ECOLOGY
The Experimental Analysis of Distribution and Abundance

Second Edition

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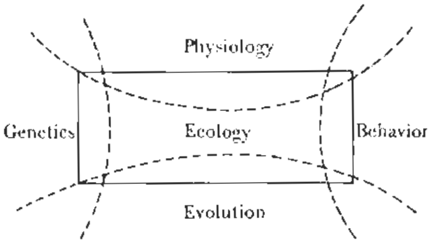
HARPER & ROW, PUBLISHERS
New York, Hagerstown, San Francisco, London

Chapter 1

Introduction to the Science of Ecology

DEFINITION

The word *ecology* came into use in the last half of the nineteenth century. Henry Thoreau in 1858 used the word in his letters, but he did not define it. Ernst Haeckel in 1869 defined *ecology* as the total relations of the animal to both its organic and its inorganic environment. This very broad definition has provoked some authors to point out that, if this is ecology, there is very little that is *not* ecology. Since four biological disciplines are closely related to ecology—genetics, evolution, physiology, and behavior—the problem of defining ecology may be viewed schematically in the following way:



Broadly interpreted, ecology overlaps each of these subjects; hence we need a more restrictive definition.

Charles Elton (1927) in his pioneering book *Animal Ecology* defined ecology as *scientific natural history*. Although this definition does point out the origin of many of our ecological problems, it is again uncomfortably vague. Eugene Odum (1963) has defined ecology as the study of the *structure and function of nature*. This statement has the merit of emphasizing the form-and-function idea that permeates biology, but it is still not a completely clear definition.

A clear and restrictive definition of ecology is this: *Ecology is the scientific study of the distribution and abundance of organisms* (Andrewartha 1961). This definition is static and leaves out the important idea of *relationships*. Ecology is about relationships, and we can modify Andrewartha's definition as follows: *Ecology is the scientific study of the interactions that determine the distribution and abundance of organisms*. This definition of ecology restricts the scope of our quest to a manageable level and forms the starting point for this book. We are interested then in *where* organisms are found, *how many* occur there, and *why*.

HISTORY OF ECOLOGY

The roots of ecology lie in natural history, which is as old as man himself. Primitive tribes, which depended on hunting, fishing, and food gathering, needed detailed knowledge of where and when their quarry might be found. The establishment of agriculture increased the need to learn about the practical ecology of plants and domestic animals.

Spectacular plagues of animals attracted the attention of the earliest writers. The Egyptians and Babylonians feared locust plagues, and supernatural powers were often believed to cause these outbreaks. The Book of Exodus (7:14–12:30) describes the plagues that God called down upon the Egyptians. In the fourth century B.C. Aristotle tried to explain these plagues of field mice and locusts in his *Historia Animalium*. He pointed out that the high reproductive rate of field mice could produce more mice than could be reduced by their natural predators, such as foxes and ferrets, or by the control efforts of man. Nothing succeeded in reducing these mouse plagues, Aristotle stated, except the rain, and after heavy rains the mice disappeared rapidly.

Ecological harmony was a guiding principle basic to the Greeks' understanding of nature, and Egerton (1968a) has traced this concept from ancient times to the modern term "balance of nature." This concept of "providential ecology," in which nature is designed to benefit and preserve each species, was implicit in the writings of Herodotus and Plato. The assumptions of this world view were that the numbers of every species remain essentially constant. Outbreaks of some populations might occur, but these could be traced usually to divine intervention for the punishment of evil-doers. Each species had a special place in nature, and extinction did not occur because it would disrupt this balance and harmony in nature.

Little conceptual advance occurred until students of natural history and human ecology began to focus the ideas of ecology and to provide an analytical framework. Graunt (1662), who described human populations in quantitative terms, can be called the father of demography (Cole 1958). He recognized the importance of measuring in a quantitative way the birth rate, death rate, sex ratio, and age structure of human populations, and he complained about the inadequate census data available in England in the seventeenth century. Graunt estimated the potential rate of population growth for London and concluded that even without immigration, London could double its population in 64 years.

