Este es el primer capítulo (con pequeñas modificaciones) del libro:

Ecology. Concepts and applications. 2019. 8th edition. Manuel C. Molles (Jr) and Anna A. Sher. Mc Graw Hill Education, New York.

Esta introducción no solo introduce el concepto de ecología, sino también sus abordajes y aplicaciones.

Chapter 1 Introduction to Ecology

CHAPTER CONCEPTS

LEARNING OUTCOME After studying this section you should be able to do the following:

1.1 Discuss the concept of environment as it pertains to the science of ecology.

What is ecology? Ecology is the study of relationships among organisms and between organisms and the physical environment. These relationships influence many aspects of the natural world, including the distribution and abundance of organisms, the variety of species living together in a place, and the transformation and flow of energy in nature. Humans are rapidly changing earth's environment, yet we do not fully understand the consequences of these changes. For instance, human activity has increased the quantity of nitrogen cycling through land and water, changed land cover across the globe, and increased the atmospheric concentration of CO_2. Changes such as these threaten the diversity of life on earth and may endanger our life support system. Because of the rapid pace of environmental change in the early twenty first century, it is imperative that we better understand earth's ecology. Behind the simple definition of ecology lies a broad scientific discipline. Ecologists may study individual organisms, entire forests or lakes, or even the whole earth. The measurements made by ecologists include counts of individual organisms, rates of reproduction, and rates of processes such as photosynthesis and decomposition. Ecologists often spend as much time studying nonbiological components of the environment, such as temperature and soil chemistry, as they spend studying organisms. Meanwhile, the “environment” of organisms in some ecological studies is other species. While you may think of ecologists as typically studying in the field, some of the most important conceptual advances have come from ecologists who build theoretical models or do ecological research in the laboratory. Clearly, our simple definition of ecology does not communicate the great breadth of the discipline or the diversity of its practitioners. To get a better idea of what ecology is, let’s briefly review its scope.

1.1 Overview of Ecology

LEARNING OUTCOMES After studying this section you should be able to do the following:

1.2 Describe the levels of ecological organization, for example, population, studied by ecologists.

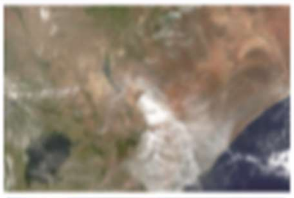
1.3 Distinguish between the types of questions addressed by ecologists working at different levels of organization.

1.4 Explain how knowledge of one level of ecological organization can help guide research at another level of organization.

Ecologists study environmental relationships ranging from those of individual organisms to factors influencing global-scale processes. This broad range of subjects can be organized by arranging them as levels in a hierarchy of ecological organization, such as that embedded in the brief table of contents and the sections of this book. Figure 1.1 attempts to display such a hierarchy graphically. Historically, the ecology of individuals, which is at the base of figure 1.1, has been the domain of physiological ecology and behavioral ecology. Physiological ecologists have emphasized the evolution (a process by which populations change over time) of physiological and anatomical mechanisms by which organisms adapt to challenges posed by physical and chemical variation in the environment. Meanwhile, behavioral ecologists have focused principally on evolution of behaviors that allow animals to survive and reproduce in the face of environmental variation. There is a strong conceptual linkage between ecological studies of individuals and of populations particularly where they concern evolutionary processes. Population ecology is centered on the factors influencing population structure and process, where a population is a group of individuals of a single species inhabiting a defined area. The processes studied by population ecologists include adaptation, extinction, the distribution and abundance of species, population growth and regulation, and variation in the reproductive ecology of species. Population ecologists are particularly interested in how these processes are influenced by nonbiological and biological aspects of the environment.

BIOSPHERE

What role does concentration of atmospheric CO_2 play in the regulation of global temperature?



REGION

How has geologic history influenced regional diversity within certain groups of organisms?

ECOSYSTEM

How does fire affect nutrient availability in grassland ecosystems?

LANDSCAPE

How do vegetated corridors affect the rate of movement by mammals among isolated forest fragments?

COMMUNITY

What factors influence the number of large mammal species living together in African grasslands?

INTERACTIONS

Do predators influence where zebras feed in the landscape?

POPULATIONS

What factors control zebra populations?

INDIVIDUALS

How do zebras regulate their internal water balance?

Figure 1.1 Levels of ecological organization and examples of the kinds of questions asked by ecologists working at each level.

