

Fundamentals of Ecology

FIFTH EDITION

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From cover: A picture of the Great Barrier Reef (Walter Allen) in breeding plumage. Fortunately, the number of these magnificent birds has recovered from long persecution by plume hunters—an excellent example illustrating how the principles of conservation biology and restoration ecology can help to restore biotic diversity at the landscape scale.

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Foreword

Fundamentals of Ecology is an icon among biology textbooks—the most influential such work as measured by the number of students recruited into the field as researchers and teachers. The rebirth here of this classic, in a much modified fifth edition, but under the original title, is welcome.

There has always been a sense of inevitability about ecology, even in the early twentieth century, when it ranked as little more than a pastiche of natural history and schools of thought. Ecology was and remains the discipline that addresses the highest and most complex levels of biological organization. It was and remains a study of holism and emergence, of the properties of life taken from the top down. Even hard-nosed laboratory scientists, who were focused on the less complex (and more accessible) levels of molecules and cells, knew in their hearts that in time, biologists must eventually arrive at this discipline. To understand ecology thoroughly would be to understand *all* of biology, and to be a complete biologist is to be an ecologist. But ecology at the time of the first edition of *Fundamentals of Ecology* was still the most distant subject, enveloped in an intellectual haze, hard to picture except as scattered fragments. Odum's book was a map by which we could take a bearing. We need him still to learn the boundaries and principal features of ecology. The effectiveness of early editions of *Fundamentals of Ecology* is illustrated in a 2002 survey of the American Institute of Biological Sciences (Barrett and Mabry 2002) ranking it as the book that has recruited the most professionals into organismic and environmental biology.

The fifth edition, in comparison with the first edition, shows how far we have advanced in substance and in experimental studies linked to sophisticated theory and models. Subjects that were rudiments at the beginning—ecosystems analysis, energy and materials cycles, population dynamics, competition, biodiversity, and others—have grown to the rank of subdisciplines. They have been increasingly linked to one another and to the biology of organisms.

Furthermore, ecology is now seen as not just a biological but a human science. The future of our species depends on how well we understand that extension and employ it in the wise management of our natural resources. We live both by a market economy—necessary for our welfare on a day-to-day basis—and by a natural economy, necessary for our welfare (indeed, our very existence) in the long term. It is equally true that the pursuit of public health is largely an application of ecology. None of this should be surprising. We are, after all, a species in an ecosystem, exactly adapted to the conditions peculiar to the surface of this planet, and subject to the same principles of ecology as all other species.

The present edition provides a balanced approach among higher levels of biological organization. It can serve as a basic ecology text for college majors—not only in ecology and general biology, but also in the emerging disciplines of conservation biology and natural resource management. Moreover, it takes a futuristic look at such important topics as sustainability, environmental problem solving, and the relationship between market and natural capital.

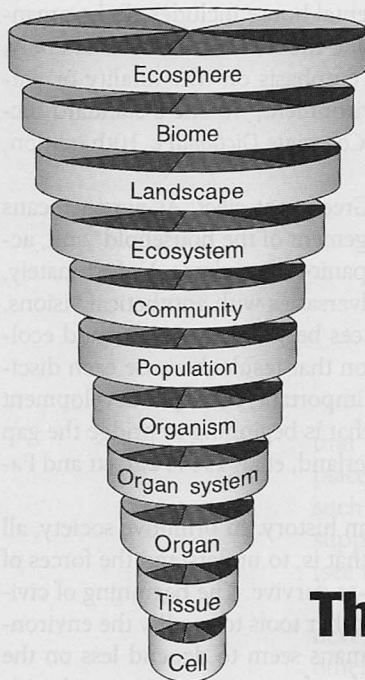
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Ecology is an old science, but its modern form as a quantitative discipline is relatively recent. The number of students recruited into the field as researchers has increased steadily since the 1950s. The field has grown in size and complexity, and it has become a discipline that addresses the most important and complex problems of our time. It is a discipline that is both broad and deep, and it is a discipline that is both theoretical and applied. The field of ecology is now a central part of the natural sciences, and it is a discipline that is both exciting and challenging. The present edition of *Ecology* is a book that is both a textbook and a reference work. It is a book that is both a guide to the field and a source of information. It is a book that is both a work of art and a work of science. It is a book that is both a pleasure to read and a source of knowledge. The field of ecology is a field that is both old and new, and it is a field that is both broad and deep. It is a field that is both theoretical and applied, and it is a field that is both exciting and challenging. The present edition of *Ecology* is a book that is both a textbook and a reference work. It is a book that is both a guide to the field and a source of information. It is a book that is both a work of art and a work of science. It is a book that is both a pleasure to read and a source of knowledge.



