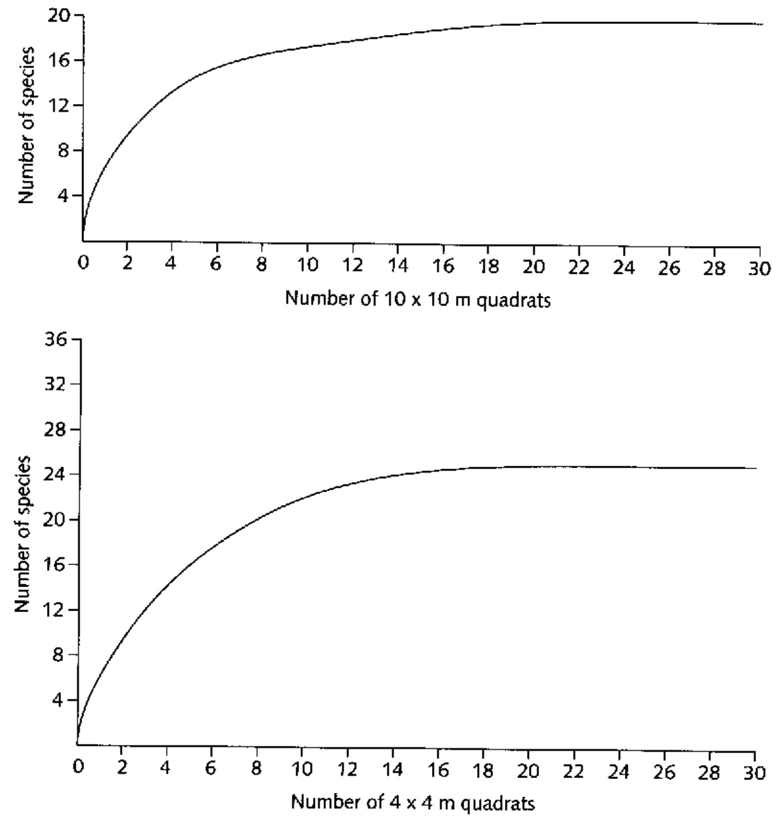

Figure 7. Species-area curves for oak-hickory forests in North Carolina. The upper curve represents trees sampled on 10 × 10–meter plots. The lower curve represents shrubs sampled on 4 × 4–meter plots. (From Oosting 1950.)

The resonance between the concepts of the human community and the natural community that must have influenced the language of ecology is clearer when one reflects on the history of human settlements. At the smallest scale, human adaptation is to microscale environmental conditions. The dwellings of a small village seem to be placed higgledly-piggledy with little relationship to other dwellings. At this level of scale the human has so little control over the environment that it is only through careful observation of the habitat that permanent habitation of a site becomes possible. Tiny raised areas are chosen and tiny depressions avoided to ensure a dry house site. As the settlement grows in scale, space becomes more organized until the stage of the large town or city is reached. At this stage, abstract principles of architecture and design can be used to organize activities and habitations. The classical design of Washington, D.C., by Pierre L'Enfant and the imperial Chinese cities designed to represent the physical body of the Buddha are illustrations. At the time ecological science was born, ecologists had all scales of settlement visible before them. Now that is no longer true, especially in developed countries. For example, in the United States even the smallest space is designed on geometrical principles, and the natural environment has relatively little influence on the design of the site or the buildings.

Community ecology shares with human ecology some of these issues. First, the focus in community ecology is on the biota (organized by species), not on the interaction of the biota and its environment, just as the focus in human ecology is on humans. Second, the community is often treated as a bounded entity. Third, the community is sometimes treated as having a single scale. Fourth, the presence of species or individuals is assumed to have causes that come from the life history of the organism or the environment. All of these assumptions raise questions that lead to research. How does selection operate on the individuals and species within a community? Can we recognize community boundaries? How is the microenvironmental scale treated? How do species respond to the diversity of environments within the habitat occupied by a community? Is the presence of species due to chance (à la Gleason) or are there design rules that lead to the most efficient or most powerful combinations of species (à la Clements)? Since biotic communities may contain thousands of species, unpacking communities and understanding the ways they are organized is a formidable challenge.

Niche

The ecologist's concept of niche is an invention of the science itself. It has, as far as we know, no deeper origin. It is concerned with a fundamental problem in ecology: how to integrate the two parts of the ecological system: the biotic element and the environmental element. The puzzle has three parts, as we have described earlier: the biotic, the environment, and the links between biota and environment. Each element in the triad is highly dynamic and changes over space/time. For example, the biota, through sexual reproduction and genetic processes, produce phenotypes that vary in fitness. The environment, through variation in the energy dynamic of the planet, changes over space/time. As a consequence, the links between the biota and the environment vary as well. There are few satisfactory models that allow the ecologist to relate the individual parts of the triad to the whole ecological system.