Leeuwenhoek studied the reproductive rate of grain beetles, carrion flies, and human lice. In 1687 he counted the number of eggs laid by female carrion flies and calculated that one pair of flies could produce 746,496 flies in three months. Thus, Leeuwenhoek made one of the first attempts to calculate theoretical rates of increase for an animal species (Egerton 1968c).

Buffon in his *Natural History* (1756) touched on many of our modern ecological problems and recognized that populations of man, other animals, and plants are subjected to the same processes. Buffon discussed, for example, how the great fertility of every species was counterbalanced by innumerable agents of destruction. He believed that plague populations of field mice were checked partly by diseases and scarcity of food. Buffon did not accept Aristotle's idea that heavy rains caused the decline of dense mouse populations but thought that control was achieved by biological agents. Rabbits, he stated, would reduce the countryside to a desert if it were not for their predators. Buffon thus dealt with problems of population regulation that are still unsolved today.

Malthus published one of the earliest controversial books on demography. In his *Essay on Population* (1798) he calculated that although the numbers of organisms can increase geometrically (1, 2, 4, 8, 16, . . .), their food supply may never increase faster than arithmetically (1, 2, 3, 4, . . .). The arithmetic rate of increase in food production seems to be somewhat arbitrary, and Malthus may have presented this rate as a reasonable maximum supposition (Flew 1957). The great disproportion between these two powers of increase led Malthus to infer that reproduction must eventually be checked by food production. The thrust of Malthus' ideas was *negative*—what prevents populations from reaching the bare subsistence level that his theory predicts? What checks operate against the tendency toward a geometric rate of increase? Two centuries later we still ask these questions. These ideas were not new, since Machiavelli had said much the same thing about 1525, and Buffon in 1751, and several others had anticipated Malthus. It was Malthus, however, who brought these ideas to general attention. Darwin used the reasoning of Malthus as one of the bases for his theory of natural selection.

Other workers questioned the ideas of Malthus. For example, in 1841 Doubleday brought out his true law of population. He believed that whenever a species was threatened, nature made a corresponding effort to preserve it by increasing the fertility of its members. Human populations that were undernourished had the highest fertility; those that were well fed had the lowest fertility. Doubleday explained these effects by the oversupply of mineral nutrients in well-fed populations. Doubleday thus observed a basic fact that we recognize today, although his explanations were completely wrong.

Interest in the mathematical aspects of demography increased after Malthus. Quetelet, a Belgian statistician, suggested in 1835 that the potential ability of a population to grow geometrically was balanced by a resistance to population growth. In 1838 his student Verhulst derived an equation describing the course of growth of a population over time. This S-shaped curve he called the *logistic curve*. This work was overlooked until modern times, and we shall return to it later in detail.

Farr (1843) was one of the earliest demographers concerned with mortality. He discovered that in England there was a relation between the density of the population and the death rate (Farr's rule), such that mortality increased as the sixth root of density:

$$R = cD^m$$

where

R = mortality rate
D = density of the population
c, m = constants (m = approx. $\frac{1}{6}$)

Farr returned in 1875 to further consideration of the human population of England. He pointed out that even though the death rate had been steadily declining in England during the 1800s, this did not automatically lead to a population increase, since the birth rate might fall an equivalent amount. Farr pointed out that Malthus' postulate that food supply increases arithmetically was not true at least in the United States, where food production had increased geometrically at a rate even greater than that of the human population.

During most of this time the philosophical background had not changed from the idea of harmony of nature of Plato's day. Providential design was still the guiding light. In the late eighteenth and early nineteenth centuries two ideas that undermined the idea of balance of nature gradually gained support: (1) that many species had become extinct and (2) that competition caused by population pressure is important in nature. The consequences of these two ideas became clear with the work of Malthus, Lyell, Spencer, and Darwin in the nineteenth century. Providential ecology and the balance of nature were replaced by natural selection and the struggle for existence (Egerton 1968b).