Bringing biological components of the environment into the picture takes us to the next level of organization, the ecology of interactions such as predation, parasitism, and competition. Ecologists who study interactions between species have often emphasized the evolutionary effects of the interaction on the species involved. Other approaches explore the effect of interactions on population structure or on properties of ecological communities. The definition of an ecological community as an association of interacting species links community ecology with the ecology of interactions. Community and ecosystem ecology have a great deal in common, since both are focused on multispecies systems. However, the objects of their study differ. While community ecologists concentrate on understanding environmental influences on the kinds and diversity of organisms inhabiting an area, ecosystem ecologists focus on ecological processes such as energy flow and decomposition. To simplify their studies, ecologists have long attempted to identify and study isolated communities and ecosystems. However, all communities and ecosystems on earth are subject to exchanges of materials, energy, and organisms with other communities and ecosystems. The study of these exchanges, especially among ecosystems, is the intellectual territory of landscape ecology. However, landscapes are not isolated either but part of geographic regions subject to largescale and long-term regional processes. These regional processes are the subjects of geographic ecology. Geographic ecology in turn leads us to the largest spatial scale and highest level of ecological organization—the biosphere, the portions of the earth that support life, including the land, waters, and atmosphere. While this description of ecology provides a brief preview of the material covered in this book, it is a rough sketch and highly abstract. To move beyond the abstraction represented by figure 1.1, we need to connect it to the work of the scientists who have created the discipline of ecology. To do so, let's briefly review the research of ecologists working at a broad range of ecological levels emphasizing links between historical foundations and some developing frontiers (fig. 1.2).

Concept 1.1 Review

1. How does the level of ecological organization an ecologist studies influence the questions he or she poses? 2. While an ecologist may focus on a particular level of ecological organization shown in figure 1.1, might other levels of organization be relevant, for example, does an ecologist studying factors limiting numbers in a population of zebras need to consider the influences of interactions with other species or the influences of food on the survival of individuals?

1.2 Sampling Ecological Research

LEARNING OUTCOMES After studying this section you should be able to do the following:

1.5 Describe some emerging frontiers in ecology.

1.6 Explain how the use of stable isotopes has extended what it is possible to know about the ecology of warblers.

1.7 Compare the spatial and temporal scales addressed by the research of Robert MacArthur, Nalini Nadkarni, and Margaret Davis.

Two rapidly developing frontiers in ecology: a) Aeroecology: the interdisciplinary study of the ecology of the earth– atmosphere boundary (Kunz et al. 2008). New tools, such as the Indigo/FLIR Merlin midthermal camera that took this thermal infrared image of flying Brazilian free-tailed bats, Tadarida brasiliensis, have opened this developing frontier in ecology. This image depicts variation in the surface temperature of these bats. Thermal infrared technology makes it possible not only to detect and record the presence of free-ranging nocturnal organisms, but also to investigate their physiology and ecology in a noninvasive manner (see chapter 5). (b) Urban ecology: the study of urban areas as complex, dynamic ecological systems, influenced by interconnected, biological, physical, and social components. As ecologists focus their research on the environment where most members of our species live, they have made unexpected discoveries about the ecology of urban centers such as the city of Baltimore (see chapter 19).

Ecologists design their studies based on their research questions, the temporal and spatial scale of their studies, and available research tools. Because the discipline is so broad, ecological research can draw from all the physical and biological sciences. The following section of this chapter provides a sample of ecological questions and approaches to research.