In "Niche, Habitat and Ecotope" (1973), Robert Whittaker, Simon Levin, and Richard Root review the history of the concept of niche; and in "On the Reasons for Distinguishing *Niche, Habitat,* and *Ecotope*" (1975), reprinted here as chapter 7, they provide a rationale for distinguishing the three concepts.

Initially, the variable in the life history of the biota that reflected its dynamic character was the capacity of organisms to move and occupy space. The distribution of organisms was related to environmental conditions. Together, these patterns represented the niche of the organism. Some ecologists equated the niche to the habitat and its properties. Other ecologists, especially those concerned with food as a resource, associated the niche with the organism.

These conversations led to a variety of insights. For example, the movement of a species into a new habitat, as occurs when an exotic animal appears for the first time on a continent, sometimes results in a successful invasion, leading eventually to its incorporation into the fauna or flora. In this case the ecologist might claim that the species moved into a vacant niche that existed in the habitat. *Niche* used in this sense seems to be a property of the place.

The Russian scientist G. F. Gause (1964) investigated the competition between species of yeast in closed chambers. In these experiments both species competed for the same resource, and one species eventually won out over the other. Gause's experiments were interpreted to mean that two species cannot occupy the same niche. In this sense niche is associated with a place but also reflects the species' ability to utilize the resources in that place. This usage comes closer to representing an integrated concept.

Finally, the English animal ecologist Charles Elton (1927, 1930), who was concerned with the feeding relationships of species, suggested that *niche* should be used in the same way that *profession* is used in everyday English, as when we observe someone walking in the street and say, "There goes the vicar." The word *vicar* conveys to the listener a particular picture of a person (especially, in this case, if one is British). Niche is the "profession" of a species. *Niche* used in the Eltonian sense is attached mainly to the species.

The modern ecologist knows of many more processes that describe the dynamic properties of the biota and the physical environment than the distribution of organisms or their feeding rates. The genotypic differences that underlie differences in the phenotype; the life history strategies that make use of cooperative, competitive, parasitic, predatory, and other relations; and our concepts of climatic and biogeochemical patterns may all contribute to a modern concept of niche. In modern ecological research, the challenge is to integrate the separate elements into a system in order to predict the success or failure of a species in an environment.

Biological Diversity

Awareness of the diversity of life is ancient. Clarence Glacken (1967: 5) attributes the term to Arthur Lovejoy (1964), who traced the term to Plato's *Timaeus* (1982). The modern concept of diversity is related to the ancient idea of plenitude. Glacken comments: "The principle of plenitude thus presupposes a richness, an expansiveness of life, a tendency to fill up, so to speak, the empty niches of nature: implicit in it is the recognition of the great variety of life and perhaps its tendency to multiply. When the principle of plenitude was fused with the Aristotelian idea of continuity, the richness and fecundity of all life was seen as manifesting itself in a scale of being from the lowest to the highest forms, and revealing itself in a visible order of nature" (6). Glacken continues by noting the importance of the concept in the Christian interpretation of nature, in natural history, and in Thomas Malthus's theory of population (1926), especially in his emphasis on fertility. One of the characteristics of Western thought about nature has been the emphasis on nature's fecundity, its capacity to multiply and overcome drought, deluge, plague, and destructive events. Many writers have observed that if a single species were allowed to breed freely, it could, given sufficient time, cover the entire earth. Darwin used this idea in his observation that even slow-breeding elephants could "stock the world in a few thousand years."

Thus, the ancient idea of plenitude has two parts. First, it recognizes the enormous variety of life that we observe in nature. And, second, it explains this variety by the tendency to propagate. If unchecked, the proliferation of life would have no end. These themes are directly relevant to ecology because the ecologist is interested in how the plenitude of life is checked and controlled by environmental factors.

When ecologists use the word *diversity,* they refer to taxonomic variety and the number of species in a community, area, or sample. As Ruth Patrick observes in "Biological Diversity in Ecology" (1983), reprinted here as chapter 8, ecologists also have applied the term to the variety of functions in an ecosystem or to the variety of ecosystems in a landscape. *Diversity* also has become a widely used word in conservation ecology as it relates to concerns about the loss of species through extirpation and extinction due to human activity. Biological diversity is one of the major interests of the world conservation movement.

