Chapter 1

INTRODUCTION: THE SCOPE OF ECOLOGY

1. ECOLOGY—ITS RELATION TO OTHER SCIENCES AND ITS RELEVANCE TO HUMAN CIVILIZATION

Man has been interested in ecology in a practical sort of way since early in his history. In primitive society every individual, to survive, needed to have definite knowledge of his environment, i.e., of the forces of nature and of the plants and animals around him. Civilization, in fact, began when man learned to use fire and other tools to modify his environment. It is even more necessary than ever for mankind as a whole to have an intelligent knowledge of the environment if our complex civilization is to survive, since the basic "laws of nature" have not been repealed; only their complexion and quantitative relations have changed, as the world's human population has increased and as man's power to alter the environment has expanded.

Like all phases of learning, the science of ecology has had a gradual, if spasmodic, development during recorded history. The writings of Hippocrates, Aristotle, and other philosophers of the Greek period contain material which is clearly ecological in nature. However, the Greeks literally did not have a word for it. The word "ecology" is of recent coinage, having been first proposed by the German biologist Ernst Haeckel in 1869. Before this, many of the great men of the biological renaissance of the eighteenth and nineteenth centuries had contributed to the subject even though the label "ecology" was not in use. For example, Anton van Leeuwenhoek, best known as a pioneer microscopist of the early 1700s, also pioneered the study of "food chains" and "population regulation" (see Egerton, 1968), two important areas of modern ecology. As a recognized distinct field of biology, the science of ecology dates from about 1900, and only in the past decade has the word become part of the general vocabulary. Today, everyone is acutely aware of the environmental sciences as indispensable tools for creating and maintaining the quality of human civilization. Consequently, ecology is rapidly becoming the branch of science that is most relevant to the everyday life of every man, woman, and child.

The word ecology is derived from the Greek *oikos*, meaning "house" or "place to live." Literally, ecology is the study of organisms "at home." Usually ecology is defined as the study of the relation of organisms or groups of organisms to their environment, or the science of the interrelations between living organisms and their environment. Because ecology is concerned especially with the biology of *groups* of organisms and with *functional* processes on the lands, in the oceans, and in fresh waters, it is more in keeping with the modern emphasis to define ecology as the study of the structure and function of nature, it being understood that mankind is a part of nature. One of the definitions in Webster's Unabridged Dictionary seems especially appropriate for the closing decades of the 20th century, namely, "*the totality or pattern of relations between organisms and their environment.*" In the long run the best definition for a broad subject field is probably the shortest and least technical one, as, for example, "environmental biology."

So much for definitions. To understand the scope and relevance of ecology, the subject must be considered in relation to other branches of biology and to "*ologies*" in general. In the present age of specialization in human endeavors, the inevitable connections between different fields are often obscured by the large masses of knowledge within the fields (and sometimes also, it must be admitted, by stereotyped college courses). At the other extreme, almost any field of learning may be so broadly defined as to take in an enormous range of subject material. Therefore, recognized "fields" need to have recognized bounds, even if these bounds are somewhat arbitrary and subject to shifting from time to time. A shift in scope has been especially noteworthy in the case of ecology as general public awareness of the subject has increased. To many, "ecology" now stands for "the totality of man and environment." But first let us examine the more traditional academic position of ecology in the family of sciences.

For the moment, let us look at the divisions of biology, "the science of life." We traditionally cut the biology "layer cake," as it were, into small pieces in two distinct ways, as shown in Figure 1–1. We may divide it "horizontally" into what are usually called "basic" divisions because they are concerned with fundamentals common to all life, or at least are not restricted to particular organisms. Morphology, physiology, genetics, ecology, evolution, molecular biology, and developmental biology are examples of such divisions. We may also divide the cake "vertically" into what may be called "taxonomic" divisions, which deal with the morphology, physiology, ecology, etc., of specific kinds of organisms. Zoology, botany, and bacteriology are large divisions of this type, and phycology, protozoology, mycology, entomology, ornithology, etc., are divisions dealing with more limited groups of organisms. Thus ecology is a basic division of biology and, as such, is also an integral part of any and all of the taxonomic divisions. Both approaches are profitable. It is often very productive to restrict work to certain taxonomic groups, because different kinds of organisms require different methods of study (one cannot study eagles by the same methods used to study bacteria) and because some groups of organisms are economically or otherwise much more important or interesting to man than others. Ultimately, however, unifying principles must be delimited and tested if the subject field is to qualify as "basic." It is the purpose of Part 1 of this book to outline briefly this aspect of ecology.