The Scope of Ecology

- 1 **Ecology: History and Relevance to Humankind**
- 2 **Levels-of-Organization Hierarchy**
- 3 **The Emergent Property Principle**
- 4 **Transcending Functions and Control Processes**
- 5 **Ecological Interfacing**
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1 Ecology: History and Relevance to Humankind

The word *ecology* is derived from the Greek *oikos*, meaning “household,” and *logos*, meaning “study.” Thus, the study of the environmental house includes all the organisms in it and all the functional processes that make the house habitable. Literally, then, **ecology** is the study of “life at home” with emphasis on “the totality or pattern of relations between organisms and their environment,” to cite a standard dictionary definition of the word (*Merriam-Webster’s Collegiate Dictionary*, 10th edition, s.v. “ecology”).

The word *economics* is also derived from the Greek root *oikos*. As *nomics* means “management,” economics translates as “the management of the household” and, accordingly, ecology and economics should be companion disciplines. Unfortunately, many people view ecologists and economists as adversaries with antithetical visions. Table 1-1 attempts to illustrate perceived differences between economics and ecology. Later, this book will consider the confrontation that results because each discipline takes a narrow view of its subject and, more important, the rapid development of a new interface discipline, *ecological economics*, that is beginning to bridge the gap between ecology and economics (Costanza, Cumberland, et al. 1997; Barrett and Farina 2000; L. R. Brown 2001).

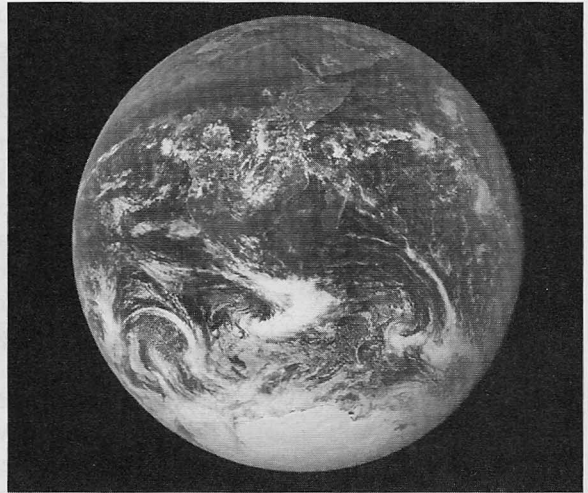
Ecology was of practical interest early in human history. In primitive society, all individuals needed to know their environment—that is, to understand the forces of nature and the plants and animals around them—to survive. The beginning of civilization, in fact, coincided with the use of fire and other tools to modify the environment. Because of technological achievements, humans seem to depend less on the natural environment for their daily needs; many of us forget our continuing dependence on nature for air, water, and indirectly, food, not to mention waste assimilation, recreation, and many other services supplied by nature. Also, economic systems, of whatever political ideology, value things made by human beings that primarily benefit the individual, but they place little monetary value on the goods and services of nature that benefit us as a society. Until there is a crisis, humans tend to take nat-

Table 1-1

A summary of perceived differences between economics and ecology

Attribute	Economics	Ecology
School of thought	Cornucopian	Neo-Malthusian
Currency	Money	Energy
Growth form	J-shaped	S-shaped
Selection pressure	<i>r</i> -selected	<i>K</i> -selected
Technological approach	High technology	Appropriate technology
System services	Services provided by economic capital	Services provided by natural capital
Resource use	Linear (disposal)	Circular (recycling)
System regulation	Exponential expansion	Carrying capacity
Futuristic goal	Exploration and expansion	Sustainability and stability

