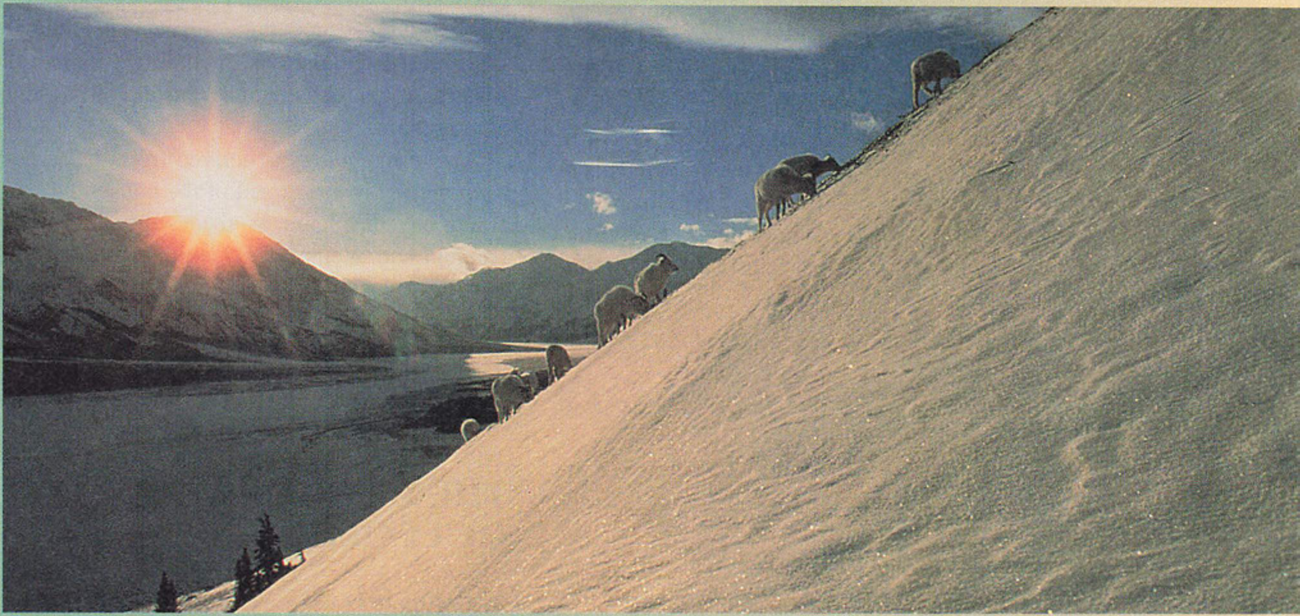
Chapter 1

Ecology: Its Meaning and Scope



Outline

Concepts

1. Ecology is the study of the structure and function of nature.
2. Ecology developed from many roots, but its beginnings trace back to natural history and plant geography.
3. Ecology has branched into many subdivisions, many of them specialized.
4. The principles of ecology form the scientific basis for the solution to many environmental problems.

ECOLOGY DEFINED

What is ecology? Ask nonecologists and they will probably answer that ecology has something to do with the environment or with saving it. Before the 1960s, few of them could have given you any answer. If you had asked a biologist in the same time period, you would probably have gotten some vague answer implying that ecology was "quantified natural history." Ecology only became a household word in the 1960s, through the environmental movement, and then its popular meaning became confused with environmentalism.

The origin of the word *ecology* is the Greek *oikos,* meaning "household," "home," "place to live." Clearly, ecology deals with the organism and its place to live, its environment. Ecologists continue to work toward a deeper definition. Here is a sampling of their attempts:

"the study of structure and function of nature." (Odum 1971:3)

"the scientific study of the distribution and abundance of animals." (Andrewartha 1961:10)

"the scientific study of the interactions that determine the distribution and abundance of organisms." (Krebs 1985:4)

"the scientific study of the relationships between organisms and their environments." (McNaughton and Wolfe 1979:1)

"the study of the relationships between organisms and the totality of the physical and biological factors affecting them or influenced by them." (Pianka 1988:4)

"the study of the adaptation of organisms to their environment." (Emlen 1973:1)

"the study of the principles which govern temporal and spatial patterns for assemblages of organisms." (Fenchel 1987:12)

"the study of the patterns of nature and how those patterns came to be, and how they change in space and time." (Kingsland 1985:1)

"the study of organisms and their environment—and the interrelationships between the two." (Putman and Wratten 1984:13)

"the study of the relationship between organisms and their physical and biological environments." (Ehrlich and Roughgarden 1987:3)

The author of the term, Ernst Haeckel, defined ecology as "the body of knowledge concerning the economy of nature—the investigation of the total relationships of the animal both to its inorganic and its organic environment; including, above all, its friendly and inimical relations with those animals and plants with which it comes directly or indirectly into contact—in a word ecology is the study of all those complex interrelations referred to by Darwin as the conditions for the struggle for existence."

None of these definitions really is satisfactory. They are either too restrictive or too vague, and the original definition relates only to animal ecology. Most definitions apply to population ecology and overlook ecosystem function. The subject has outgrown them.

For now, let us use a wider working definition. *Ecology* is the study of the structure and function of nature. Structure includes the distribution and abundance of organisms as influenced by the biotic and abiotic elements of the environment; and function includes all aspects of the growth and interaction of populations, including competition, predation, parasitism, mutualism, and transfers of nutrients and energy among them.