Perhaps the best way to delimit modern ecology is to consider it in terms of the concept of *levels of organization* visualized as a sort of "biological spectrum" as shown in Figure 1–2. Community, population, organism, organ, cell, and gene are widely used terms for several major biotic levels shown in hierarchial arrangement from large to small in Figure 1–2. Interaction with the physical environment (energy and matter) at each level produces characteristic functional systems. By a *system* we mean just what Webster's Collegiate Dictionary defines as "regularly interacting and interdependent components forming a unified whole." Systems containing living components (biological systems or biosystems) may be conceived at any level in the hierarchy illustrated in Figure 1–2, or at any intermediate position convenient or practical for analysis. For example, we might consider not only gene systems, organ systems, and so on, but also host-parasite systems as intermediate levels between population and community.

Ecology is concerned largely with the right-hand portion of this spectrum, that is, the system levels beyond that of the organism. In ecology the term *population*, originally coined to denote a group of people, is broadened to include groups of individuals of any one kind of organism. Likewise, *com-*

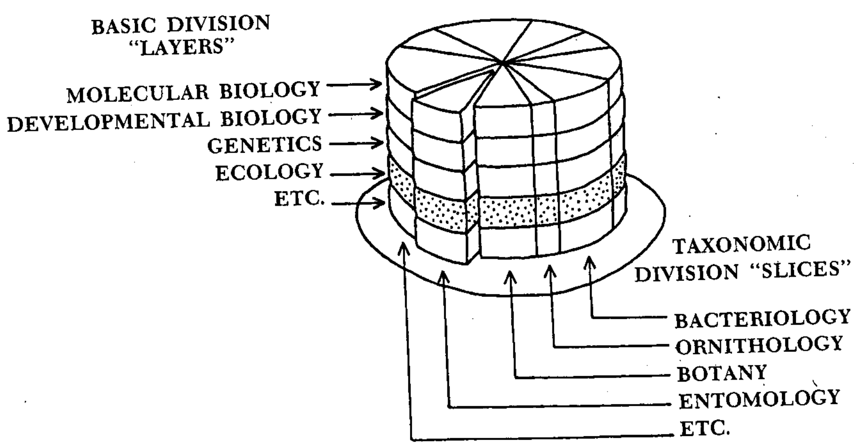

Figure 1–1. The biology "layer cake," illustrating "basic" (horizontal) and "taxonomic" (vertical) divisions.

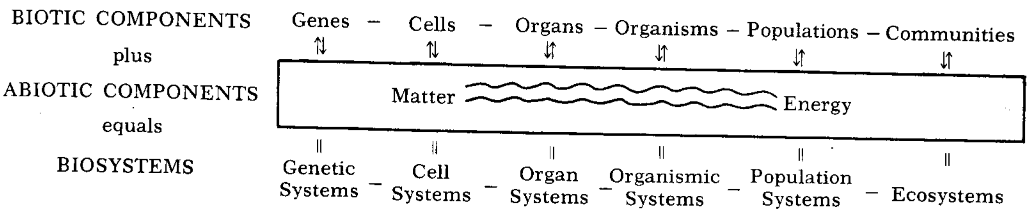

Figure 1–2. Levels of organization spectrum. Ecology focuses on the right-hand portion of the spectrum, that is, the levels of organization from organisms to ecosystems.

munity in the ecological sense (sometimes designated as "biotic community") includes all of the populations occupying a given area. The community and the nonliving environment function together as an ecological system or *ecosystem. Biocoenosis* and *biogeocoenosis,* terms frequently used in the European and Russian literature, are roughly equivalent to community and ecosystem respectively. The largest and most nearly self-sufficient biological system we know about is often designated as the *biosphere* or *ecosphere,* which includes all of the earth's living organisms interacting with the physical environment as a whole so as to maintain a steady-state system intermediate in the flow of energy between the high energy input of the sun and the thermal sink of space.