While ecologists consider diversity an important parameter and an indicator of the health and well-being of a biotic community, diversity is difficult to measure. Very few complete censuses have been made in communities (though in unusual situations, such as hot springs, the diversity is often greatly reduced and as a consequence may have been completely sampled). Overall, we lack a good understanding of the size and variety of the biota in our forests, grasslands, and rivers. The problem with inventories usually lies with the microorganisms, such as bacteria and protozoa. In some instances we are not even certain if the species concept can be applied to these organisms. Edward O. Wilson, citing a Norwegian study of a single gram of beech forest soil in which between four and five thousand species were found, says: "The bacteria await

biologists as the black hole of taxonomy. Few scientists have even tried to dream of how all that diversity can be assayed and used" (1992: 148). As a consequence, diversity studies often focus on groups of organisms that can be sampled by conventional techniques, such as plants in quadrats or insects in Malaise traps. Ecologists assume that the patterns demonstrated for these easily recognized partial samples represent the whole community—that, for example, the diversity of herbivores is related to the diversity of the plants that serve as their food. But it is difficult to test such assumptions.

Stability

Stability is a fundamental concept in ecology that touches upon essentially every research project and crops up in every textbook. The idea that the earth is elegantly teleological comes from the earliest recorded statements of the ancient world. In Glacken's words:

> Geographically, it was a most important idea: if there were harmonious relationships in nature . . . the spatial distribution of plants, animals and man conformed to and gave evidence of this plan; there was a place for everything and everything was in its place . . . the idea of a design with all its parts well in place and adapted to one another in an all-embracing harmony implied stability and permanence; nature and human activity within it were a great mosaic, full of life and vigor, conflict and beauty, its harmony persisting among the myriads of individual permutations, an underlying stability. (1967: 147–48)

An orderly and harmonious cosmos is a stable cosmos.

Frank Egerton, who has made the most complete study of the balance of nature, comments that in ecology the concept has been a "background assumption rather than a hypothesis or theory" (1973: 324). And, as a consequence, the concept has been poorly articulated and defined and therefore is seldom examined explicitly. Like Daniel Simberloff (1980 [reproduced in this volume]), Egerton pins the origin of the idea of teleology to Greek philosophy and science which assumed that nature was "constant and harmonious." In the *History,* Herodotus (1862), for example, notes the correlation between reproductive capacity and the habits of species, which were evidence for the design of nature by divine Providence. In the *Timaeus,* Plato (1982) accounts for the creation of the universe by an intelligent being, meaning that the universe itself has an intelligible design. These classical ideas, supported by evidence from natural history, provided the basis for the Christian concept of an orderly nature operating by divine plan. Much of theoretical ecology's emphasis on stability and equilibrium, in the words of philosopher Mark Sagoff, "blurs the line between science and religion" (1997: 888).

As Egerton shows, the balance of nature is at the core of Carolus Linnaeus's famous concept of an "economy of nature." In a 1744 essay, Linnaeus attempts to explain how the world was stocked with plants and animals. Linnaeus imagines the Garden of Eden as a tropical mountain with Arctic species at the top, temperate species in the middle, and tropical species at the bottom, in a pattern familiar to ecologists as life zones. Species in these zones increased in number and spread out over the earth. In a later (1749) essay, he speculates that the "economy of nature" is maintained by the propagation, preservation, and destruction of plants and animals. The balance between these regulatory functions became an organizing theory of the new science. Frederic Clements's superorganism ontology (1916 [reproduced in this volume]) is founded on the *a priori* assumption of design and balance in nature.

In contemporary ecology the balance-of-nature concept has been largely rejected. Charles Elton is perfectly clear: "'The balance of nature' does not exist and perhaps never has existed" (1930). The problem is that species vary continuously in time and space and their regulation comes from factors both within and without the organism. The notion of specific variation with each case study fits the nature of observation in a postmodern world in which relativity is a major explanatory element. Yet the concept of balance or stability continues to reemerge. The field naturalist and ecologist continue to find in nature order and continuity at one scale and variety and change at other scales. For example, Eugene Odum states, "Questions of stability versus aging of mature systems may be academic in many situations where disease, storms, fires and so on hasten the death of the community at or before climax and start a new cycle of several stages. . . . But acute perturbations can also be stabilizing if they occur in the form of regular pulses that can be utilized by adapted species as an extra energy subsidy" (1993: 203, 202).

So, even though the teleological view of nature has been severely criticized, the connection between biotic diversity and system stability remains an important theme in ecology. David Tilman and John Downing (1994) have demonstrated that ecosystems with high species diversity are more likely to contain species that can do well under a perturbed environment and will compensate for species that are negatively affected. In their studies of grasslands affected by an unusual drought, they found that drought resistance of the system was significantly related to the predrought species richness of the community. Both resistance to drought and resilience, or the capacity to recover from drought, were related nonlinearly to species richness.