Figure 1-1. Earthscape as viewed from Apollo 17 traveling toward the Moon. View of the ecosphere from “outside the box.”



ural goods and services for granted; we assume they are unlimited or somehow replaceable by technological innovations, even though we know that life necessities such as oxygen and water may be recyclable but not replaceable. As long as the life-support services are considered free, they have no value in current market systems (see H. T. Odum and E. P. Odum 2000).

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 ancient Greece clearly contain references to ecological topics. However, the Greeks did not have a word for ecology. The word *ecology* is of recent origin, having been first proposed by the German biologist Ernst Haeckel in 1869. Haeckel defined *ecology* as “the study of the natural environment including the relations of organisms to one another and to their surroundings” (Haeckel 1869). Before this, during a biological renaissance in the eighteenth and nineteenth centuries, many scholars had contributed to the subject, even though the word *ecology* was not in use. For example, in the early 1700s, Antoni van Leeuwenhoek, best known as a premier microscopist, also pioneered the study of food chains and population regulation, and the writings of the English botanist Richard Bradley revealed his understanding of biological productivity. All three of these subjects are important areas of modern ecology.

As a recognized, distinct field of science, ecology dates from about 1900, but only in the past few decades has the word become part of the general vocabulary. At first, the field was rather sharply divided along taxonomic lines (such as plant ecology and animal ecology), but the biotic community concept of Frederick E. Clements and Victor E. Shelford, the food chain and material cycling concepts of Raymond Lindeman and G. Evelyn Hutchinson, and the whole lake studies of Edward A. Birge and Chauncy Juday, among others, helped establish basic theory for a unified field of general ecology. The work of these pioneers will be cited often in subsequent chapters.

What can best be described as a worldwide environmental awareness movement burst upon the scene during two years, 1968 to 1970, as astronauts took the first photographs of Earth as seen from outer space. For the first time in human history, we were able to see Earth as a whole and to realize how alone and fragile Earth hovers in space (Fig. 1-1). Suddenly, during the 1970s, almost everyone became con-

cerned about pollution, natural areas, population growth, food and energy consumption, and biotic diversity, as indicated by the wide coverage of environmental concerns in the popular press. The 1970s were frequently referred to as the “decade of the environment,” initiated by the first “Earth Day” on 22 April 1970. Then, in the 1980s and 1990s, environmental issues were pushed into the political background by concerns for human relations—problems such as crime, the cold war, government budgets, and welfare. As we enter the early stages of the twenty-first century, environmental concerns are again coming to the forefront because human abuse of Earth continues to escalate. We hope that this time, to use a medical analogy, our emphasis will be on prevention rather than on treatment, and ecology as outlined in this book, can contribute a great deal to prevention technology and ecosystem health (Barrett 2001).

The increase in public attention had a profound effect on academic ecology. Before the 1970s, ecology was viewed largely as a subdiscipline of biology. Ecologists were staffed in biology departments, and ecology courses were generally found only in the biological science curricula. Although ecology remains strongly rooted in biology, it has emerged from biology as an essentially new, integrative discipline that links physical and biological processes and forms a bridge between the natural sciences and the social sciences (E. P. Odum 1977). Most colleges now offer campus-wide courses and have separate majors, departments, schools, centers, or institutes of ecology. While the scope of ecology is expanding, the study of how individual organisms and species interface and use resources intensifies. The multilevel approach, as outlined in the next section, brings together “evolutionary” and “systems” thinking, two approaches that have tended to divide the field in recent years.