The Ecology of Forest Birds: Old Tools and New Robert MacArthur gazed intently through his binoculars. He was watching a small bird, called a warbler, searching for insects in the top of a spruce tree. To the casual observer it might have seemed that MacArthur was a weekend bird-watcher. Yes, he was intensely interested in the birds he was watching, but he was just as interested in testing ecological theory. The year was 1955, and MacArthur was studying the ecology of five species of warblers that live together in the spruce forests of northeastern North America. All five warbler species, Cape May (Dendroica tigrina), yellow-rumped (D. coronata), black-throated green (D. virens), blackburnian (D. fusca), and bay-breasted (D. castanea), are about the same size and shape and all feed on insects. Theory predicted that two species with identical ecological requirements would compete with each other and that, as a consequence, they could not live in the same environment indefinitely. Mac Arthur wanted to understand how several warbler species with apparently similar ecological requirements could live together in the same forest. The warblers fed mainly by gleaning insects from the bark and foliage of trees. MacArthur predicted that these warblers might be able to coexist and not compete with each other if they fed on the insects living in different zones within trees. To map where the warblers fed, he subdivided trees into vertical and horizontal zones. He then carefully recorded the amount of time warblers spent feeding in each. MacArthur's prediction proved to be correct. His quantitative observations demonstrated that the five warbler species in his study area fed in different zones in spruce trees. As figure 1.3 shows, the Cape May warbler fed mainly among new needles and buds at the tops of trees. The feeding zone of the blackburnian warbler overlapped broadly with that of the Cape May warbler but extended farther down the tree. The blackthroated green warbler fed toward the trees' interiors. The bay-breasted warbler concentrated its feeding in the middle sections of trees. Finally, the yellow-rumped warbler fed mostly on the ground and low in the trees. MacArthur's observations showed that though these warblers live in the same forest, they extract food from different parts of that forest. He concluded that feeding in different zones may reduce competition among the warblers of spruce forests. MacArthur's study (1958) of foraging by warblers is a true classic in the history of ecology. However, like most studies it raised as many questions as it answered. Scientific research is important both for what it teaches us directly about nature and for how it stimulates other studies that improve our understanding. MacArthur's work stimulated numerous studies of competition among many groups of organisms, including warblers. Some of these studies produced results that supported his work and others produced different results. All added to our knowledge of competition between species and of warbler ecology.

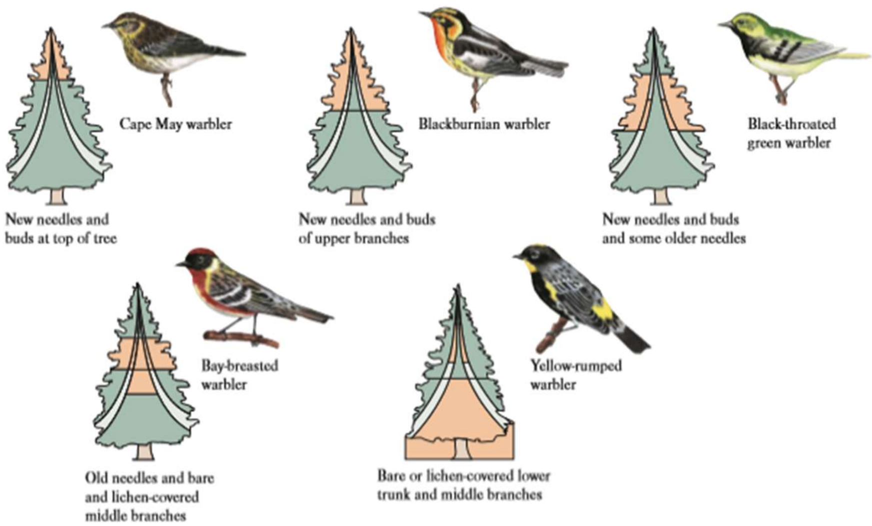


Figure 1.3 Warbler feeding zones shown in beige. The several warbler species that coexist in the forests of northeastern North America feed in distinctive zones within forest trees.

Nearly half a century after Robert MacArthur studied the feeding ecology of warblers through the lenses of his binoculars, a team of Canadian and U.S. scientists led by Ryan Norris (Norris et al. 2005) worked to develop tools capable of penetrating the feeding habitats of wide-ranging migratory birds. The object of their study was the American redstart (Setophaga ruticilla), another colorful member of the warbler family Parulidae (fig. 1.4). American redstarts, like the warblers studied by MacArthur, are long-distance migrants, nesting in temperate North America but spending their winters mainly in tropical Central America, northern South America, and the Caribbean islands. Historically, studies of wide-ranging bird species, such as the American redstart, have focused mainly on their temperate breeding grounds. However, observations by ecologists had long suggested that the success of an individual migratory bird during the breeding season may depend critically on the environmental conditions it experienced on its tropical wintering grounds. For example, it has been well established that male migratory birds, arriving early on the breeding grounds, are generally in better physical condition compared to those arriving later. Early arrivals also generally obtain the best breeding territories and have higher reproductive success. Variation in arrival times and physical condition led ecologists to ponder the connection between events on the wintering grounds and subsequent reproductive success among birds in their breeding habitats. To answer such a question, we need a great deal of information, including where individual birds live on the wintering grounds, how the winter habitat correlates with physical condition during migration, how winter habitat influences time of arrival on the breeding grounds, and whether winter habitat correlates with reproductive success on the breeding grounds. Clearly, the amount of information required to answer such questions, concerning environments separated by thousands of kilometers (fig. 1.5), exceeds what one person, or even a large team, can learn through the lenses of binoculars.