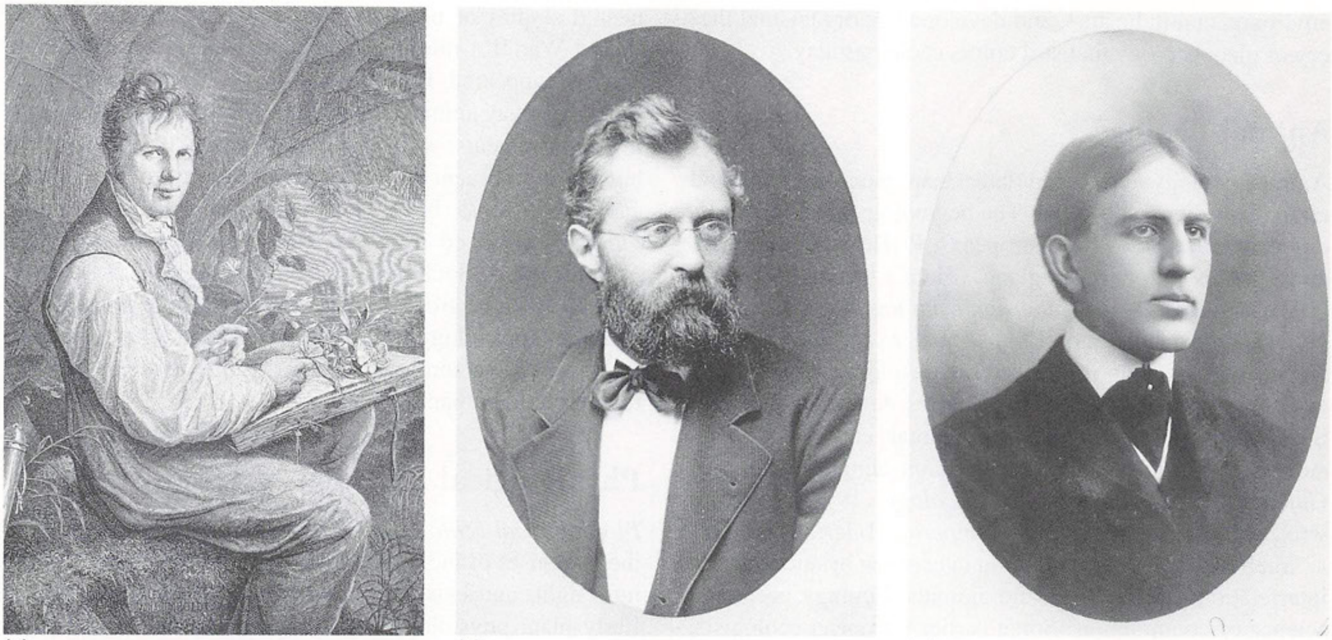
The term *ecology* is derived from the same root word as *economics,* "management of the household." Ecology, then, could be considered as the economics of nature. Wells, Huxley, and Wells (1939) commented that "Ecology is really an extension of economics to the whole world of life." Some economic concepts, such as resource allocation, cost-benefit ratios, and optimization theory, have found a place in ecology.

THE DEVELOPMENT OF ECOLOGY

Just as there is no consensus on the definition of ecology, so there is no agreement on its beginnings. It is more like a multistemmed bush than a tree with a single trunk. Some historians trace the beginnings of ecology to Darwin, Thoreau, and Haeckel; others to the Greek scholar Theophrastus, a friend and associate of Aristotle, who wrote about the interrelationships between organisms and the environment.

Plant Ecology

The modern impetus to ecology came from the plant geographers. They discovered that, although plants differed in various parts of the world, certain similarities and differences demanded explanation. They looked to climate as a possible answer, because similar climates supported similar vegetation. Carl Ludwig Willdenow (1765–1812), one of the early influential plant geographers, championed this explanation. His ideas caught the attention of a wealthy young Prussian naturalist, Friedrich Heinrich Alexander von Humboldt (1769–1859) (Figure 1.1a). He sailed in 1799 with the French botanist Aimé Bonpland for a five-year expedition through tropical Spanish America. They traveled though Mexico, Cuba, Venezuela, and Peru, and explored the Orinoco and Amazon Rivers. Humboldt described these travels and tropical America's plant and animal life in a 30-volume work, *Voyage to the Equatorial Regions.* In these books Humboldt described vegetation in terms of physiognomy, correlated vegetation types with environmental characteristics, and coined the term *association.*



(a) (b) (c)

Figure 1.1 Plant geographers. (a) Friedrich Heinrich Alexander von Humboldt. (b) Johannes Warming. (c) F. E. Clements.

Travel to the tropics continued to stimulate plant ecology. A Danish botanist, Johannes Warming (1841–1924), spent three years studying tropical vegetation in Brazil (Figure 1.1b). Thirty years later he described the vegetation in a book in which he introduced such concepts as dominants and subdominants and noted the effects of fire and time. His major contribution was the book *Plantesamfund: Grundtrak af den okologiske Plantegeografi,* published in 1895. In this book he unified plant morphology, physiology, taxonomy, and biogeography and emphasized the importance of moisture, temperature, and soil for vegetation. The book fixed the modern concept of ecology and greatly influenced its development. Following Warming, another tropical traveler, the German botanist Andreas Schimper (1856–1901) published *Plant Geography on a Physiological Basis,* a book heavy on plant morphology and light on plant physiology. Schimper explained regional differences in vegetation as a function of moisture and temperature.

Other plant geographers stayed closer to home. Nevertheless they made major advances in plant ecology, especially the emerging concept of plant succession—vegetation change over time. Anton Kerner (1831–1898) was one of these geographers. Commissioned to survey the vegetation of eastern Hungary and Transylvania, he described plant succession in *Plant Life of the Danube Basin.* He pioneered the use of experimental transplant gardens at various elevations in the Tyrolean Alps to study the growth and behavior of plants taken from alpine and lowland sites. Later, the Polish botanist Jozef Paczoski (1864–1941) described how plants modify their environment by creating microenvironments and introduced such concepts as shade tolerance, competition, plant succession, and the role of fire. Because his book was published in Slavic, it was belatedly discovered by ecologists outside the Slavic world. He is now recognized as the father of plant sociology or *phytosociology.*

The study of plant communities developed along separate paths in Europe and America. In Europe plant ecologists concentrated on describing the plant community. Christen Raunkiaer (1860–1938) of Denmark contributed a scheme of life form classification and quantitative methods of sampling vegetation, the data from which could be treated statistically. Later Josias Braun-Blanquet developed methods of community sampling, data reduction, and the classification and nomenclature of plant communities. A. E. Tansley, however, urged a more experimental approach to plant ecology. His views on ecology and research anticipated by years the type of ecological studies that emerged in the 1970s.