Many of the early developments in ecology came from the applied fields of agriculture, fisheries, and medicine. Work on the insect pests of crops has been one important source of ideas. The regulation of population size in insect pests is a basic problem that has long been under study. In 1762 the mynah bird was introduced from India to the island of Mauritius to control the red locust. By 1770 the locust threat was a negligible problem (Moutia and Mamet 1946). Forskål wrote in 1775 about the introduction of predatory ants from nearby mountains into date palm orchards to control other species of ants feeding on the palms in southwestern Arabia. In subsequent years an increasing knowledge of insect parasitism and predation led to many such introductions all over the world in the hope of controlling introduced and native agricultural pests (Doutt 1964). We discuss this problem of *biological control* in Chapter 18.

Medical work on infectious diseases such as malaria around the 1890s gave rise to the study of epidemiology and interest in the spread of disease through a population. Before malaria could be controlled adequately, it was necessary to know in detail the ecology of mosquitoes. The pioneering work of Ross (1908, 1911) attempted to describe in mathematical terms the propagation of malaria, which is transmitted by mosquitoes. In an infected area the propagation of malaria is determined by two continuous and simultaneous processes: (1) The number of new infections among people depends on the number and infectivity of mosquitoes; (2) the infectivity of mosquitoes depends on the number of people in the locality and the frequency of malaria among them. Ross could write these two processes as two simultaneous differential equations:

$$\begin{array}{l}\text{Rate of increase}\\ \text{of infected humans}\end{array} = \left(\underset{\substack{\downarrow \\ \textit{(depends on number of} \\ \textit{infected mosquitoes)}}}{\begin{array}{l}\text{new infections per}\\ \text{unit time}\end{array}} - \text{recoveries per unit time} \right)$$

$$\begin{array}{l}\text{Rate of increase of}\\ \text{infected mosquitoes}\end{array} = \left(\underset{\substack{\downarrow \\ \textit{(depends on number of} \\ \textit{infected humans)}}}{\begin{array}{l}\text{new infections per}\\ \text{unit time}\end{array}} - \begin{array}{l}\text{deaths of infected}\\ \text{mosquitoes per unit time}\end{array} \right)$$

Ross had described an ecological process with a mathematical model, and his work represents a pioneering attempt at *systems analysis* (see Chapter 27). Such models can help us to clarify the problem—we can now analyze these components—and predict new situations (Lotka 1923).

Production ecology had its beginnings in agriculture, and Egerton (1969) has traced this back to the eighteenth-century botanist Richard Bradley. Bradley recognized the fundamental similarities of animal and plant production, and he proposed methods of maximizing agricultural yields (and hence profits) for vineyards, trees, poultry, rabbits, and fish. The conceptual framework that Bradley used—monetary investment vs. profit—could be applied to any organism. This *optimum-yield problem* is an important part of applied ecology (see Chapter 17).

Recognition of communities of living organisms in nature is very old, but specific recognition of the interrelations of the organisms in a community is relatively recent. Edward Forbes in 1844 described the distribution of animals in British coastal waters and part of the Mediterranean Sea, and he wrote of zones of differing depths which were distinguished by the associations of species they contained. Forbes noted that some species are found only in one zone and that other species have a maximum of development in one zone but occur sparsely in other adjacent zones. Mingled in are stragglers that do not fit the zonation pattern. Forbes recognized the dynamic aspect of the interrelations between these organisms and their environment. As the environment changed, one species might die out, another might increase in abundance. Similar ideas were expressed by Karl Möbius in 1877 in a classic essay on the oyster-bed community as a unified collection of species. Möbius coined the word *biocoenosis* to describe such a community.