It is important to note that no sharp lines or breaks were indicated in the above "spectrum,"* not even between the organism and the population. Since in dealing with man and higher animals we are accustomed to think of the individual as the ultimate unit, the idea of a continuous spectrum may seem strange at first. However, from the standpoint of interdependence, interrelations and survival, there can be no sharp break anywhere along the line. The individual organism, for example, cannot survive for long without its population any more than the organ would be able to survive for long as a self-perpetuating unit without its organism. Similarly, the community cannot exist without the cycling of materials and the flow of energy in the ecosystem.

One reason for listing the levels of organization horizontally instead of vertically is to emphasize that, in the long run, no one level is any more or less important or any more or less deserving of scientific study than any other level. Some attributes, obviously, become more complex and variable as we proceed from the left to the right, but *it is an often overlooked fact that other attributes become less complex and less variable as we go from the small to the large unit.* Because homeostatic mechanisms, that is, checks and balances, forces and counter forces, operate all along the line, a certain amount of integration occurs as smaller units function within larger units. For example, the rate of photosynthesis of a forest community is less variable than that of individual leaves or trees within the community, because when one part slows down another may speed up in a compensatory manner. *When we consider the unique characteristics which develop at each level,* there is no reason to suppose that any level is any more difficult or any easier to study quantitatively. For example, growth and metabolism may be effectively studied at the cellular level or at the ecosystem level by using technology and units of measurement of a different order of magnitude. Furthermore, the findings at any one level *aid in the study of another level, but never completely explain the phenomena occurring at that level.* This is an important point because persons sometimes contend that it is useless to try to work on complex populations and communities when the smaller units are not yet fully understood. If this idea was pursued to its logical conclusion, all biologists would concentrate on one level, the cellular, for example, until they solved the problems of this level; then they would study tissues and organs. Actually, this philosophy was widely held until biologists discovered that each level had characteristics which knowledge of the next lower level explained only *in part.* In other words, not all attributes of a higher level are predictable if we know only the properties of the lower level. Just as

* Actually the "levels" spectrum, like a radiation spectrum or a logarithmic scale, theoretically can be extended infinitely in both directions.

the properties of water are not predictable if we know only the properties of hydrogen and oxygen, so the characteristics of ecosystems cannot be predicted from knowledge of isolated populations; one must study the forest (i.e., the whole) as well as the trees (i.e., the parts). Feibleman (1954) has called this important generalization the "theory of integrative levels."

In summary, the principle of *functional integration involving additional properties with increasing complexity of structure* is an especially important one for the ecologist to note. Advances in technology in the past 10 years have made it possible to deal quantitatively with large, complex systems such as the ecosystem. Tracer methodology, mass chemistry (spectrometry, colorimetry, chromatography, etc.), remote sensing, automatic monitoring, mathematical modeling, and computer technology are providing the tools. Technology is, of course, a two-edged sword; it can be the means of understanding the wholeness of man and nature or of destroying it.

2. THE SUBDIVISIONS OF ECOLOGY

In regard to subdivisions, ecology is sometimes divided into *autecology* and *synecology*. Autecology deals with the study of the individual organism or an individual species. Life histories and behavior as a means of adaptation to the environment are usually emphasized. Synecology deals with the study of groups of organisms which are associated together as a unit. Thus, if a study is made of the relation of a white oak tree (or of white oak trees in general) or a wood thrush (or of wood thrushes in general) to the environment, the work would be autecological in nature. If the study concerned the forest in which the white oak or the wood thrush lives, the approach would be synecological. In the former instance attention is sharply focused on a particular organism with the purpose of seeing how it fits into the general ecological picture, much as one might focus attention on a particular object in a painting. In the latter instance the picture as a whole is considered, much as one might study the composition of a painting.