In America plant ecologists were far more interested in how plant communities develop. Settlement was destroying the original forests and grasslands, creating profound changes in vegetation. Interest in these disturbances led to pioneer studies of the dynamics of vegetation, especially plant succession. A doctoral study on the succession of plant life on the Indiana sand dunes by H. E. Cowles (1897) established plant succession as one of the central concepts of modern ecology.

F. E. Clements (1916) further developed the concept of succession by investigating its causes and consequences. Dogmatic and convincing, Clements quickly became the major theorist of plant ecology in the United States (Figure 1.1c). He gave ecology a hierarchical framework, introduced innumerable terms (no longer used) and the idea of environmental indicators, and developed an organismal theory of plant ecology that still colors ecology today.

Animal Ecology

Animal ecology developed later than plant ecology and along lines divorced from it. The beginnings of animal ecology can be traced to two Europeans, R. Hesse of Germany and Charles Elton of England. Elton's *Animal Ecology* (1927) and Hesse's *Tiergeographie auf logischer grundlage* (1924), translated into English as *Ecological Animal Geography,* strongly influenced the development of animal ecology in the United States. Charles Adams and Victor Shelford were two pioneering animal ecologists there. Adams published the first textbook on animal ecology, *A Guide to the Study of Animal Ecology* (1913). Shelford wrote *Animal Communities in Temperate America* (1913).

Shelford gave a new direction to ecology by stressing the interrelationship of plants and animals. Ecology became a science of communities. Some earlier European ecologists, particularly the marine biologist Karl Mobius, had developed the general concept of the community. In his essay "An Oyster Bank Is a Biocenose" (1877), Mobius explained that the oyster bank, although dominated by one animal, was really a complex community of many interdependent organisms. He proposed the word *biocenose* for such a community. The word comes from the Greek meaning "life having something in common."

The appearance in 1949 of the encyclopedic *Principles of Animal Ecology* by five second generation ecologists from the University of Chicago—W. C. Allee, A. E. Emerson, Thomas Park, Orlando Park, and K. P. Schmidt—pointed the direction modern ecology was to take. It emphasized trophic structure and energy budgets, population dynamics, and natural selection and evolution.

Still another area of biology, animal behavior, grafted its branch onto ecology. Although Darwin, Wallace, and others described activities of animals, the formal study of animal behavior began with George John Romanes (1848–1894), who introduced the comparative method of studying nonhuman animals to gain insights into human behavior. His approach depended largely on inferences, but C. Lloyd Morgan (1852–1936), an English behaviorist, emphasized the use of direct observation and experiment.

After the early 1900s, animal behavior study developed along four major lines. One was the study of behavioral mechanisms, perceptual and physiological. It became known as *behaviorism.* A second, more relevant to ecology, was the study of the function and evolution of behavior, including comparative physiology. This study became known as *ethology.* The three major founders of ethology were Konrad Lorenz, noted for his studies of genetically programmed behavior; Niko Tinbergen, who developed the scheme of four areas of inquiry (causation, development, evolution, and function); and Karl von Frisch, who pioneered studies of bee communication and behavior. After World War II a third field of animal behavior, wedded to ecology, appeared. It was *behavioral ecology,* which investigates the way animals interact with their living and nonliving environments, with a special emphasis on how that behavior is influenced by natural selection. Behavioral ecology in 1975 begot a controversial offspring, *sociobiology,* pioneered by E. O. Wilson in *Sociobiology: The New Synthesis.* Sociobiology, concentrating on field observations of social groups of animals, applies the principles of evolutionary biology to the study of social behavior in animals. It became controversial when some writers attempted to apply it to humans.

Physiological Ecology

Physiological ecology, or *ecophysiology,* is concerned with the responses of individual organisms to temperature, moisture, light, nutrients, and other factors of the environment. Early plant physiologists studied photosynthesis and plant growth, including the influence of environment on growth. Justus Leibig (1840) investigated the role of limited supplies of nutrients on the growth and development of plants and came up with the "law of the minimum." F. F. Blackman (1905) extended this idea of limiting factors to include a maximum—a plant could get too much of a good thing. Soon both plant physiologists and plant ecologists began to work out the physiological relationships among plants, climate, atmosphere, and soil. As plant physiologists deciphered the mechanisms of photosynthesis and water relations in plants, ecophysiologists related these functions to plant distributions and adaptations. After World War II, the field grew rapidly. New instrumentation, experimental techniques, and rapidly advancing knowledge allowed ecophysiologists to study the interactions of plant physiology and enviromental responses in the field and in laboratory growth chambers.

Animal ecophysiology developed out of animal physiology, concerned at first with the functioning of the human body. V. E. Shelford (1911) stimulated the study of animal ecophysiology when he applied the concept of limiting factors to animals in a "law of tolerance." This law linked the physiology of an organism to its environment. He suggested that organisms have both a negative and an optimal response to environmental conditions, and that these responses influence their distribution. This idea stimulated investigations into how such physiological responses as thermoregulation, energy metabolism, and water balance relate to the environmental conditions in which animals live.

