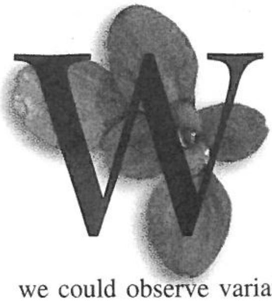


What is ecology? **Ecology** can be defined as the study of relationships between organisms and the environment. Humans have been students of ecology as long as we have existed as a species. Our survival has depended upon how well we could observe variations in the environment and predict the responses of organisms to those variations. The earliest hunters and gatherers had to be familiar with the habits of their animal prey. They also had to know where to find food plants and when they would ripen. Later, farmers and ranchers had to be aware of variations in weather and soils and of how they might affect their crops and livestock.

Today, most of earth's human population lives in cities and most of us have little direct contact with nature. More than ever before, though, the future of our species depends on how well we understand the relationships between organisms and the environment. We must study these relationships because our species is rapidly changing earth's environment, but we do not fully understand the consequences of these changes. For instance, human activity has greatly increased the quantity of nitrogen cycling through the biosphere, changed land use 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. At the dawn of the twenty-first century, it is imperative that we once again become ardent students of ecology.

Behind the simple definition of ecology lies a broad scientific discipline that almost defies definition. 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, or rates of processes such as photosynthesis and decomposition. Ecologists often spend as much time studying nonbiological components of the environment, such as temperature or soil chemistry, as they spend studying organisms. Meanwhile, the "environment" of organisms in some ecological studies may be other species. While you may think of ecologists as typically studying in the field, some of the most important conceptual advances in ecology have come from ecologists who build theoretical models of ecological systems 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 the research approaches of a few ecologists.

The Ecology of Forest Birds: Using Field Studies to Test Theory

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 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. MacArthur 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 1.1 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 black-throated green warbler fed toward the trees' interiors. The bay-breasted warbler concentrated its feeding in the interior 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.

One ecologist whose studies extended our knowledge of warbler ecology a great deal was Douglass Morse (1980, 1989). His research addressed several questions raised by MacArthur's work, including whether warblers use the same feeding zones in the absence of one or more of the other species. Morse studied this possibility by comparing the feeding zones of warblers living in the presence or absence of other warbler species.