Often, ecologists have pioneered the use of more powerful research tools, as the complexity of their questions have increased. A tool to which ecologists turn increasingly to understand the ecology of migratory birds is stable isotope analysis (see chapter 6). Isotopes of a chemical element, for example, isotopes of carbon, have different atomic masses as a result of having different numbers of neutrons. Carbon, for instance, has three isotopes (listed in order of increasing mass): 12C, 13C, and 14C. Of these three, 12C and 13C are stable isotopes because they do not undergo radioactive decay, whereas 14C decays radioactively and is therefore unstable. Stable isotopes have proven useful in the study of ecological processes—for example, identifying food sources, because the proportions of various isotopes differ across the environment. Stable isotope analysis provides ecologists with a new type of “lens” capable of revealing ecological relationships that would otherwise remain invisible. For example, ecologists using stable isotope analysis can track habitat use by American redstarts on their wintering grounds. In Jamaica, older male American redstarts, along with some females, spend the winter in higher-productivity mangrove forest habitats, pushing most females and younger males into poorer quality, dry scrub habitat. The dominant plants in these two habitats and the insects that feed on them contain different proportions of the carbon isotopes 12C and 13C. Therefore, the tissues of the birds spending their winters in the productive mangrove habitat (lower 13C) and those spending the winters in the poor scrub habitat (higher 13C) are in effect chemically tagged. As a consequence, today’s ecologist can analyze a very small sample of blood from an American redstart when it arrives on its temperate breeding ground and know the habitat where it spent the winter. When Ryan Norris and his research team made such measurements, they found that male redstarts that had spent the winter in the more productive mangrove habitat arrived on the breeding grounds earlier and produced significantly more young birds that survived to fledging. Stable isotope analysis and the role that it has played in elucidating the ecology of a diversity of organisms will thread its way through the text. As is often the case in science, new tools create new research frontiers. Another of those frontiers is to be found in the canopies of forests.

Forest Canopy Research: A Physical and Scientific Frontier Studies of warblers showcase how ecologists approach studies of one or a few species. Other ecologists have been concerned with the ecology of entire forests, lakes, or grasslands, which they treat as ecosystems. An ecosystem includes all the organisms that live in an area and the physical environment with which those organisms interact. Many ecosystem studies have focused on nutrients, the raw materials that an organism must acquire from the environment to live. For ecologists who study the budgets of nutrients such as nitrogen, phosphorus, or calcium, one of the first steps is to inventory their distribution within an ecosystem. Inventories by Nalini Nadkarni (1981, 1984a, 1984b) changed our ideas of how tropical and temperate rain forests are structured and how they function. On the rain forest floor, she had wondered about the diversity of organisms and ecological relationships that might be hidden in the canopy high above. Her wonder soon gave way to determination. With the aid of mountain-climbing equipment, Nadkarni slowly made her first ascent into the canopy of the Costa Rican rain forest, a world explored by few others and where she was to become a pioneer (fig. 1.6). Nadkarni not only visited the canopy but also was among the first to explore the ecology of this unseen world. Because of leaching by heavy rains, many rain forest soils are poor in nutrients such as nitrogen and phosphorus. The low availability of nutrients in many rain forest soils has produced one of ecology's puzzles. How can the prodigious life of rain forests be maintained on such nutrient-poor soils? Many factors contribute to the maintenance of this intense biological activity. Nadkarni's research in the treetops uncovered one of those factors, a significant store of nutrients in the rain forest canopy. The nutrient stores in the rain forest canopy are associated with epiphytes. Epiphytes are plants, such as many orchids and ferns, that live on the branches and trunks of other plants. Epiphytes are not parasitic: they do not derive their nutrition from the plant they grow on. As they grow on the branches of a tree they begin to trap organic matter, which eventually forms a mat. Epiphyte mats increase in thickness up to 30 cm, providing a complex structure that supports a diverse community of plants and animals.