S. A. Forbes (1887), in a classical paper on "The Lake as a Microcosm," suggested that the species assemblage in a lake was an organic complex and that by affecting one species we exerted some influence on the whole assemblage. Thus each species maintains a "community of interest" with the other species, and we cannot limit our studies to a single species. Forbes believed that there was a steady balance of nature, which held each species within limits year after year, even though each species was always trying to increase its numbers.

Studies of communities were greatly influenced by the Danish botanist Warming (1895, 1909). Warming raised questions about the structure of plant communities and the associations of species in these communities. The dynamics of vegetation change was emphasized first by North American plant ecologists. In 1899 H. C. Cowles described *plant succession* on the sand dunes at the southern end of Lake Michigan. This aspect of the development of vegetation was analyzed by Clements (1916) in a classic book that began a long controversy about the nature of the community (see Chapter 20).

Thus by about 1900 ecology was started on the road to becoming a science with the recognition of the broad problems of populations and communities. The roots of ecology lie in natural history, human demography, biometry (mathematical approach), and applied problems of agriculture and medicine.

Until the 1960s ecology was not considered an important science. The continuing increase of the human population and the associated destruction of natural environments with pesticides and pollutants has awakened the public to the world of ecology. Much of this recent interest centers on the human environment and human ecology. Unfortunately the word *ecology* became identified in the public mind with the much broader problems of the human environment, and "ecology" came to mean everything and anything about the environment. The science of ecology is concerned with the environments of all plants and animals and is not solely concerned with humans. As such, ecology has much to contribute to some of the broad questions about humans and their environment. Ecology should be to environmental science as physics is to engineering. Just as we humans are constrained by the laws of physics when we build airplanes and bridges, so also we should be constrained by the principles of ecology when altering the environment.

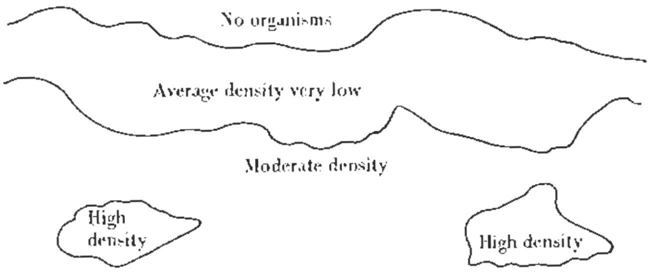
BASIC PROBLEMS AND APPROACH

We can approach the study of ecology from three points of view—*descriptive*, *functional*, or *evolutionary*. The descriptive point of view is mainly natural history and proceeds by describing the vegetation groups of the world, such as the temperate deciduous forests, tropical rain forests, grasslands, and tundra, and by describing the animals and plants and their interrelationships for each of these ecosystems. The functional point of view, on the other hand, is oriented more toward *relationships* and seeks to identify and analyze general problems common to most or all of the different areas. Functional studies deal with populations and communities as they exist and can be measured now. The evolutionary point of view considers organisms as historical products of evolution. Functional ecology studies *proximate* causes—the responses of populations and communities to immediate factors of the environment. Evolutionary ecology studies *ultimate* causes—the historical reasons why natural selection has favored the particular adaptations we now see. Functional ecologists ask "how," How does the system operate? Evolutionary ecologists ask "why," Why does natural selection favor this particular ecological solution? Since evolution has occurred not only in the past but is also going on at the present time, the evolutionary ecologist must work closely with the functional ecologist to understand ecological systems (Orians 1962). The environment of an organism contains all the selective forces which shape its evolution, and hence ecology and evolution are two viewpoints of the same reality.

All three approaches to ecology can have shortcomings. The primary difficulty with the descriptive approach is that one can get entirely lost in it. We could use all the space in this book just to describe the temperate deciduous forests of North America. With the functional approach there is a tendency to get far removed from reality, in the absence of detailed biological knowledge. The evolutionary approach can degenerate into undisciplined speculation about past events and provide hypotheses that can never be tested in the real world. In this book I shall use a mixture of the functional and evolutionary approaches and emphasize the general problems of ecology.