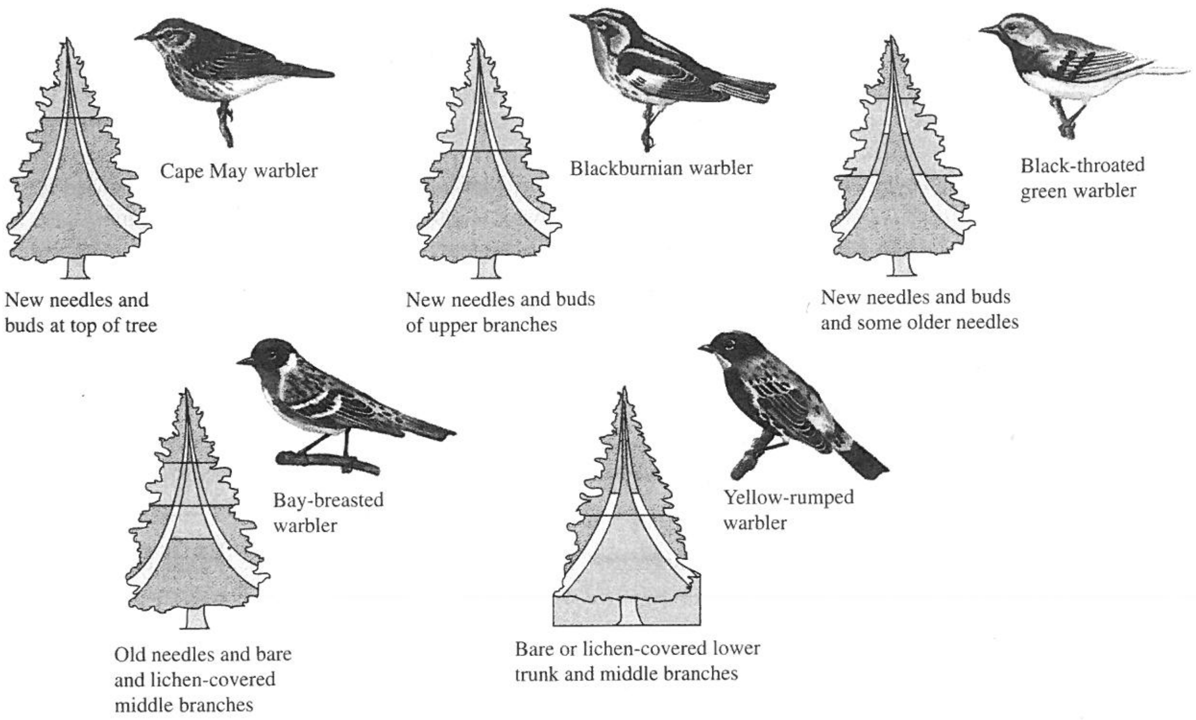


FIGURE 1.1 *Warbler feeding zones.*

Morse compared the feeding zones of warblers in spruce forests on the mainland of Maine to their feeding zones on small islands. The islands were 0.2 to 1.5 km offshore and were inhabited by one to three species of warblers. Two of the warbler species that lived on the islands, the black-throated green warbler and the yellow-rumped warbler, also lived in MacArthur's study areas. Morse found that the black-throated green warbler maintained approximately the same feeding zone whether it lived on the mainland, with many other warbler species, or on islands, with only two other warbler species. In contrast, the yellow-rumped warbler moved its feeding zone upward on islands where the black-throated green warbler was absent. This shift in feeding zone by island populations of yellow-rumped warblers is shown in figure 1.2.

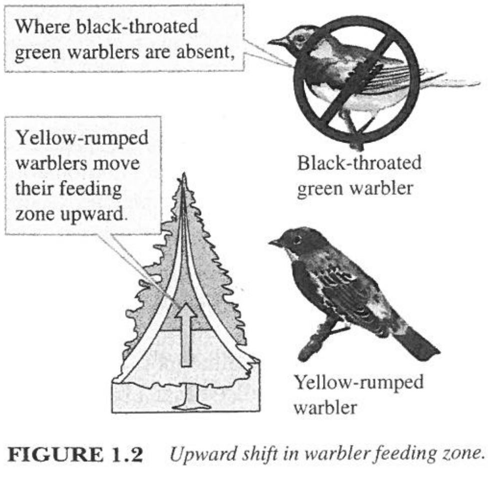


FIGURE 1.2 *Upward shift in warbler feeding zone.*

Why doesn't the yellow-rumped warbler feed higher in the trees when black-throated green warblers are present? Morse found that the feeding zones of spruce-forest warblers are at least partially maintained by aggressive interactions between species. He also discovered that the black-throated green warbler is socially dominant over yellow-rumped warblers. Consequently, aggression by black-throated green warblers can exclude yellow-rumped warblers from potential feeding areas. Morse proposed that aggressive interactions between warbler species help maintain differences in feeding zones of the kind described by MacArthur.

The studies of MacArthur and Morse show how field studies can be used to address important ecological questions. Field studies can also be combined with laboratory studies to yield even more detailed information about ecological systems. As we shall see in the following example, this approach has revealed a great deal about the ecology of bumblebees.

The Ecology of Bumblebees: Contributions of Field and Laboratory Studies

Complex ecological problems may require a combination of field and laboratory studies. Field studies provide information within a natural context. Laboratory studies can provide precise measurements within controlled environments. The two approaches provide complementary information.

Bernd Heinrich has tackled many complex ecological problems using a combination of field and laboratory studies.

In one of his research projects he pointed out that bumblebees live in most of the cool regions of the earth. They live in all temperate regions, on cool tropical mountaintops, and above the Arctic Circle. Two species live farther north than any humans. In all these regions, bumblebees keep their thoraxes, the part of the body that houses the flight muscles and to which the wings and legs are attached, warm when they are active. Maintaining a warm body temperature in a cool environment requires energy. Heinrich realized that to understand the ecology of bumblebees he needed to quantify their gains and losses of energy.

Figure 1.3 summarizes how Heinrich used a combination of field and laboratory studies to estimate the energy budgets of bumblebees feeding on different kinds of flowers at different temperatures. First, what is an **energy budget?** The budget that Heinrich had in mind is similar to a financial budget. He wanted to know the rate at which feeding bumblebees take in energy (income) relative to the rate at which they expend energy (cost). Why should an ecologist be interested in an energy budget? An energy budget would give Heinrich an estimate of the amount of energy available for maintaining the bumblebee colony. The difference between energy intake and energy expended while feeding on particular flowers at particular temperatures is the energy gain or loss from foraging in that environment. Energy gains may be invested in the production of honey to feed the bumblebee colony and in reproduction. Foraging that results in a net loss of energy means less food and dwindling reproduction and cannot be sustained for long.

