CHAPTER 1

The Science of Plant Ecology

The biological science of **ecology** is the study of the relationships between living organisms and their environments, the interactions of organisms with one another, and the patterns and causes of the abundance and distribution of organisms in nature. In this book we consider ecology from the perspective of terrestrial plants. Plant ecology is both a subset of the discipline of ecology and a mirror for the entire field. In *The Ecology of Plants,* we cover some of the same topics that you might find in a general ecology textbook, while concentrating on the interactions between plants and their environments over a range of scales. We also include some subjects that are unique to plants, such as photosynthesis and the ecology of plant-soil interactions, and others that have unique aspects in the case of plants, such as the acquisition of resources and mates.

Ecology as a Science

Ecologists study the function of organisms in nature and the systems they inhabit. Some ecologists are concerned in particular with the application of ecological principles to practical environmental problems. Sometimes the distinction between basic and applied ecology becomes blurred, as when the solution to a particular applied problem reveals fundamental knowledge about ecological systems. In both basic and applied ecology, the rules and protocols of the sciences must be rigorously followed.

What ecology is *not* is environmental or political activism, although ecologists are sometimes environmental activists in their personal lives, and environmental activists may rely on ecological research. Ecology is not about one's feelings about nature, although ecologists may have strong feelings about what they study. Ecological systems are complex things, with a great many parts, each of which contributes to the whole in different ways. Nevertheless, ecology is indeed a science, and it works like other scientific disciplines.

How do we know whether something is true? Science is one way of knowing about the world—not the only way, but a spectacularly successful one. In contrast to some of the other ways of knowing that are part of our lives, the legitimacy of science is based not on authority, or opinion, or democratic principles, but on the weight of credible, repeatable evidence.

The Genesis of Scientific Knowledge

Throughout this book we examine how ecologists have come to their current knowledge and understanding of organisms and systems in nature. Ecology has both a strong and a rich theoretical basis and has developed from a foundation based on an enormous collective storehouse of information about natural history.

Ecology, like all of science, is built on a tripod of pattern, process, and theory. **Patterns** consist of the relationships between pieces or entities of the natural world. **Processes** are the causes of those patterns. **Theories** are the explanations of those causes. When ecologists carry out original scientific research, they seek to document patterns, understand processes, and ultimately to put together theories that explain what they have found out.

There is a distinction between the kind of research a scientist does and the kind of research done for a term paper, or by any member of the public trying to gather information about a topic using library books or material posted on Web sites. Although there are exceptions, research carried out by students or the general public is usually **secondary research**: gathering data or confirming facts that are already known. This sort of research is not only useful, it is essential: every scientific study must begin by assessing what is already known. But the heart of what research scientists do is **primary research**: gathering information or finding out facts that no one has ever known before. That experience of discovery is what makes doing science so incredibly exciting and fun.

Scientists gain knowledge by using the **scientific method**. They carry out a series of steps, although not always in a fixed order (Figure 1.1). In ecology, these steps can be summarized as follows: observation, description, quantification, posing hypotheses, testing those hypotheses using experiments (in a broad sense of the word, as discussed below), and verification, rejection, or revision of the hypotheses, followed by retesting of the new or modified hypotheses. Throughout this process, ecologists gather various kinds of information, look for patterns or regularities in their data and propose processes that might be responsible for those patterns. They often put together some sort of model to help in advancing their understanding. Eventually, they construct theories, using assumptions, data, models, and the results of many tests of hypotheses, among other things. The building of comprehensive scientific theories proceeds simultaneously from multiple directions by numerous people, sometimes working in synchrony and sometimes at cross-purposes. Science in operation can be a messy and chaotic process, but out of this chaos comes our understanding of nature.

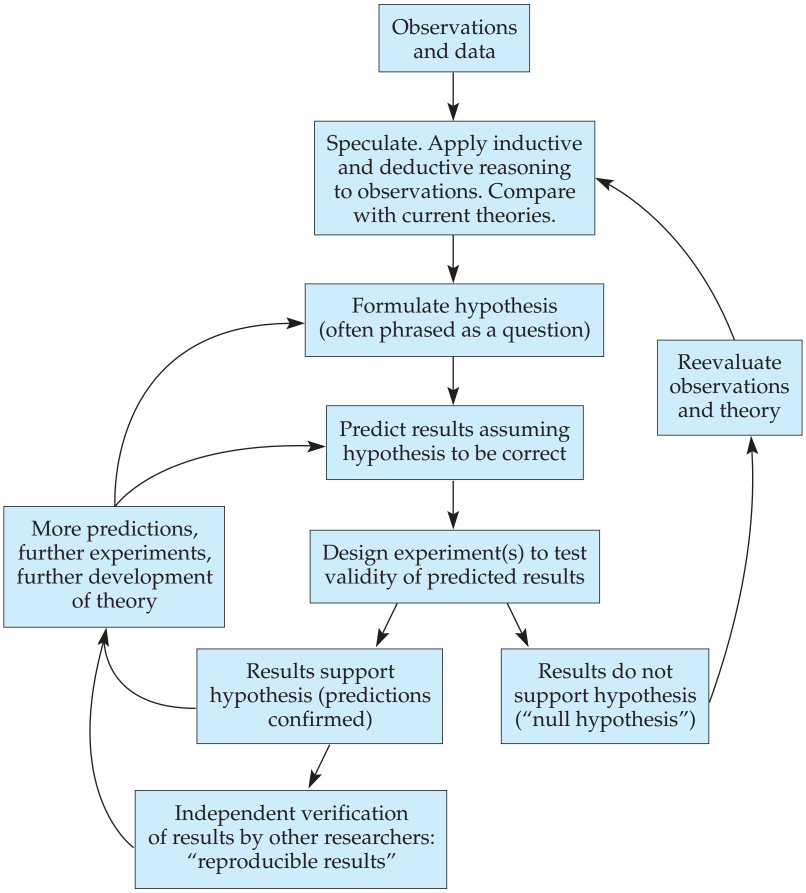

Figure 1.1
The scientific method. The cycle of speculation, hypothesis, and experimentation is circular, as new questions constantly emerge from the answers scientists obtain.