2 Levels-of-Organization Hierarchy

Perhaps the best way to delimit modern ecology is to consider the concept of **levels of organization**, visualized as an ecological spectrum (Fig. 1-2) and as an extended ecological hierarchy (Fig. 1-3). **Hierarchy** means “an arrangement into a graded series” (Merriam-Webster’s Collegiate Dictionary, 10th edition, s.v. “hierarchy”). Interaction with the physical environment (energy and matter) at each level produces characteristic functional systems. A **system**, according to a standard definition, consists of “regularly interacting and interdependent components forming a unified

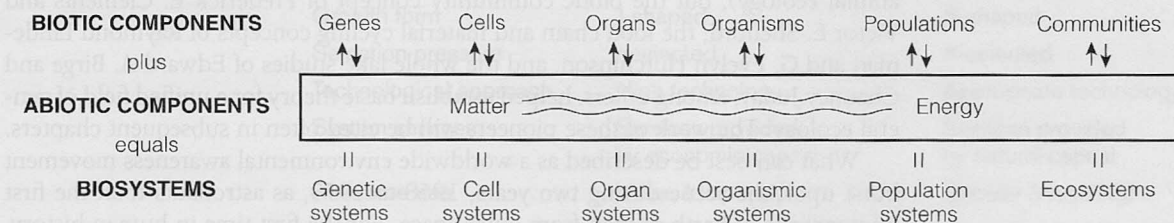
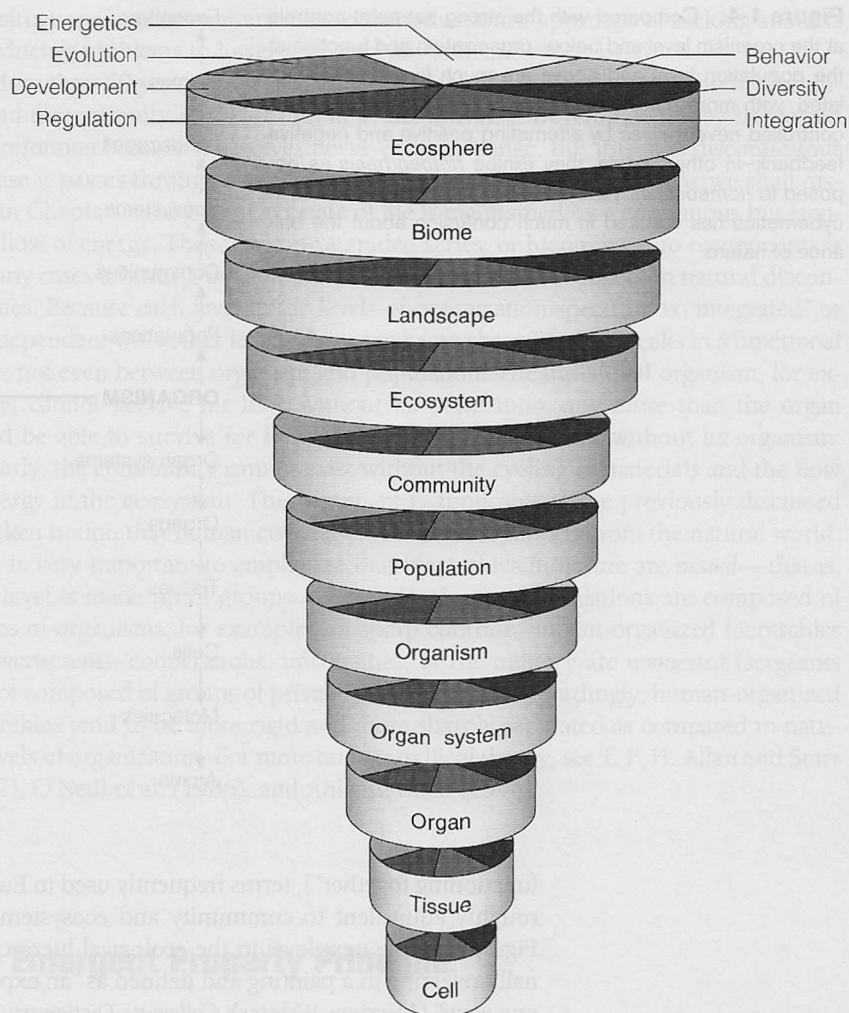


Figure 1-2. Ecological levels-of-organization spectrum emphasizing the interaction of living (biotic) and nonliving (abiotic) components.