Epiphyte mats contain significant quantities of nutrients. Nadkarni estimated that these quantities in some tropical rain forests are equal to about half the nutrient content of the foliage of the canopy trees. In the temperate rain forests of the Olympic Peninsula in Washington, the mass of epiphytes is four times the mass of leaves on their host trees. Nadkarni's research showed that in both temperate and tropical rain forests, trees access these nutrient stores by sending out roots from their trunks and branches high above the ground. These roots grow into the epiphyte mats and extract nutrients from them. As a consequence of this research, we now know that to understand the nutrient economy of rain forests the ecologist must venture into the treetops. Easier means of working in the rain forest canopy have been developed, and this research is no longer limited to the adventurous and agile. New ways to access the forest canopy range from hot air balloons and large cranes (see

Investigating the Evidence 16 in Appendix A) to aerial drones (fig. 1.7). Research projects supported—and made far easier—by these technologies have included the ecology of migratory birds in the forest canopy, photosynthesis by epiphytes living at different canopy heights, and vertical stratification of habitat use by bats and beetles (Ozanne et al. 2003). Nadkarni points out, in response to these developments, that the canopy as a physical frontier may be closing, but its exploration as a scientific frontier is just beginning, particularly as we attempt to predict the ecological consequences of climate change.

Climatic and Ecological Change: Past and Future The earth and its life are always changing. However, many of the most important changes occur over such long periods of time or at such large spatial scales that they are difficult to study. Two approaches that provide insights into long-term and large-scale processes are studies of pollen preserved in lake sediments and of evolutionary change. Margaret B. Davis (1983, 1989) carefully searched through a sample of lake sediments for pollen. The sediments had come from a lake in the Appalachian Mountains, and the pollen they contained would help her document changes in the community of plants living near the lake during the past several thousand years. Davis is a paleoecologist trained to think at very large spatial scales and over very long periods of time. She has spent much of her professional career studying changes in the distributions of plants during the Quaternary period, particularly during the most recent 20,000 years. Some of the pollen produced by plants that live near a lake falls on the lake surface, sinks, and becomes trapped in lake sediments. As lake sediments build up over the centuries, this pollen is preserved and forms a historical record of the kinds of plants that lived nearby. As the lakeside vegetation changes, the mix of pollen preserved in the lake's sediments also changes. In the example shown in figure 1.8, pollen from spruce trees, Picea spp., first appears in lake sediments about 12,000 years ago; then pollen from beech, Fagus grandifolia, occurs in the sediments beginning about 8,000 years ago. Chestnut pollen does not appear in the sediments until about 2,000 years ago. The pollen from all three tree species continues in the sediment record until about 1920, when chestnut blight killed most of the chestnut trees in the vicinity of the lake. Thus, the pollen preserved in the sediments of lakes can be used to reconstruct the history of vegetation in the area. Margaret B. Davis, Ruth G. Shaw, and Julie R. Etterson reviewed extensive evidence that during climate change, plants evolve, as well as disperse (Davis and Shaw 2001; Davis, Shaw, and Etterson 2005). As climate changes, plant populations simultaneously change their geographic distributions and undergo the evolutionary process of adaptation, which increases their ability to live in the new climatic regime. Meanwhile, evidence of evolutionary responses to climate change has been found in many animal groups. William Bradshaw and Christina Holzapfel (2006) summarized several studies documenting evolutionary change in northern animals, ranging from birds and insects to small mammals (fig. 1.9), in response to longer growing seasons with global warming (see chapter 23). Such research will be essential to predicting ecological responses to global climate change. In the remainder of this book we will fill in the details of the sketch of ecology presented in this chapter. This brief survey has only hinted at the conceptual basis for the research described. Throughout this book we emphasize the conceptual foundations of ecology. We also explore some of the applications associated with the focal concepts of each chapter. Of course, the most important conceptual tool used by ecologists is the scientific method (see Investigating the Evidence 1 in Appendix A). We continue our exploration of ecology in section I with natural history and evolution. Natural history is the foundation on which ecologists build modern ecology for which evolution provides a conceptual framework. A major premise of this book is that knowledge of natural history and evolution improves our understanding of ecological relationships.

Concept 1.2 Review

1. How were the warbler studies of Robert MacArthur and those that focused on the American redstart similar? How did they differ? 2. What aspects of Nalini Nadkarni's research identify it as "ecosystem ecology"? Give examples of research in forest canopies that would address other levels of ecological organization (for examples, see fig. 1.1). 3. The discussion of the research by Margaret Davis and her colleagues did not identify the questions that they addressed. What research questions can we infer from the above description of their work?

   Applications: Ecology Can Inform Environmental Law and Policy

   LEARNING OUTCOMES After studying this section you should be able to do the following:

   1.8 Describe the purposes of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) and the U.S. Endangered Species Act (ESA).