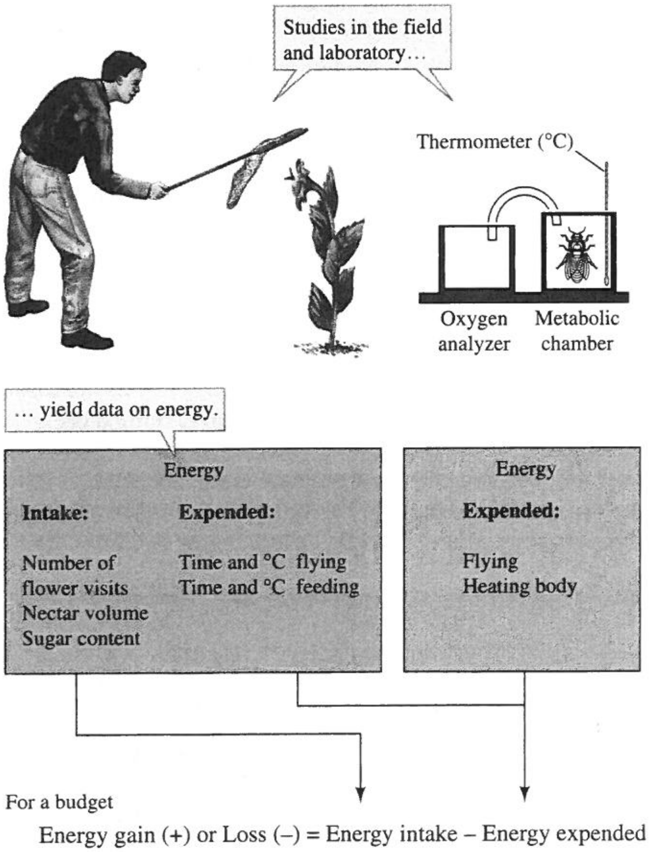


FIGURE 1.3 *Estimating the energy budgets of foraging bumblebees.*

Heinrich followed individual bumblebees as they gathered nectar from various species of flowers to estimate their rate of energy intake. He recorded the number and kinds of flowers visited and also measured the volume and sugar content of nectar produced by each species. He followed one bumblebee as it visited 145 flowers. This particular bumblebee only visited a species of hawkweed that produces orange flowers. Later, Heinrich followed a second bumblebee as it visited 184 flowers. This bumblebee fed almost exclusively on the yellow flowers of a different species. The behavior of these two bumblebees was typical; that is, most of the bumblebees usually visited only a single flower species. This fidelity to a single plant species simplified Heinrich's estimates of the amount of sugar gathered by a bee during a foraging trip.

To estimate the energy expended by a foraging bumblebee, Heinrich needed to know how much energy bumblebees use while flying and feeding. To make these estimates, he needed to know the amount of time bumblebees spend flying and feeding and the temperatures of their thoraxes while doing so. In the field, Heinrich used a stopwatch to measure the time they spent flying and feeding. He also caught flying and feeding bumblebees and measured their thoracic temperatures.

In the laboratory, Heinrich estimated the amount of energy used during flight and the amount of energy bumblebees expend to heat their bodies. He estimated the energetic costs of flight by measuring the rate at which flying bumblebees consume oxygen. How can oxygen consumption be used to estimate energy expenditure? Remember that during respiration all aerobic organisms derive energy from the **oxidation** of organic molecules such as sugars and fats. Consequently, the amount of oxygen consumed can be converted directly into the amount of organic molecules oxidized. The amount of organic molecules can be converted directly into energy equivalents such as calories. Heinrich found that the amount of energy expended during flight was approximately the same regardless of air temperature. This was convenient because he needed only to record the time bumblebees spent flying to know their energy expenditure for flight.

Heinrich found that bumblebees maintain the temperature of their thoraxes at 30° to 37°C, even at air temperatures as low as 0°C. How do bumblebees in cold environments maintain elevated thoracic temperatures? They elevate the temperatures of their thoraxes by contracting their flight muscles. When they are heating, bumblebees simultaneously contract the muscles that raise the wings and those that lower them. Consequently, instead of flying, they shiver.