Distribution and abundance

The basic problem of ecology is to determine the causes of the distribution and abundance of organisms. Every organism lives in a matrix of space and time that can be considered as a unit. Consequently these two ideas of distribution and abundance are closely related, although at first glance they may seem quite distinct. What we observe for many species is this:



Thus we can view the average density of any species as a contour map, with the provision that the contour map may change with time. Now, throughout the area of distribution, the abundance of an organism must be greater than zero, and the limit of distribution equals the contour of zero abundance. Thus distribution may be considered as a facet of abundance, and distribution and abundance may be said to be reverse sides of the same coin (Andrewartha and Birch 1954). The factors that affect the distribution of a species may also affect its abundance.

The problems of distribution and abundance can be analyzed at the level of the single species population or at the level of the community which contains many species. The complexity of the analysis may increase as more and more species are considered in a community, and consequently in this book we shall consider first the simpler problems involving single species populations.

There is considerable overlap between ecology and its related disciplines which we cannot cover thoroughly in this book. Environmental physiology has developed with a wealth of information that impinges on problems of distribution and abundance. Population genetics and ecological genetics are two additional foci of interest that we shall touch only peripherally. Behavioral ecology is another interdisciplinary area that has implications for the study of distribution and abundance.

Levels of integration

In ecology we are dealing primarily with the three starred* levels of integration:

Biosphere ↑
*Ecosystems
*Communities
*Populations
Organisms
Organ systems
Organs
Tissues
Cells
Subcellular organelles
Molecules

decreasing
scientific
understanding

On one side, ecology overlaps with environmental physiology and behavior in studies of individual organisms, and on the other side, ecology fades into meteorology, geology, and geochemistry when we consider the biosphere, the whole-earth ecosystem. The boundaries of the sciences are not sharp but diffuse, and nature does not come in discrete packages.

Each level of integration involves a separate and distinct series of attributes and problems. For example, a population has a *density* (e.g., number of deer per square mile), a property that cannot be attributed to an individual organism. A community has a *species diversity*, which is an attribute without meaning at the population level. In general, a scientist dealing with a particular level of integration seeks his explanatory mechanisms from lower levels of integration and his biological significance from higher levels. Thus to understand mechanisms of changes in a population, an ecologist will study mechanisms that operate on individual organisms and will try to view the significance of these population events in a community and ecosystem framework.

Some ecologists have suggested that the ecosystem, the biotic community and its abiotic environment, is the basic unit of ecology (Tansley 1935, Rowe 1961, Evans 1956). There may be a particular significance attached to the ecosystem level from the viewpoint of human ecology, but it is only one of the levels of organization at which ecologists operate. There are meaningful and important questions to be asked at each level of integration, and none of them should be neglected.

The extent of scientific understanding varies with the level of integration. We know a good deal about the molecular and cellular levels of organisms; we know something about organs and organ systems, and about whole organisms; but we know relatively little about populations and even less about communities and ecosystems. This point is illustrated very nicely when you look at the levels of integration—ecology comprises about one-third of biology from this viewpoint. But no basic biology curriculum could be one-third ecology and do justice to *current* biological knowledge. The reasons for this are not hard to find—they include the increasing complexity of these higher levels and the inability to deal with them in the laboratory.

Whatever the reasons for this decrease in knowledge at the higher levels, it has serious implications for the study we are about to undertake. You will not find in ecology the strong theoretical framework that you find in physics, chemistry, molecular biology, or genetics. It is not always easy to see where the pieces fit in ecology, and we shall encounter many isolated parts of ecology that are well developed internally but are not clearly connected to anything else. This is typical of a young science. Many students unfortunately think of science as a monumental pile of facts that must be memorized. But science is more than a pile of precise facts—it is a search for systematic relations, for explanations to problems, and for unifying concepts. This is the growing end of science, which is so evident in a young science like ecology. It involves many unanswered questions and much more controversy. A scientific discipline like ecology can be viewed as a mine—to the casual observer what is obvious and important is the increasing pile of facts on the ground surface; to the more serious student what is less obvious but probably more important is the actual working area at the bounds of knowledge.