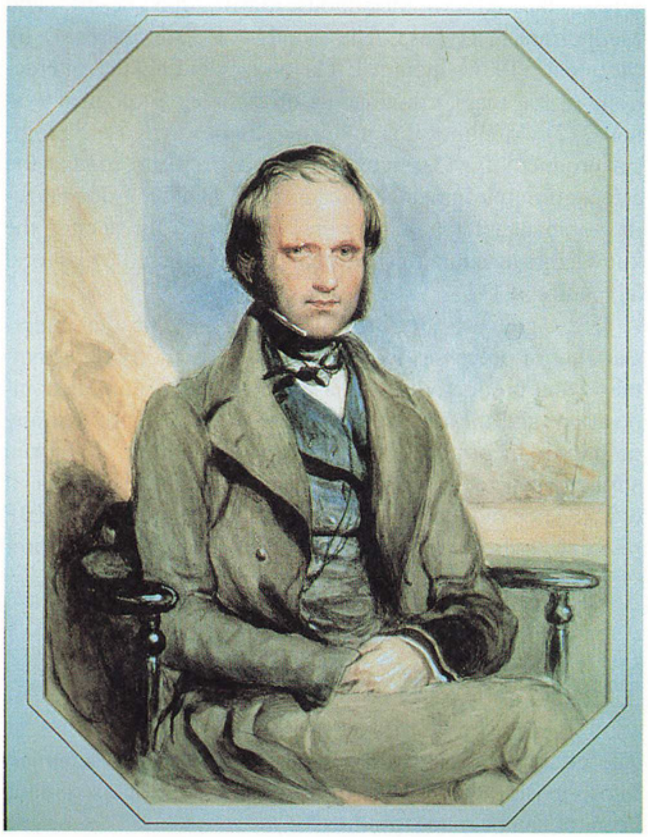
Observers noted that certain plants and animals use chemical substances for defense, and that some plant exudates inhibit the growth of associated species. They began to investigate chemical substances in the natural world. There were studies of the role of chemicals in species recognition, courtship, and defense as well as studies of the chemicals themselves. Such work has grown into the specialized field of *chemical ecology*.

Population Ecology

As plant ecology was arising out of plant geography, other developments were under way. One was the voyage of Charles Darwin on the *Beagle,* during which he collected numerous biological specimens, made detailed notes, and mentally framed his view of life on Earth (Figure 1.2). Darwin (1809–1882) observed the relationships between organisms and environment. He attributed the similarities and dissimilarities of organisms within continental land masses and among continents to geographical barriers separating the inhabitants. He noted from his collection of fossils how successive groups of plants and animals, distinct yet obviously related, replaced one another over geological time.

In developing his theory, Darwin was influenced by the writings of Thomas Malthus (1766–1834). An economist, Malthus (1798) advanced the principle that populations grew in geometric fashion, doubling after some period of time. Experiencing such rapid growth, a population would outstrip its food supply. Ultimately the population would be restrained by a "strong, constantly operating force—among plants and animals the waste of seeds, sickness, and premature death. Among mankind, misery and vice."

Figure 1.2 Charles Darwin.



From this concept Darwin developed the idea of "the survival of the fittest" as a mechanism of natural selection and evolution.

Meanwhile, unknown to Darwin, an Austrian monk, Gregor Mendel (1822–1884), was studying in his garden the transmission of inheritable characters from one generation of pea plants to another. The work of Mendel would have answered a number of Darwin's questions on the mechanisms of inheritance and provided for his theory of natural selection the firm base it needed. Belatedly, Darwin's theory of evolution and Mendelian genetics were combined to form the study of evolution and adaptation, two central themes in ecology. The theoretical basis of the role of inheritance in evolution was advanced by Sewell Wright (1931), R. S. Fisher (1930), and J. Haldane (1932, 1954), who developed the field of *population genetics.*

The Malthusian concept of population growth and limitations stimulated the study of population dynamics. P. F. Verhulst (1838) of Italy formulated the mathematical basis for population growth under limiting conditions. Verhulst's work, expanded by R. Pearl and L. J. Reed (1929), was the basis for the contributions of A. Lotka and V. Volterra (1926) to the study of population growth, predation, and interspecific competition. Their work established the foundations of *population ecology,* concerned with population growth, regulation, and intraspecific and interspecific competition. The mathematical models of Lotka and Volterra were tested experimentally in the Soviet Union by G. F. Gause (1934) with laboratory populations of protozoans and in the United States by Thomas Park (1954) with flour beetles. Many of the concepts of population genetics have been combined with ideas from population ecology to make up the field of *evolutionary ecology,* concerned with the interactions of population dynamics, genetics, natural selection, and evolution.

Ecologists now have a body of theory relating to competition, population growth, life-history strategies, resource utilization, niche, coevolution, community structure, food webs, and the like. Theoretical ecologists take theories and equations developed in pure mathematics, physics, and even economics and apply them to ecological questions. They attempt to provide a substantial mathematical foundation for ecological concepts, upon which predictions can be based. Theoretical ecologists have stimulated new insights into relationships among species, utilization of resources, and life-history patterns. Critics of theoretical ecology argue that it suffers from too many hypotheses that are untested or untestable in the field.

Ecosystem Ecology

Early plant ecologists were concerned mostly with terrestrial vegetation; but in Europe a group of biologists was interested in the natural history of fresh waters. Prominent among these biologists were A. Thienemann (1931) and

F. A. Forel (1901). Thienemann developed an ecological approach to freshwater biology. He introduced the ideas of organic nutrient cycling and trophic feeding levels, using the terms *producers* and *consumers.* Forel was more interested in the physical parameters of freshwater habitats, particularly lakes. He described thermal stratification and internal seiches within lakes. In his monograph on Lake Leman, he introduced the term *limnology* for the study of freshwater life. In a way limnology became the forerunner of ecosystem ecology.