Thus, the expression of a modern concept of the balance of nature or system stability is still alive in its general sense. But it is changed from the original definition because it recognizes change and variation; and as Odum and Tillman and Downing suggest, change maintains balance. In "Stability in Ecological Communities" (1987), reprinted here as chapter 9, Andrew Redfearn and Stuart Pimm identify five different meanings of *stability* and demonstrate how the early stability-diversity of Elton (1958) and Robert MacArthur (1955)—i.e., that more complex communities are more stable than simpler ones—has been supplanted by the view "that there is nothing inherently unstable about simple systems."

Where some ecologists see a degree of balance or stability in nature, others see chaos. Chaos theory derives from the mathematics of meteorology. It proposes that complex systems, such as ecosystems, behave in unpredictable, nonlinear, nondeterministic ways. Chaos theory replaces conventional stability or equilibrium theory with nonlinear, nonequilibrium behavior. The behavioral sequences of such systems partly depend upon the initial conditions. Very small differences, which were ignored as unimportant to system behavior under earlier theory, in chaos theory are recognized as causing widely different system patterns. Entropicists also believe chaos is creative. James Gleick, for example, states: "Unpredictability was only the attention grabber. Those studying chaotic dynamics discovered that the disorderly behavior of simple systems acted as a creative process. It generated complexity; richly organized patterns, sometimes stable and sometimes unstable, sometimes finite and sometimes infinite, but always with the fascination of living things" (1987: 43). Stuart Kauffman (1995) suggests that a new kind of order emerges at "the edge of chaos"—to use Christopher Langton's (1989) phrase—between fixed deterministic order, which is a static or deathlike condition, and chaos, which is unpredictable behavior. Between these two conditions, patches of order in a chaotic landscape create conditions for new forms of dynamic order to emerge, exist, and eventually disappear.

Chaos theory has not yet been applied to the problems of community theory except in a negative and critical way. If we are to find a new model that fits our explanation more effectively, then it must also be expressed in ways that fit both our scientific experience and our personal observations. Until that happens we have a job of translation before us.

Conclusion

Consideration of the background and history of several concepts in wide use in ecology indicates that there is a rich area of philosophic exploration within ecological science. Some of the concepts have deep roots that take us back to antiquity. The ideas of plenitude and order continue to inform our interpretations of nature. In addition, however, ecologists have invented new concepts to describe or make clear their insights. The concept of niche is an example of this theme. Other concepts are created by analogy from other sciences or from human experience generally. A case in point is the community concept in ecology. Möbius was among the first to write about the community, but he gave it a unique name, the *biocönose,* to distinguish the ecological community from the human community. Thus, ecological concepts are grounded in many ways other than the evolutionary, systems, and natural history themes discussed in the earlier chapters. Each concept deserves analysis, which will lead to greater precision in thought and method.

CHAPTER 6

An Oyster Bank Is a Biocönose, or a Social Community

Karl Möbius

The history of the impoverishment of the French oyster-beds is very instructive. When the beds of Cancale had been nearly deprived of all their oysters, by reason of excessive fishing, with no protection, the cockle (*Cardium edule*) came in and occupied them in place of the oyster; and vast hordes of edible mussels (*Mytilus edulis*) under similar circumstances appeared upon the exhausted beds near Rochefort, Marennes, and the island of Oléron. The territory of an oyster-bed is not inhabited by oysters alone but also by other animals. Over the Schleswig-Holstein sea-flats, and also along the mouths of English rivers, I have observed that the oyster-beds are richer in all kinds of animal life than any other portion of the sea-bottom. As soon as the oyster-men have emptied out a full dredge upon the deck of their vessel, one can see nimble pocket-crabs (*Carcinus moenas*) and slow horn-crabs (*Hyas aranea*) begin to work their way out of the heap of shells and living oysters, and try to get to the water once more. Old abandoned snail-shells begin to move about, caused by the hermit-crabs (*Pagarus bernhardus*), which have taken up their residence in them, trying to creep out of the heap with their dwelling. Spiral-shelled snails (*Buccinum undatum*) stretch their bodies as far out of the shell as they can, and twist from side to side, trying, with all their power, to roll themselves once more into the water. Red starfish (*Asteracanthion rubens*), with five broad arms, lie flat upon the deck, not moving from the place, although their hundreds of bottle-shaped feet are in constant motion. Sea-urchins (*Echinus miliaris*), of the size of a small apple, bristling with greenish spines, lie motionless in the heap. Here and there a ring-worm (*Nereis pelagica*), of a changeable bluish color, slips out of the mass of partially dead, partially living, animals. Black edible mussels (*Mytilus edulis*) and white cockles (*Cardium edule*) lie there with shells as firmly closed as are those of the oysters.

From *The Oyster and Oyster-Culture,* trans. H. J. Rice. In *Documents of the Senate of the United States for the Third Session of the Forty-sixth Congress and the Special Session of the Forty-seventh Congress (1880–1881),* pp. 721–24. Notes omitted.