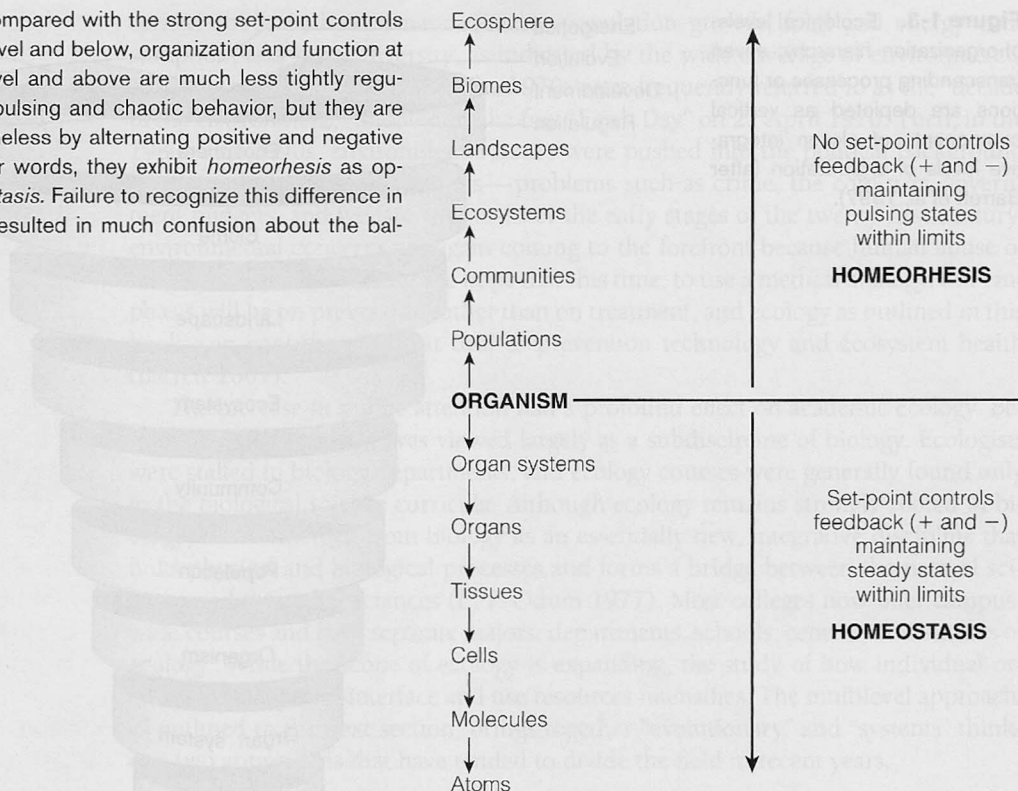
Figure 1-3. Ecological levels-of-organization hierarchy; seven transcending processes or functions are depicted as vertical components of eleven integrative levels of organization (after Barrett et al. 1997).



whole" (*Merriam-Webster's Collegiate Dictionary*, 10th edition, s.v. "system"). Systems containing living (biotic) and nonliving (abiotic) components constitute *biosystems*, ranging from genetic systems to ecological systems (Fig. 1-2). This spectrum may be conceived of or studied at any level, as illustrated in Figure 1-2, or at any intermediate position convenient or practical for analysis. For example, host-parasite systems or a two-species system of mutually linked organisms (such as the fungi-algae partnership that constitutes the lichen) are intermediate levels between population and community.