Early concepts were further developed by S. A. Forbes, an entomologist at the University of Illinois and the Illinois State Laboratory of Natural History (Illinois Natural History Survey). He wrote a classic of ecology, "The Lake as a Microcosm," about the interrelations of life in a lake, particularly through food chains, and the role of natural selection in the regulation of numbers of predators and prey.

Unrelated to limnology, but destined to have an important influence on its future and that of ecology, was the work of Edgar Transeau in an Illinois cornfield. Transeau was not an ecologist, much less a limnologist. He was interested in improving farm production by understanding the photosynthetic efficiency of the corn plant. His landmark paper "The Accumulation of Energy in Plants" (1926) marked the beginning of the study of primary production and energy budgets.

Thienemann's and Transeau's work stimulated the study of lakes by E. A. Burge and by C. Juday of the Wisconsin Natural History Survey. In a classic paper, "The Annual Energy Budget of an Inland Lake," Juday summarized not only the accumulation of energy by aquatic plants over a year but also its movement through various feeding groups, including the decomposers.

The work of Juday and Birge influenced a young limnologist at the University of Minnesota, R. A. Lindeman. Lindeman was interested in exploring plant succession in terms of energy. He turned his attention to Cedar Bog Lake in Minnesota. In a 1942 paper, "The Trophic-Dynamic Aspect of Ecology," Lindeman described succession in terms of energy flow through the lake ecosystem. He showed how short-term processes of feeding or trophic relationships affected the long-term changes in the lake. This paper, a significant advance in ecology, marked the beginning of *ecosystem ecology.*

Preceding Lindeman's contribution was the theoretical work of a physical chemist, A. J. Lotka. In his book *Elements of Physical Biology* he introduced thermodynamic principles of energy transformations in biology along the lines of physical chemistry. He considered food webs and the cycles of carbon dioxide, phosphorus, nitrogen, and water; and he viewed Earth as a single energy-transforming system. Most ecologists overlooked Lotka's contribution. However, his ideas and Lindeman's study stimulated further pioneering work on energy flow and nutrient budgets by G. E. Hutchinson (1957, 1969) and H. T. and E.P. Odum in the 1950s. J. Ovington (1962) in England and Rodin and Bazilevic (1967) in the Soviet Union investigated nutrient cycling in forests. The increased ability to measure energy flows and nutrient cycling by means of radioactive tracers and to analyze large amounts of data with computers permitted the development of *systems ecology,* the application of general systems theory and methods to ecology.

Cooperative Studies

Ecology has developed from so many roots and has grown so many branches that it probably will always remain, as Robert McIntosh (1980) calls it, "a polymorphic discipline." Attempts to reduce ecology to a set of basic principles have not been successful. Ecology ranges over many diverse areas—marine, freshwater, and terrestrial. It involves all taxonomic groups, from bacteria and protozoa to mammals and forest trees, at all levels—individuals, populations, ecosystems. Any of these levels and groups may be studied from various points of view—behavioral, physiological, mathematical, chemical. As a result ecology, by necessity, involves isolated groups of specialists.

Pulling some of these groups together in the 1960s was the International Biological Program, known as IBP. A growing concern over environmental problems facing the world prompted the program. In the United States the IBP, initiated in 1967, focused on a cooperative study and analysis of ecosystems, including the tundra, the coniferous forest, the eastern deciduous forest, the desert, and Mediterranean types. The goals, as summarized by McIntosh (1976) included: (1) understanding the interactions of the many components of complex ecological systems; (2) exploiting this understanding to increase biological productivity; (3) increasing the capacity to predict the effects of environmental impacts; (4) enhancing the capacity to manage natural resources; and (5) advancing the knowledge of human genetic, physiological, and behavioral adaptations.

IBP's greatest contribution was to increase our understanding of processes in ecosystems, particularly photosynthesis and productivity, water and mineral cycling, decomposition, and the role of detritus. IBP did not provide any definitive theoretical foundations for ecology. It lacked strong organization and coordinated direction. However, it did advance modern ecosystem ecology. Summaries of IBP research, still being published in numerous volumes, provide a base for future ecological research.

TENSIONS WITHIN ECOLOGY

The complexity of ecology's past has led some scientists into opposing camps. Often these deep controversies have been, or can be made, productive.

Plant Versus Animal Ecology

The first major split in ecology was the failure of plant ecology and animal ecology to meet on common ground. In England plant ecology was influenced strongly by A. E. Tansley and animal ecology by Charles Elton. At that time one journal, *The Journal of Ecology,* sponsored by the British Ecological Society, covered the field of ecology. In a few years Elton started *The Journal of Animal Ecology.* The two, plant ecology and animal ecology, went their separate ways.

In the United States, the split was less amicable. Early on, a controversy developed over the term *ecology.* Botanists decided at the Madison (Wisconsin) Botanical Congress in 1893 to drop the *o* from *oecology* and adopt an anglicized spelling. Zoologists refused to recognize the term at all. The entomologist William Morton Wheeler complained that botanists had usurped the word, and had distorted the science. He urged zoologists to drop the term and adopt the word *ethology.*

The schism was widened by a more fundamental difference in approach. Plant ecologists ignored any interaction between plants and animals. In effect, they viewed plants as growing in a world without parasitic insects and grazing herbivores. For years plant and animal ecologists went their separate ways. F. E. Clements and V. E. Shelford began to bring the two sides together with *Bio-Ecology* (1939), in which they suggested that plants and animals be considered as interacting components of broad biotic communities or biomes.