The amount of energy that bumblebees expend to heat their thoraxes decreases as air temperature increases. In other words, a bumblebee expends less energy to heat itself and can heat itself faster in warm environments than in cold environments (fig. 1.4). Heinrich calculated that a bumblebee perched on a flower in an air temperature of 25°C does not have to produce any heat beyond that produced during flights between flowers to maintain its thoracic temperature at 30°C. In con-

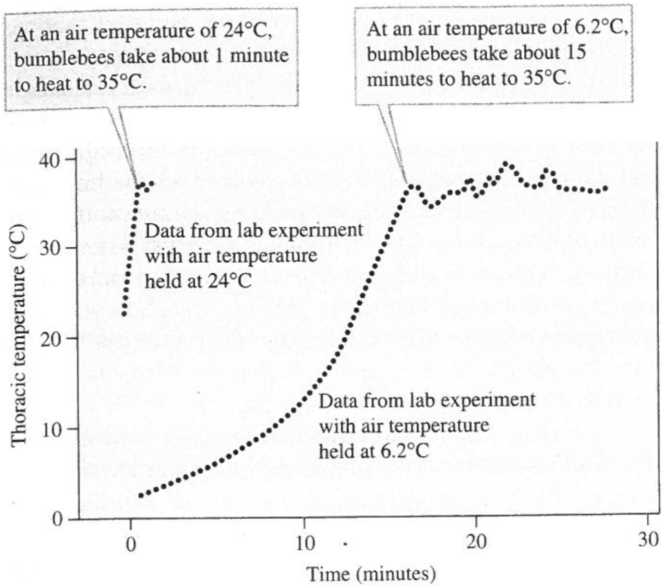


FIGURE 1.4 *Environmental temperature and bumblebee heating rate measured in a laboratory experiment (data from Heinrich 1993).*

trast, a bumblebee perched on a flower in an air temperature of 5°C must burn enough sugar to produce half a calorie of heat per minute to maintain a thoracic temperature of 30°C.

Heinrich estimated that a bumblebee feeding on fireweed flowers would have to visit one to two flowers per minute to obtain enough energy for 1 minute of flying. However, Heinrich found that bumblebees visited fireweed flowers at a rate of 20 to 30 per minute, gathering enough energy to meet their energy needs during flight, to keep themselves warm on cold days, and to take honey back to the colony.

Bernd Heinrich's research (1979, 1993) on bumblebees has focused on the behavior and physiology of individuals in their natural environments. He has combined field measurements with laboratory studies of physiology to estimate the energy budgets of bumblebees. Such studies help us to understand the ecology of individual species and interactions between 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.

Forest Nutrient Budgets: Inventories and Large-Scale Experiments

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. 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. 1.5). She stood on the rain forest floor and 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, and she not only visited the canopy but 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. Ecologists have often asked how the prodigious life of rain forests can 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

FIGURE 1.5 *Exploring the rain forest canopy. What Nalini Nadkarni discovered helped solve a puzzle.*

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.