Ecology is largely, but not entirely, concerned with the system levels beyond that of the organism (Figs. 1-3 and 1-4). 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, **community**, in the ecological sense (sometimes designated as "biotic community"), includes all the populations occupying a given area. The community and the nonliving environment function together as an ecological system or **ecosystem**. *Biocoenosis* and *biogeocoenosis* (literally, "life and Earth

Figure 1-4. Compared with the strong set-point controls at the organism level and below, organization and function at the population level and above are much less tightly regulated, with more pulsing and chaotic behavior, but they are controlled nevertheless by alternating positive and negative feedback—in other words, they exhibit *homeorhesis* as opposed to *homeostasis*. Failure to recognize this difference in cybernetics has resulted in much confusion about the balance of nature.



functioning together”), terms frequently used in European and Russian literature, are roughly equivalent to community and ecosystem, respectively. Referring again to Figure 1-3, the next level in the ecological hierarchy is the landscape, a term originally referring to a painting and defined as “an expanse of scenery seen by the eye as one view” (Merriam-Webster’s *Collegiate Dictionary*, 10th edition, s.v. “landscape”). In ecology, **landscape** is defined as a “heterogenous area composed of a cluster of interacting ecosystems that are repeated in a similar manner throughout” (Forman and Godron 1986). A *watershed* is a convenient landscape-level unit for large-scale study and management because it usually has identifiable natural boundaries. *Biome* is a term in wide use for a large regional or subcontinental system characterized by a major vegetation type or other identifying landscape aspect, as, for example, the Temperate Deciduous Forest biome or the Continental Shelf Ocean biome. A *region* is a large geological or political area that may contain more than one biome—for example, the regions of the Midwest, the Appalachian Mountains, or the Pacific Coast. The largest and most nearly self-sufficient biological system is often designated as the **ecosphere**, which includes all the living organisms of Earth interacting with the physical environment as a whole to maintain a self-adjusting, loosely controlled pulsing state (more about the concept of “pulsing state” later in this chapter).

Hierarchical theory provides a convenient framework for subdividing and examining complex situations or extensive gradients, but it is more than just a useful rank-order classification. It is a holistic approach to understanding and dealing with com-

plex situations, and is an alternative to the reductionist approach of seeking answers by reducing problems to lower-level analysis (Ahl and Allen 1996).

More than 50 years ago, Novikoff (1945) pointed out that there is both continuity and discontinuity in the evolution of the universe. Development may be viewed as continuous because it involves never-ending change, but it is also discontinuous because it passes through a series of different levels of organization. As we shall discuss in Chapter 3, the organized state of life is maintained by a continuous but stepwise flow of energy. Thus, dividing a graded series, or hierarchy, into components is in many cases arbitrary, but sometimes subdivisions can be based on natural discontinuities. Because each level in the levels-of-organization spectrum is "integrated" or interdependent with other levels, there can be no sharp lines or breaks in a functional sense, not even between organism and population. 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. This argument is applicable to the previously discussed mistaken notion that human civilization can exist separately from the natural world.

It is very important to emphasize that hierarchies in nature are *nested*—that is, each level is made up of groups of lower-level units (populations are composed of groups of organisms, for example). In sharp contrast, human-organized hierarchies in governments, cooperations, universities, or the military are *nonnested* (sergeants are not composed of groups of privates, for example). Accordingly, human-organized hierarchies tend to be more rigid and more sharply separated as compared to natural levels of organization. For more on hierarchical theory, see T. F. H. Allen and Starr (1982), O'Neill et al. (1986), and Ahl and Allen (1996).

3 The Emergent Property Principle

An important consequence of hierarchical organization is that as components, or subsets, are combined to produce larger functional wholes, new properties emerge that were not present at the level below. Accordingly, an **emergent property** of an ecological level or unit cannot be predicted from the study of the components of that level or unit. Another way to express the same concept is **nonreducible property**—that is, a property of the whole not reducible to the sum of the properties of the parts. Though findings at any one level aid in the study of the next level, they never completely explain the phenomena occurring at the next level, which must itself be studied to complete the picture.