Organismal Versus Individualistic Ecology

Although the division between plant and animal ecology narrowed, a new division was to plague ecology. It had its roots in the ideas of Clements, who strongly influenced philosophical ideas in ecology. Clements viewed the plant community as an organism. Like an individual organism, vegetation moved through several stages of development, from youthful colonization of bare ground to a mature, self-reproducing climate in balance with its climate determined environment. The climax was the end or goal toward which all vegetation progressed. If disturbed, vegetation responded by retracing its developmental stages to the climax again.

Clements' organismal approach was not lost on animal ecologists. In the United States the zoologist and animal behaviorist William Morton Wheeler, an international authority on ants and termites, advanced the idea that ant colonies behave as organisms. They carry out such functions as food gathering, nutrition, self-defense, and reproduction. Basing his ideas on those of C. Lloyd Morgan, a biological philosopher, Wheeler applied **emergence theory** to ecology. He proposed that natural associations have certain emergent properties as aggregations of organisms—predators and prey, parasites and hosts—that arose from lower levels of organization. All levels occurred together in an ecological community or *biocenosis.* The biocenosis modified its component species through behavioral changes and new levels of integration. Everything in the biocenosis was related to everything else. His view of a tight but orderly nature contrasted with the chaotic effect imposed on nature by humans.

This organismic, levels-of-hierarchy view of nature advanced by Clements and Wheeler captured the thinking of that influential group of ecologists at the University of Chicago, the authors of *The Principles of Animal Ecology,* Allee, Park, Park, Emerson, and Schmidt. In that book they stated that the organismic concept of ecology was "one of the fruitful ideas contributed by biological science to modern civilization."

Although the organismal concept dominated ecology until the early 1960s, many ecologists refused to accept it. Clement's organismic concept had its critics, notably H. A. Gleason and A. E. Tansley. In 1926 Gleason published "The Individualistic Concept of the Plant Association." In it he argued that the plant association was hardly an organism capable of self-reproduction. Instead, he argued, each community is unique. It arises randomly through environmental selection of seeds, spores, and other reproductive parts of plants that enter a particular area. The English ecologist A. E. Tansley, once enamored with the organismic concept, ultimately rejected it too. Vegetation, he allowed, might be called a quasi-organism, but certainly not an organism or a complex organism. In fact, Tansley rejected the whole idea of a biotic community as anthropomorphic. No social relationship exists among plants or between plants and animals as the term connotes, he argued. In its place Tansley substituted the term **ecosystem.** He viewed plants and animals as components of a system that also included physical factors.

Holism Versus Reductionism

By the mid-1960s the individualistic concept of Gleason had supplanted the organismic concept—almost. Many of its philosophical and functional attributes lived on in the "new ecology" of the 1960s. The new ecology, as defined by E. P. Odum (1964, 1971), is a "systems ecology," an "integrative discipline that deals with supraindividual levels of organization."

According to this concept ecosystems develop from youth to maturity. Each stage of development exhibits some of its own unique characteristics. Interactions among populations and between plants and animals result in a hierarchical organization. This organization involves interacting components that produce large functional wholes. The outcome is the emergence of new system properties that are not evident at the level below (Odum 1971, 1982). These emergent properties account for most of the changes in species and growth that take place over time. The approach is **holistic** (studying the total behavior or attributes of a complex system) because systems are considered too complex to study in bits. Because the whole is greater than the sum of its parts, ecosystems can be studied only as functional units.

This holistic approach has critics who take a **reductionist** approach. They consider that the ecosystem is in fact the sum of its parts. By understanding how each part—the species, their numbers, and characteristics—functions, we can discover how the whole system operates. Rather than guiding the evolution of species, the nature of ecosystems results from the evolution of species.

Fenchel (1987:17) puts the reductionist's point of view well: "I find the entire argument as nonsensical as stating that an alarm clock is qualitatively different from its constituent wheel, bolts, and springs. A holist approach to an alarm clock . . . is to observe that when wound it will run. To arrive at a real understanding of the device one must take it apart in order to see how it works . . . to take a reductionist's approach."

The holist would counter that studying the wheels, bolts, and springs tells nothing about the way the whole system functions, what the clock really does. You could study a few separate components, but they are outside the context of the whole clock. Only when all parts of the system are functioning as a unit can the clock function. Then its emergent property, telling time, becomes apparent.

Is the sum of the parts of the clock greater than the whole or not? Allen and Starr (1982) in their book *Hierarchy* argue that the whole problem of emergent properties is a matter of scale and assert that some properties of the whole are emergent and cannot be derived from the behavior of the parts alone. They also point out that ecosystem models of holists are simply large-scale reductionism. Ecosystem ecologists cannot possibly study a model of an entire ecosystem. They can only study pieces of it. The only major difference between a reductionist and a holist is that the holist studies larger pieces, made up of assembled parts studied by the reductionists.

What keeps ecosystem ecologists (holists) and population and evolutionary ecologists (reductionists) apart is their approach to ecology. Population ecologists focus on species' interactions with their environment in the broadest sense. They are interested in the historical or ultimate reasons why natural selection favored different adaptive responses among species over evolutionary time. Ecosystem ecologists are more interested in the how of current or proximate outcomes of the functional interactions at the population, community, and ecosystem levels. These differences may not be as great as they appear.

What can bring the two groups together? Population ecologists could approach population growth and population interactions such as mutualism, parasitism, predation, and competition as interacting systems (Berry 1981) and as components of a hierarchy of systems. Systems ecologists could integrate some evolutionary theory into system models, particularly in the area of ecosystem development and organization (Loehle and Peckmann 1988). Food web theory, for example, crosses the line into both evolutionary and systems ecology, involving both species interactions and the transfer of energy and nutrients through a hierarchy. Ecosystem functioning ultimately depends upon species adaptations, which are the outcomes of evolution. For example, efficiency of water use by certain ecosystems such as grasslands and deserts results from the water use efficiency of the individual plants. The natural assemblage of plants and animals that comprise the living component of an ecosystem is not a random collection of species but rather one that has been determined by the competitive abilities and other attributes of the component species (H. Odum 1983).