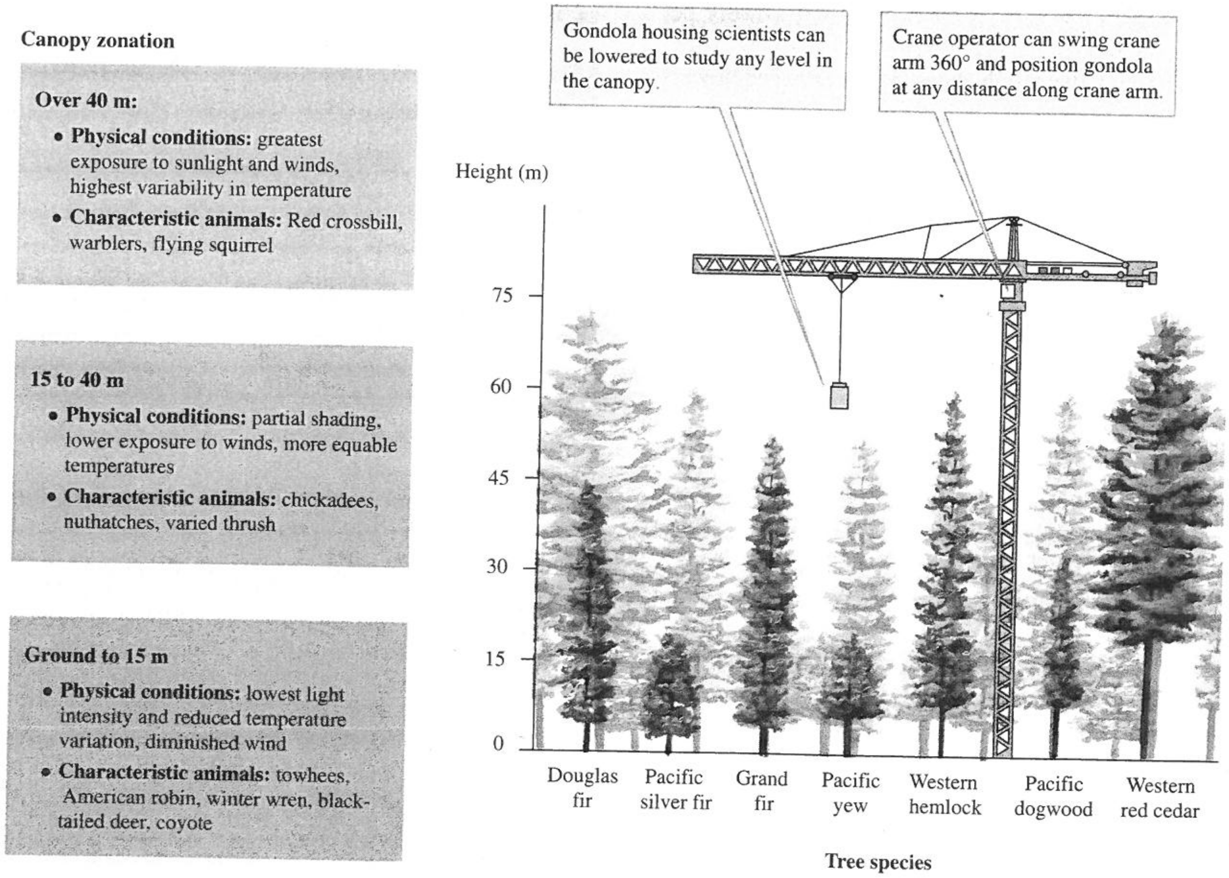
Epiphyte mats contain significant quantities of nutrients. Nadkarni estimated that these quantities in some tropical rain forests are equal to about half the nutrient content of the foliage of the canopy trees. In the temperate rain forests of the Olympic Peninsula in Washington, the mass of epiphytes 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 get into the forest canopy range from hot air balloons and aerial trams to large cranes. The Wind River Canopy Crane offers scientists access to any level within a 70 m tall coniferous forest in a 2.3 ha area near the Columbia River Gorge in Washington (fig. 1.6). Research projects supported—and made far easier—by this crane 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. Nadkarni points out that the canopy as a physical frontier may be closing, but its exploration as a scientific frontier is just beginning.

The researchers we have considered so far have described a population or an environment by working with small pieces of their ecological system. While Heinrich followed individual bumblebees and Nadkarni climbed individual trees in search of ecological knowledge, other researchers manipulated entire lakes or forests. One team of researchers studied how forests affect the movement of plant nutrients across landscapes.

As Gene Likens and Herbert Bormann watched, work crews felled the trees covering an entire stream basin in the Hubbard Brook Experimental Forest of New Hampshire. The felling of these trees was a key part of an experiment that Likens and Bormann had designed to study how forests affect the loss of nutrients, such as nitrogen, from forested lands (Bormann and Likens 1994, Likens and Bormann 1995). They had studied two small stream valleys for 3 years before cutting the trees in one of the valleys. The undisturbed stream valley would act as a control against which to compare the response of the deforested stream valley. Likens and Bormann



Canopy zonation

Over 40 m:

- **Physical conditions:** greatest exposure to sunlight and winds, highest variability in temperature
- **Characteristic animals:** Red crossbill, warblers, flying squirrel

15 to 40 m

- **Physical conditions:** partial shading, lower exposure to winds, more equable temperatures
- **Characteristic animals:** chickadees, nuthatches, varied thrush

Ground to 15 m

- **Physical conditions:** lowest light intensity and reduced temperature variation, diminished wind
- **Characteristic animals:** towhees, American robin, winter wren, black-tailed deer, coyote

Gondola housing scientists can be lowered to study any level in the canopy.

Crane operator can swing crane arm 360° and position gondola at any distance along crane arm.

FIGURE 1.6 *Providing access to the forest canopy.*

combined biology with physical sciences, including geochemistry, hydrology, micrometeorology, and applied disciplines, including forestry.

The central hypothesis guiding their experiment was that organisms, especially plants, regulate the rate of nutrient loss from northern hardwood forests. Their study area, the Hubbard Brook Experimental Forest, covers approximately 3,000 ha and ranges in altitude from 200 to 1,000 m. The Hubbard Brook valley was nearly completely deforested by 1917, and most of the present-day forest has grown up since that time. The forest is fairly representative of second-growth forests across northern New England and is dominated by sugar maple, beech, and yellow birch, along with some red spruce, balsam fir, and white birch.