   1.9 Discuss how subject areas covered in this text are applicable to identifying and managing endangered species.

   Because ecological science concerns relationships between organisms and the environment, it is natural to turn to ecology when environmental concerns arise. Consequently, ecology has contributed prominently to the development of environmental law and policy. For example, ecologists have been essential to evaluating the effects of pollution on the diversity of species in terrestrial and aquatic communities and on the functioning of ecosystems. One area where ecology, which includes how the environment influences the distribution and abundance of species (covered in chapters 9–12), has played a particularly significant role is in evaluating the status of individual species threatened by human impacts on the environment. Ecological studies of animal and plant populations are essential to determining when species populations have declined in numbers to the point where they are in danger of extinction (see chapter 9). Reports of such declines in the 1960s eventually led to the establishment of international treaties and national laws to protect endangered species. Two prominent protections came into force in 1973. The first was the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES), an international treaty to protect endangered species from the threat of wildlife trafficking and trade. The second was the U.S. Endangered Species Act, or ESA. The ESA extended protection to all threatened and endangered vertebrate animals, invertebrate animals, and plants in the United States and to species elsewhere around the globe listed as endangered under the CITES treaty. The species protected by the ESA have ranged from the large and charismatic, such as grizzly bears and whales, to inconspicuous plants and insects. Later amendments to the ESA required that management agencies, such as the U.S. Fish and Wildlife Service, identify "critical habitat" for threatened and endangered species. This requirement brought studies of the adaptations of species to the environment (chapters 4–8) as well as community, ecosystem, landscape, and geographic ecology (chapters 16–22), into greater prominence as tools for endangered species management. Because human-caused changes to the environment now extend to the entire planet, global ecology (chapter 23) is increasingly relevant to long-term endangered species protection. Ecological studies are also essential to determining whether protected populations have recovered sufficiently to be removed from the ESA's list of endangered species, a process called delisting. There have been a number of high- profile species that have been delisted in recent years, including the gray whales of the eastern North Pacific Ocean and bald eagles of the contiguous 48 states. In summary, ecological science has been essential to identifying, protecting, and managing species vulnerable to extinction.

Ecologists study environmental relationships ranging from those of individual organisms to factors influencing global-scale processes. The research focus and questions posed by ecologists differ across the levels of ecological organization studied. Ecologists design their studies based on their research questions, the temporal and spatial scale of their studies, and available research tools. With this brief review of research approaches and topics, we return to the question asked at the beginning of the chapter: What is ecology? Ecology is indeed the study of relationships between organisms and the environment. However, as you can see from the studies reviewed, ecologists study those relationships over a large range of temporal and spatial scales using a wide variety of approaches. Ecology includes Davis's studies of vegetation moving across the North American continent over a span of thousands of years. Ecology also includes the observational studies of birds in contemporary forests by MacArthur. Ecologists may study processes on plots measured in square centimeters or, like those studying the ecology of migratory birds, study areas may span thousands of kilometers. Important ecological discoveries have come from Nadkarni's probing of the rain forest canopy and from traces of stable isotopes in a droplet of blood. Ecology includes all these approaches and many more. Because ecological science concerns relationships between organisms and the environment, it is often consulted when environmental concerns arise. Ecological science has been particularly important to identifying, protecting, and managing species vulnerable to extinction.

Review Questions

1. Faced with the complexity of nature, ecologists have divided the field of ecology into subdisciplines, each of which focuses on one of the levels of organization pictured in figure 1.1. What is the advantage of developing such subdisciplines within ecology? 2. What are the pitfalls of subdividing nature in the way it is represented in figure 1.1? In what ways does figure 1.1 misrepresent nature? 3. What could you do to verify that the distinct feeding zones used by the warblers studied by MacArthur (see fig. 1.3) are the result of ongoing competition between the different species of warblers? How might you examine the role of competition in keeping some American redstarts out of the most productive feeding areas on their wintering grounds? 4. Although Nalini Nadkarni's studies of the rain forest canopy addressed a question related to ecosystem structure, the patterns Review Questions of nutrient storage in rain forest canopy resulted from the biology of individual organisms, populations of organisms, and communities of species. Explain. 5. What do the studies of Margaret Davis tell us about the composition of forests in the Appalachian Mountains during the past 12,000 years (see fig. 1.8)? Based on this research, what predictions might you make about the future composition of these forests? 6. During the course of the studies reviewed in this chapter, each scientist or team of scientists measured certain variables. What major variable studied by Margaret Davis and her research team distinguishes their work from that of the other research reviewed in the chapter?