Theoretical Versus Applied Ecology

Ecological theories and models help us understand the human impact on environments. They provide a basis for ecosystem and natural resource management, preservation, and restoration. All of these activities make up *applied ecology*. For years theoretical and academic ecologists viewed applied ecology as an intellectual lightweight. Applied ecologists, for their part, often ignored theory, even when it could be of practical use. Fortunately ecologists of both persuasions now recognize that solutions applied to environmental problems must be based on sound theory developed through research.

Applied ecology began to take shape in the 1930s. In 1932 Herbert Stoddard pointed out the role of fire in the control of plant succession in his book *The Bobwhite Quail.* This topic was ignored by academic plant ecologists. Aldo Leopold pioneered the application of ecological principles to the management of wildlife in his classic *Game Management* (1933). In *Forest Soils* (1954) H. L. Lutz and R. F. Chandler discussed nutrient cycles and their role in the forest ecosystem. J. Kittredge pointed out the impact of forests on the environment in *Forest Influences* (1948).

We have begun to apply ecosystem and theoretical ecology more intensively to resource management in the past decade, even though economics often takes precedence over protection. Forestry, once concerned with the raising of trees for harvest, now emphasizes biomass accumulation, nutrient cycling, the effects of timber harvesting on nutrient budgets, and the role of fire in forest ecosystems. Specialists in range management are interested in the functioning of grassland ecosystems, the effects of grazing intensities on aboveground and belowground production by plants, and the structure of grassland communities. Wildlife managers, who once emphasized only game species, now consider the entire wildlife spectrum, including species not hunted. The range of interest covers both population ecology of wildlife and the maintenance and management of plant communities as wildlife habitat. Wildlife managers have developed an interest in population genetics, especially as it relates to the effects of hunting on game species and to the restoration of endangered species.

A related developing field comprising both applied and theoretical ecology is *conservation biology*. It has been defined as "the science of scarcity and diversity" (Soule 1986). Conservation biology addresses the problems of gross habitat destruction and a great reduction in population size of species.

A second developing field tied to applied ecology is **landscape ecology.** It is concerned with spatial patterns in landscape and how they develop, with emphasis on the role of disturbance, including human impacts (Forman and Godron 1986).

A third new field is **restoration ecology.** It applies experimental research to the restoration of ecosystems on highly disturbed lands (Jordan et al. 1987).

Although applied ecology has been around since the early 1930s, it did not gain visibility until the 1970s, when ecology became involved in social, political, and economic issues. This involvement grew out of public awareness of the problems of pollution, toxic wastes, overpopulation, and a degraded environment. Although the public treated these issues as if they were new, ecologists had grappled with environmental problems for years. The ecological movement had its roots in Europe, especially Germany. An early founder of political ecology was Ernst Haeckel, who coined the term *ecology.* From Germany it moved to northern Europe, Great Britain, and the United States. In England the animal ecologist Charles Elton helped found the Nature Conservancy. The plant ecologist A. E. Tansley founded the British Ecological Society and was active in the conservation movement.

In the United States George Perkin Marsh in 1885 called attention to the effects of poor land use on the human environment in his dramatic book *Man and Nature.* In the 1930s F. E. Clements urged that the Great Plains be managed as grazing land and not be broken by the plow. The plant ecologist Paul Sears wrote *Deserts on the March* (1935) in response to the Great Plains Dust Bowl of the 1930s. William Vogt's *Road to Survival* (1948) and Fairfield Osborn's *Our Plundered Planet* called attention to the growing population-resource problem. Aldo Leopold's *A Sand County Almanac* (1949), which called for an ecological land ethic, was read largely by those interested in wildlife management until the 1970s, when it became the bible of the environmental movement.

Rachel Carson did more than anyone else to bring environmental problems to the attention of the public (Figure 1.3). Since the publication of her book *Silent Spring* (1962), people have become more aware that chemical poisons and other pollutants are recycled through the environment. Once castigated as more fiction than fact, Carson's predictions came only too true as carnivorous birds fell victim to toxic chemicals. With a ban on DDT in the United States, some eagles, hawks, and osprey began a gradual comeback. Carson made people quick to recognize other continuing chemical dangers, such as dioxin and PCBs.

Figure 1.3 Rachel Carson.

In the past quarter century since people became concerned about growing environmental degradation, how has the situation changed? We started off well enough with environmental legislation: the National Environmental Policy Act (1969), designed to protect the environment from overzealous development and to mitigate losses, the Endangered Species Act (1975, amended 1982 and 1994), and the Clean Water Act (1977, amended 1981, 1987, 1994), among others. The early enthusiasm for a quality environment, however, has dampened; government is less sensitive about environmental issues, and funding for environmental protection and research, especially at the federal level, has shrunk. During the 1980s there was even an environmental backlash at the federal level, as the administration attempted to undo all the environmental progress made during the previous two decades.