The researchers organized their studies around small stream basins that included small tributaries of Hubbard Brook. The natural topographic boundaries of these stream basins offered the opportunity for measuring the movement of nutrients. Before they deforested the experimental basin, Likens and Bormann inventoried the distribution of nutrients. Those measurements indicated that over 90% of the nutrients in the ecosystem were tied up in soil organic matter. Most of the rest, 9.5%, was in vegetation. They estimated the rates at which some organisms fix atmospheric nitrogen and the rates at which weathering releases nutrients from the granite bedrock of the stream basins. They also measured the input of nutrients to the forest ecosystem from precipitation and nutrient outputs with stream water. The nutrient outputs in streamflow amounted to less than 1% of the amount contained within the forest ecosystems.

After this preliminary work, they cut the trees on their experimental stream basin. They used herbicides to suppress regrowth of vegetation at their experimental site and continued to apply herbicides for 3 years. As figure 1.7 indicates, cutting the forest dramatically increased rates of nutrient loss from the experimental stream basin. Losses of nitrate (NO_3^-) were approximately 40 to 50 times higher. The average concentrations of other major elements in the stream draining the deforested basin increased by 177% to 1,558%. Clearly, this type of temperate forest exerts strong controls on the movement of nutrients across the landscape.

This study by Likens and Bormann gave ecologists new insights into the influences of vegetation on nutrient movements. The study is also notable because it was conducted on a much larger scale than most ecological studies. However, there are ecologists who think and work at even larger scales.

Vegetation Change: Information from Pollen Records and Modeling

The earth and its life are always changing. However, many of the most important changes occur over such a long period 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 theoretical modeling.

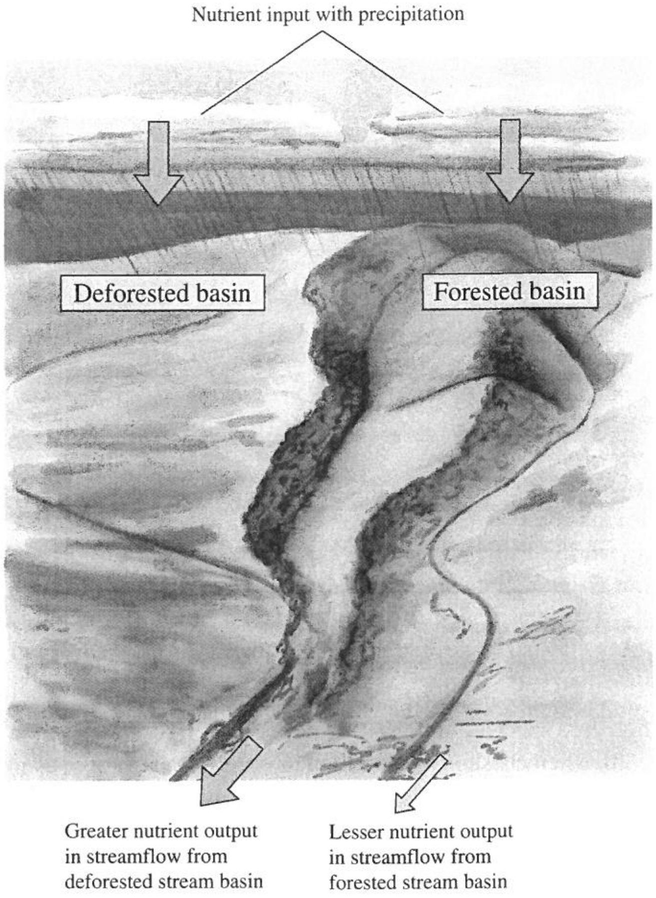


FIGURE 1.7 *Influence of forests on nutrient budgets.*

Margaret 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 plants living near the lake during the past several thousands of 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, the earliest appearance of pollen from spruce trees, *Picea* spp., is in the lake sediments from about 12,000 years ago and pollen from beech, *Fagus grandifolia,* first appears in the sediments from about 8,000 years ago. Chestnut pollen does not appear in the sediments until about 2,000 years ago. The pollen from all