For the purpose of this textbook the subject of ecology is subdivided in three ways. In Part 1 the chapters are arranged according to the levels of organization concept, as discussed in the previous section. We shall start with the ecosystem, since this is the level with which we must ultimately deal, and then consider in sequence communities, populations, species and individual organisms. Then we shall return to the ecosystem level in order to consider the development, evolution and modeling of nature.

In Part 2 the subject is subdivided according to the kind of environment or habitat, namely freshwater ecology, marine ecology, and terrestrial ecology. Although the basic principles are the same, the kinds of organisms, interrelationships with man, and the methods of study may be quite different for different environments. Subdivision by habitat is also convenient as preparation for field trips and for the presentation of descriptive data on the biota.

In Part 3 applications are considered under such subdivisions as "natural resources," "pollution," "space travel" and "applied human ecology" in order to relate basic principles to problems.

As was discussed for biology in general, ecology also may be subdivided along taxonomic lines, for example, plant ecology, insect ecology, microbial ecology and vertebrate ecology. Orientation within a restricted taxonomic group is profitable since attention is focused on the unique or special features in the ecology of that group, as well as on the development of detailed methods. In general, problems which pertain only to restricted groups are beyond the scope of this text since they are best considered after the general principles have been outlined.

Subdivisions in ecology, as in any other subject, are useful because they facilitate discussion and understanding as well as suggest profitable ways to specialize within the field of study. From the brief discussion in this section, we see that one might concentrate on processes, levels, environments, organisms, or problems and make valuable contributions to the overall understanding of environmental biology.

3. ABOUT MODELS

A model is a formulation that mimics a real-world phenomenon, and by means of which predictions can be made. In simplest form, models may be verbal or graphic (i.e., informal). Ultimately, however, models must be statistical and mathematical (i.e., formal) if quantitative predictions are to be reasonably good. For example, a mathematical formulation that mimics numerical changes taking place in a population of insects, and by means of which numbers in the population at some point in time could be predicted, would be considered a biologically useful model. If the population in question is a pest species, the model could also become economically important.

Computer operations of models make it possible to predict probable outcomes as parameters in the model are changed, new parameters added, or old ones removed. In other words, a mathematical formulation can often be "tuned" by computer operations to improve the "fit" to the real-world phenomenon. Above all, models are extraordinarily useful as summaries of what is understood about the situation being modeled, and thereby are useful in delimiting aspects needing new or better data or new principles. When a model does not work, i.e., is a poor mimic of the real world, computer operations often can provide clues to the refinements or changes needed. Once a model proves to be a useful mimic, then opportunities for experimentation are unlimited since one can introduce new factors or perturbations and see how they would affect the system.

Contrary to the feeling of many skeptics when it comes to modeling complex nature, information about only a relatively small number of variables is often a sufficient basis for effective models because "key factors" or "integrative factors" (as were discussed in Section 2 of this introductory chapter) often dominate or control a large percentage of the action. Watt (1963), for example, states that "We do not need a tremendous amount of information about a great many variables to build revealing mathematical models for population dynamics." When we move up to the level of whole nature, or the ecological system, this principle should still hold, provided the formulations used in the model are also brought up to that level. In summary, models are not intended to be exact copies of the real world but simplifications that reveal the key processes necessary for prediction.

In the chapters that follow in Part 1 of this book the paragraphs headed by the word "**Statement**" are, in effect, "word" models of the ecological principle in question. In many cases graphic or circuit models will also be presented and in some cases simplified mathematical formulations are included to clarify quantitative relationships. An introduction to the procedures used in mathematical modeling is presented as the final chapter in Part 1 under the title of "Systems Ecology." Most of all, what this text attempts to provide are the principles, simplifications, and abstractions that one must deduce from the real world of nature before one can even start to construct a mathematical model of it.