Two examples, one from the physical realm and one from the ecological realm, will suffice to illustrate emergent properties. When hydrogen and oxygen are combined in a certain molecular configuration, water is formed—a liquid with properties utterly different from those of its gaseous components. When certain algae and coelenterate animals evolve together to produce a coral, an efficient nutrient cycling mechanism is created that enables the combined system to maintain a high rate of productivity in waters with a very low nutrient content. Thus, the fabulous produc-

Newton has made major contributions. For example, research at the cellular and molecular levels has established a firm basis for the future cure and prevention of cancers at the level of the organism. However, cell-level science will contribute very little to the well-being or survival of human civilization if we understand the higher levels of organization so inadequately that we can find no solutions to population overgrowth, pollution, and other forms of societal and environmental disorders. Both holism and reductionism must be accorded equal value—and simultaneously, not alternatively (E. P. Odum 1977; Barrett 1994). Ecology seeks synthesis, not separation. The revival of the holistic disciplines may be due at least partly to citizen dissatisfaction with the specialized scientist who cannot respond to the large-scale problems that need urgent attention. (Historian Lynn White's 1980 essay "The Ecology of Our Science" is recommended reading on this viewpoint.) Accordingly, we shall discuss ecological principles at the ecosystem level, with appropriate attention to organism, population, and community subsets and to landscape, biome, and ecosphere suprasets. This is the philosophical basis for the organization of the chapters in this book.

Fortunately, in the past 10 years, technological advances have allowed humans to deal quantitatively with large, complex systems such as ecosystems and landscapes. Tracer methodology, mass chemistry (spectrometry, colorimetry, chromatography), remote sensing, automatic monitoring, mathematic modeling, geographical information systems (GIS), and computer technology are providing the tools. Technology is, of course, a double-edged sword; it can be the means of understanding the wholeness of humans and nature or of destroying it.

4 Transcending Functions and Control Processes

Whereas each level in the ecological hierarchy can be expected to have unique emergent and collective properties, there are basic functions that operate at all levels. Examples of such **transcending functions** are behavior, development, diversity, energetics, evolution, integration, and regulation (see Fig. 1-3 for details). Some of these (energetics, for example) operate the same throughout the hierarchy, but others differ in *modus operandi* at different levels. Natural selection evolution, for example, involves mutations and other direct genetic interactions at the organism level but indirect coevolutionary and group selection processes at higher levels.

It is especially important to emphasize that although positive and negative feedback controls are universal, from the organism down, control is *set point*, in that it involves very exacting genetic, hormonal, and neural controls on growth and development, leading to what is often called **homeostasis**. As noted on the right-hand side of Figure 1-4, there are no set-point controls above the organism level (no chemostats or thermostats in nature). Accordingly, feedback control is much looser, resulting in pulsing rather than steady states. The term **homeorhesis**, from the Greek meaning "maintaining the flow," has been suggested for this pulsing control. In other words, there are no equilibriums at the ecosystem and ecosphere levels, but there are *pulsing balances*, such as between production and respiration or between oxygen and carbon dioxide in the atmosphere. Failure to recognize this difference in *cybernetics* (the science dealing with mechanisms of control or regulation) has resulted in much confusion about the realities of the so-called "balance of nature."

tivity and diversity of coral reefs are emergent properties only at the level of the reef community.

Salt (1979) suggested that a distinction be made between emergent properties, as defined previously, and **collective properties**, which are summations of the behavior of components. Both are properties of the whole, but the collective properties do not involve new or unique characteristics resulting from the functioning of the whole unit. *Birth rate* is an example of a population level collective property, as it is merely a sum of the individual births in a designated time period, expressed as a fraction or percent of the total number of individuals in the population. New properties emerge because the components interact, not because the basic nature of the components is changed. Parts are not “melted down,” as it were, but integrated to produce unique new properties. It can be demonstrated mathematically that integrative hierarchies evolve more rapidly from their constituents than nonhierarchical systems with the same number of elements; they are also more resilient in response to disturbance. Theoretically, when hierarchies are decomposed to their various levels of subsystems, the latter can still interact and reorganize to achieve a higher level of complexity.