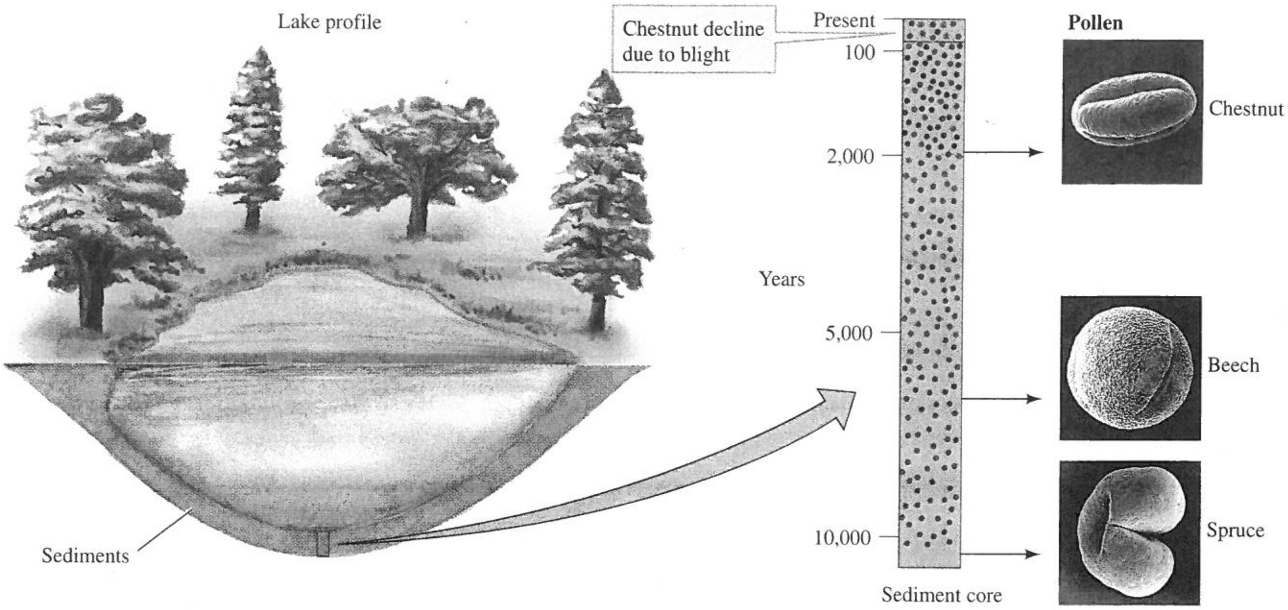


FIGURE 1.8 *History from lake sediments.*

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 individual lakes can be used to reconstruct the history of vegetation in the area.

By studying many different lakes, Davis could study changes in vegetation across entire continents. Her studies have demonstrated how forests in eastern North America changed with changing climate. Some of her work has been particularly valuable in reconstructing the history of the deciduous forests of eastern North America.

Today, the greatest diversity of deciduous trees in eastern North America is in the Appalachian Mountains. This pattern led ecologists to propose that these mountains have long been a center of diversity for deciduous trees in North America. One hypothesis proposed that deciduous trees survived the last glacial period in the southern Appalachian Mountains. However, by studying the pollen record in lakes across eastern North America, Davis showed that during the height of the last glaciation, about 18,000 years ago, the southern Appalachian Mountains were covered by coniferous trees. At that time, the nearest deciduous forests were in the lower Mississippi Valley, a pattern largely unsuspected until Davis and others studied pollen preserved in lake sediments.

Theoretical models can also provide insights into long-term ecological change. Theoretical analyses by Bruce Milne and his colleagues (1996) provide ecologists with ways to characterize spatial and temporal changes in vegetation. Some of their recent work has focused on ecotones. **Ecotones** are transitions from one type of ecosystem to another, for instance the transition from a woodland to a grassland. Milne models ecotones as a kind of **phase transition.** Typical phase transitions involve changes in the state of matter, such as the change of water from a liquid to a solid state as temperature decreases. The change from liquid water to ice involves fundamental changes in the organization of water, including the average distance between water molecules and their distributions. The change along an ecotone involves analogous changes in the structure of vegetation. In the case of an ecotone, vegetation changes from one place to another rather than over time. Consequently, Milne and his colleagues speak of spatial phase transitions.

Often, a phase transition takes place abruptly under some critical conditions. For instance, water shifts abruptly from liquid to ice as its temperature falls to 0°C. Milne's analyses of the ecotones between woodland and grassland attempt to identify the critical tree densities at which there is an abrupt transition from one vegetation type to another. This transition occurs at the densities where tree cover changes abruptly from a fragmented landscape of small patches of trees to a landscape where the tree canopies are interconnected. While this may seem like a purely geometrical exercise, Milne points out that the locations of these critical densities may be used to identify the critical environmental conditions that regulate the transition from one vegetation to another.