The theoretical framework of ecology may be weak at the present time, but this must not be interpreted as a terminal condition. Eighteenth-century chemistry was perhaps in a comparable state of theoretical development as ecology at the present time. Sciences are not static, and ecology is in a strong growth phase.

Methods of approach

Ecology has been attacked on three broad fronts: the *mathematical*, the *laboratory*, and the *field*. These three approaches are interrelated, but some problems have arisen when the results of one approach fail to verify those of another. For example, mathematical predictions may not be borne out in field data. We are primarily interested in understanding the distribution and abundance of organisms in *nature*, that is, in the *field*. Consequently this will always be our criterion of comparison, our basic standard.

Some authors divide ecology into *autecology*, the study of the individual organism in relation to its environment, and *synecology*, the study of groups of organisms in relation to their environment. Synecology may then be further subdivided into population, community, and ecosystem ecology. This subdivision of ecology has the bad feature of suggesting that the environmental factors relevant to individuals are somehow different from the environmental factors relevant to groups of organisms. Much of what is traditionally considered as autecology is really environmental physiology and may or may not be necessary for answering specific questions about distribution and abundance.

Plant and animal ecology have tended to develop along separate paths. Historically, plant ecology got off to a faster start than animal ecology. Since animals are highly dependent on plants, many of the concepts of animal ecology are patterned on those of plant ecology. *Succession* is one example. Also, since plants are the ultimate source of energy for all animals, to understand animal ecology, we must also know a good deal of plant ecology. This is illustrated particularly well in the study of community relationships.

There are, however, some important differences separating plant and animal ecology. First, animals tend to be highly mobile, whereas plants are stationary. Thus a whole series of new techniques and ideas must be applied to animals, for example, to determine population density. Second, animals fulfill a greater variety of functional roles in nature—some are herbivores, some are carnivores, some are parasites. This distinction is not complete because there are carnivorous plants and parasitic plants, but the possible interactions are on the average more numerous for animals than for plants.

Historically, plant ecology has been mostly community ecology, and animal ecology has been mostly population ecology. This distinction has fortunately broken down during the last 20 years, so that population ecology is a strong area of development in plant ecology, and zoologists are increasingly dealing with problems of community ecology. Many plants are long-lived and further complicate their study as populations by being very large and producing dormant seeds. These problems are well illustrated in forests, which change slowly and often imperceptibly over many years. Other plants are often vegetative reproducers, which makes it difficult to define an individual plant. By contrast, the complex interrelationships among animals has slowed community analysis in the past, and zoologists typically have begun with the study of single-species populations rather than multispecies communities.

In spite of these differences, I shall attempt to integrate plant with animal ecology. The problems of ecology, of distribution and abundance, are common to all organisms.

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Questions and problems

1. "The definition . . . 'ecology is the branch of biological science that deals with relations of organisms and environments' would provide the title for an encyclopaedia but does not delimit a scientific discipline" (Richards 1939, p. 388). Discuss.

2. Is it necessary to define a scientific subject before one can begin to discuss it? Contrast the introduction to several textbooks of ecology with those of some areas of physics and chemistry, as well as other biological areas, such as genetics and physiology.

3. Is it necessary to study the methodology and philosophy of science in order to understand ecology? Consider this question before and after reading the essays by Popper (1963) and Platt (1964).

4. Ask several of your nonbiologist friends how they would define "ecology," and discuss the distinction between *ecology* and *environmental studies.*

5. Discuss the application of the distribution and abundance model on page 9 to the human population.