Some attributes, obviously, become more complex and variable as one proceeds to higher levels of organization, but often other attributes become less complex and less variable as one goes from the smaller to the larger unit. Because feedback mechanisms (checks and balances, forces and counterforces) operate throughout, the amplitude of oscillations tends to be reduced as smaller units function within larger units. Statistically, the variance of the whole-system level property is less than the sum of the variance of the parts. 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 component slows down, another component may speed up to compensate. When one considers both the emergent properties and the increasing homeostasis that develop at each level, not all component parts must be known before the whole can be understood. This is an important point, because some contend that it is useless to try to work on complex populations and communities when the smaller units are not yet fully understood. Quite the contrary, one may begin study at any point in the spectrum, provided that adjacent levels, as well as the level in question, are considered, because, as already noted, some attributes are predictable from parts (collective properties), but others are not (emergent properties). Ideally, a system-level study is itself a threefold hierarchy: system, subsystem (next level below), and suprasystem (next level above). For more on emergent properties, see T. F. H. Allen and Starr (1982), T. F. H. Allen and Hoekstra (1992), and Ahl and Allen (1996).

Each biosystem level has emergent properties and reduced variance as well as a summation of attributes of its subsystem components. The folk wisdom about the forest being more than just a collection of trees is, indeed, a first working principle of ecology. Although the philosophy of science has always been holistic in seeking to understand phenomena as a whole, in recent years the practice of science has become increasingly reductionist in seeking to understand phenomena by detailed study of smaller and smaller components. Laszlo and Margenau (1972) described within the history of science an alternation of reductionist and holistic thinking (*reductionism-constructionism* and *atomism-holism* are other pairs of words used to contrast these philosophical approaches). The law of diminishing returns may very well be involved here, as excessive effort in any one direction eventually necessitates taking the other (or another) direction.

The reductionist approach that has dominated science and technology since Isaac

ogy was frequently based on **multidisciplinary** approaches (multi = “many”), especially during the 1960s and 1970s. Unfortunately, the multidisciplinary approaches lacked cooperation or focus. To achieve cooperation and define goals, institutes or centers were established on campuses throughout the world, such as the Institute of Ecology located on the campus of the University of Georgia. These **crossdisciplinary** approaches (cross = “traverse”; Fig. 1-10) frequently resulted in polarization toward a specific monodisciplinary concept, a poorly funded administrative unit, or a narrow mission. A crossdisciplinary approach also frequently resulted in polarized faculty reward systems. Institutions of higher learning, traditionally built on disciplinary structures, have difficulties in administering programs and addressing environmental problems as well as taking advantage of opportunities at greater temporal and spatial scales.

To address the dilemma, **interdisciplinary** approaches (inter = “among”) were employed, resulting in cooperation on a higher-level concept, problem, or question. For example, the process and study of natural ecological succession provided a higher-level concept resulting in the success of the Savannah River Ecological Laboratory (SREL) during its conception. Researchers theorized that new system properties emerge during the course of ecosystem development and that it is these properties that largely account for species and growth form changes that occur (E. P. Odum 1969, 1977; see Chapter 8 for details). Today, interdisciplinary approaches are common when addressing problems at ecosystem, landscape, and global levels.

Much remains to be done, however. There is an increased need to solve problems, promote environmental literacy, and manage resources in a **transdisciplinary** manner. This multilevel, large-scale approach involves entire education and innovation systems (Fig. 1-10). This integrative approach to the need for unlocking cause-and-effect explanations across and among disciplines (achieving a transdisciplinary understanding) has been termed *consilience* (E. O. Wilson 1998), *sustainability science* (Kates et al. 2001), and *integrative science* (Barrett 2001). Actually, the continued development of the science of ecology (the “study of the household” or “place where we live”) will likely evolve into that much-needed integrative science of the future. This book attempts to provide the knowledge, concepts, principles, and approaches to underpin this educational need and learning process.



Figure 1-9. Ecosystem model showing energy flow and nutrient cycling. The diagram illustrates the flow of energy and nutrients through various components of an ecosystem, including producers, consumers, and decomposers, and their interactions with the environment.