We may ask where the edge is between one type of vegetation and another. Human intervention makes the edge between a cultivated field and a woodlot obvious. However, the edge between one natural vegetation type and another may be difficult to identify. Figure 1.9 contrasts the sharpness of ecotones in landscapes with and without strong human influences.

Milne and his research group are searching for the edge that defines critical densities of vegetation along ecotones. Their analyses have led to a number of significant insights about the geometry of ecotones and their sensitivity to environmental change. One of their results concerns the distances between edges defined by different plant densities. For in-

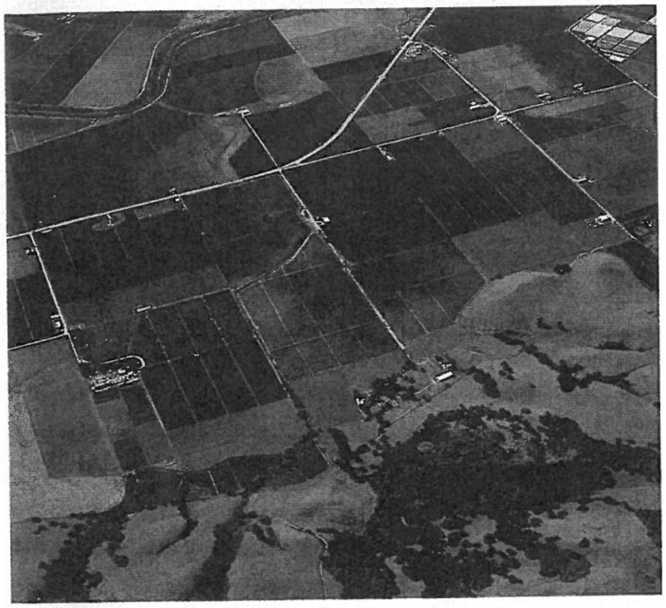


FIGURE 1.9 *Boundaries within landscapes created by human activity (background) and natural environmental gradients (foreground).*

stance, the edge between a woodland and a grassland might be defined by the places on the landscape where there is 41% tree cover or 59% tree cover. The distance between ecotonal edges defined by different densities of vegetation may indicate differences in the environmental gradient along the ecotone.

Milne points out that where edges overlap or are very close to each other, the environmental gradient is likely to be steep. Where edges defined by different densities of vegetation are more widely spaced, the environmental gradient is likely to be more gradual. Milne and his colleagues suggest that it is these areas of gradual environmental change within a landscape where we are most likely to see biological responses to environmental change. Davis's studies of pollen trapped in lake sediments document changes in vegetation in response to past climate change, while Milne's studies thrust us into the future. His analyses of the geometry of ecotones suggest where we should concentrate our studies of ecological response to future environmental change.

The Nature and Scope of Ecology

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 we have reviewed, ecologists study those relationships over a large range of temporal and spatial scales using a wide variety of approaches. Ecology includes Heinrich's studies of bumblebees living around a single bog in New England and Davis's studies of vegetation moving across the North American continent. Ecology also includes the observational studies of MacArthur and Morse. Ecologists may study processes on plots measured in square centimeters or, like Likens and Bormann, study an entire stream valley. Important ecological discoveries have come from Nadkarni's probing of the rain forest canopy and Milne's manipulating landscape images on a computer screen. Ecology includes all these approaches and many more.

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. Each chapter focuses on a few ecological concepts. We also explore some of the applications and tools associated with the concepts introduced.

We continue our exploration of ecology in section I with the natural history of life on land and in water. Natural history was the foundation upon which ecologists built modern ecology. A major premise of this book is that knowledge of natural history improves our understanding of ecological relationships.

ON THE NET

Bernd Heinrich
http://www.uvm.edu/~biology/Faculty/Heinrich.html

The Thermal Warriors
http://www.hup.harvard.edu/newsroom/press.thermal.war.html

International Canopy Network
http://esnet.edu/ican/

Research in Rainforest Canopies
http://heg-school.awl.com/bc/companion/omr2e/activity/rg/RFCBiolo.htm

Hubbard Brook Experimental Forest
http://lternet.edu/about/sites/08_hbr.html

Bruce T. Milne
http://algodones.unm.edu/~bmilne/homepage.html

Margaret B. Davis
http://biosci.cbs.umn.edu/eeb/faculty.DavisMargaret.html