There has, of course, been progress. Water quality has improved considerably, and the air above some of our cities is cleaner. However, we have discovered that our environmental problems are not only more difficult to solve than once believed; many are growing worse. Toxic wastes pollute groundwater and land. Air is becoming more polluted worldwide. Haze has cut visibility in the eastern United States by more than 50 percent in the past 40 years. Acid rain affects lakes and streams. Increased concentrations of carbon dioxide and ozone threaten climatic stability. Roads

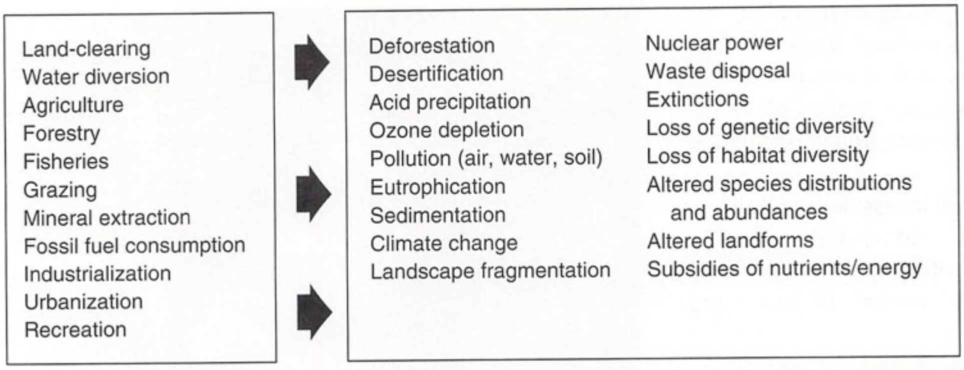


Figure 1.4 Human activities lessen the sustainability of the biosphere.

cut into open country and suburban expansions eat away at the hinterlands and farmlands. Continued deforestation in both temperate and tropical regions is fragmenting wildlife habitat, increasing the rate of extinction. A rapidly growing urban and suburban population with increasing interest in outdoor recreation is placing intolerable pressures on state and national parks that threaten their ecological integrity. Even the oceans have not escaped, as human debris and chemicals have been deadening the seas and destroying marine life. In spite of surplus agricultural production, wetlands are still being drained for more cropland at an alarming rate, threatening the very existence of already dangerously declining wetland wildlife. All of these activities have impacted regional and global ecological processes and have lessened Earth's ability to support a diversity of life, including humans (Figure 1.4). With the human population growing at the rate of 1.8 percent annually, its pressures on Earth's resources will accelerate.

Among the many environmental problems facing humanity, three broad areas are critical: global change, biological diversity, and sustainability. We have made worldwide changes in climate, in land and water use, and in landscape patterns. We are causing dramatic change in the distribution, abundance, and number of species. The loss of diversity can affect the stability of communities and populations upon which our economy depends, as exemplified by the loss of commercially important fish species. This rapid diminution of Earth's resources affects our ability to sustain both natural and managed ecosystems and human life itself.

The basis and solution of our environmental problems are ecological in nature. To this end The Ecological Society of America has developed a three-pronged Sustainable Biosphere Initiative, involving research, education, and environmental decision-making (Lubchenco et al. 1991). Research priorities focus on the critical areas of global change, biological diversity, and sustainable ecological systems. Researchers seek answers to such problems as the responses of ecological systems to stress, development and application of ecological theory to the management of ecological systems, and an ecological understanding of the effects of introduced species, pests, and pathogens.

Unfortunately, attempts to apply sound ecological principles to environmental problems often run headlong into economic, political, and social opposition, as witnessed by the debates over old-growth forest, regulation of fishing, land zoning, and wetland preservation. Successful application requires a citizenry that understands ecology and its importance. We need ecological education at all levels. Ecological principles need to be clearly understood by economists, engineers, lawyers, businespeople, and politicians, all of them decision makers who can hurt or improve the environment. Most decision-makers are unaware of the facts, do not understand basic ecological concepts, or are even hostile to environmental considerations for political, economic, or special reasons. An educated public can make decision-makers more responsible.

The future of human life on Earth depends on far more ecological knowledge than we now possess, even though we are not applying all we know. For the first time in the history of Earth, *Homo sapiens* has become the completely dominant organism, changing Earth and its diversity of life at will with little regard for the consequences. It is little wonder, then, that some of the most intellectually challenging problems in ecology lie in that transition zone between theoretical and applied ecology.

SUMMARY

Ecology, difficult to define precisely, is the study of the interrelations of organisms with their total environment, physical and biological. Its origins are diverse, but a main root goes back to early natural history and plant geography. They evolved into the study of plant communities, ecosystems, trophic levels, and energy budgets. A major branch that developed out of the natural history of animals was the study of natural selection and evolution, beginning with the major contributions of Darwin and Wallace. It further branched into evolutionary ecology, population genetics, population ecology, and theoretical ecology. Another branch gave rise to behavioral ecology, concerned with the way animals interact with their living and nonliving environment as influenced by natural selection, and to physiological ecology, concerned with the physiological responses of individual organisms to environmental factors. Studies of chemical reactions of organisms to their environment stimulated the development of chemical ecology. It concerns the uses of chemicals by plants and animals as attractants, repellents, and defensive mechanisms, their evolution and chemical structure. Ecology has so many roots and branches that we call it polymorphic.

As its various disciplines expand, ecology is becoming fragmented into specialties with a growing lack of communication among them. One tension developed between organismic and individualistic ecology. Another persists between holistic ecosystem ecology and reductionist evolutionary and population ecology. The differences, however, are not insuperable.

Applied ecology is concerned with the application of ecological principles to major environmental and resource management problems. Traditionally, applied ecology meant forest, range, wildlife and fishery management. Recently applied ecology has spawned the new fields of conservation biology, restoration ecology, and landscape ecology. The future quality of human life in all its aspects and the sustainability of Earth depend upon our ability to recognize and apply ecological principles to its management.

REVIEW QUESTIONS

1. Define ecology.
2. Why was plant geography a stimulus for the development of modern ecology?
3. What differences separate the organismal concept of ecology from the individualistic concept?
4. How do the two concepts in question 3 relate to holism and reductionism in ecology?
5. What is applied ecology, and how does it relate to theoretical and ecosystem ecology?
6. Refer to *The Sustainable Biosphere Initiative* (Lubchenco et al. 1991), select one of the research topics, and discuss how the results of such research would relate to our environmental problems.
7. Why is ecology not taken as seriously as it should be by the public and decision-makers?