The word “theory” has a very different meaning in science than it does in common usage. A scientific theory is a broad, comprehensive explanation of a large body of information that, over time, must be supported and ultimately confirmed (or rejected) by the accumulation of a wide range of different kinds of evidence (Table 1.1). In popular usage, the word “theory” usually refers to a limited, specific conjecture or supposition, or even a guess or “hunch.” Equating the meaning of a scientific theory with “a guess” has caused no end of mischief in the popular press and in public debates on politically charged issues.

When a theory is buttressed over many years with strong evidence, with new findings consistently supporting and amplifying the theory while producing no serious contradictory evidence, it becomes an accepted framework or pattern of scientific thought from which new speculation can spring. This is what has occurred with Newton’s theory of gravity, Darwin’s theory of evolution, and Einstein’s theory of relativity. Scientists use such overarching theories to organize their thinking and derive additional predictions about nature.

A scientific **hypothesis** is a possible explanation for a particular observation or set of observations. A hypothesis is smaller in scope than a fully developed theory. Hypotheses must be testable: they must contain a prediction or statement that can be verified or rejected using scientific evidence. Experiments are the heart of science, and we discuss their design and use in more detail later in this chapter. A crucial characteristic of science is the need to revise or reject a hypothesis if the evidence does not support it. Science does not accept hypotheses on faith.

Some of the most important tools in the scientist's toolkit are models. A **model** is an abstraction or simplification that expresses structures or relationships. Models are one of the ways in which the human mind attempts to understand complex structures and relationships, whether in science or in everyday life. Building a model airplane from a kit can tell you a lot about the basic form of an airplane; civil engineers often build small models of structures such as bridges or buildings (either physical models or three-dimensional images on a computer) before construction is begun. You have no doubt seen models of DNA and of chemical reactions, and you may have heard about global climate models, which we will discuss at length in Chapter 22.

Models can be abstract or tangible, made of plastic or words. They can be diagrams on paper, sets of equations, or a complex computer program. In science, models are used to define patterns, summarize processes, and generate hypotheses. One of the most valuable uses of models is to make predictions. Ecologists deal almost exclusively with abstract models that can range from a simple verbal argument to a set of mathematical equations. One reason the models often rely on mathematics is that ecologists are so often concerned with the numbers of things (for instance, is a species' population size so small that it is becoming endangered? How rapidly is an invasive species spreading? How many species can coexist in a community, and how does this change as conditions change?). Mathematical models offer well-defined methods for addressing questions in both qualitative and quantitative terms.

All models are necessarily based on simplifications and rest on a set of assumptions. Those (implicit and explicit) simplifications and assumptions are critical to recognize because they can alert you to the limitations of the model, and because faulty assumptions and unjustified simplifications can sink even the most widely accepted or elegant model.

Table 1.1 The components of a theory

Component	Description
Domain	The scope in space, time, and phenomena addressed by the theory
Assumptions	Conditions or structures needed to build the theory
Concepts	Labeled regularities in phenomena
Definitions	Conventions and prescriptions necessary for the theory to work with clarity
Facts	Confirmable records of phenomena
Confirmed generalizations	Condensations and abstractions from a body of facts that have been tested
Laws	Conditional statements of relationship or causation, or statements of process that hold within a universe of discourse
Models	Conceptual constructs that represent or simplify the natural world
Translation modes	Procedures and concepts needed to move from the abstractions of a theory to the specifics of application or test
Hypotheses	Testable statements derived from or representing various components of the theory
Framework	Nested causal or logical structure of the theory

Source: Pickett et al. 1994.

Objectivity, Subjectivity, Choice, and Chance in Scientific Research

When you read a typical scientific paper, it may at first seem arcane and dull. The format follows a rigid protocol, designed for efficiently conveying essential information to other scientists. Ideas are tightly packaged, with a clear logical line running from start to finish. It may seem as if the researchers knew exactly what they would find even before they began. We will let you in on an open secret: That is not usually how real science works. The justifications for the research presented in a paper's introduction may have been thought up or discovered long after the research project began, or even after the work was finished. Because of serendipitous discoveries, laboratory or field disasters, or unusual natural occurrences, the original purpose of a research project is sometimes modified or, occasionally, entirely discarded and replaced with something else.

Ideas in science, especially in ecology, come from a variety of sources. While everyone knows that science is objective and rational, that is only half the story. In order to reach a genuinely new understanding, subjectivity and creativity must also come into play. While one must be objective in, for example, examining the weight of evidence in support of a hypothesis, subjectivity plays a subtle but important role throughout all of scientific research. What one chooses to study, where one chooses to look for answers, and what is or is not a valid topic for scientific research are all subjective decisions scientists must routinely make. To a large extent, these choices depend on the questions one asks. While determining the answers must be objective, choosing what questions to ask, and how to ask them, is largely subjective.

Many scientific endeavors are highly creative as well. Coming up with a good experiment, looking at a seemingly intractable problem from a new perspective, switching gears after a disastrous laboratory failure to extract a successful outcome from the jaws of catastrophe, and pulling a large number of disparate facts together to build a comprehensive theory are all highly creative activities.

Many scientific discoveries start with casual observations, such as Newton's proverbial apple. Or an idea may arise as a "what if" thought: What if the world works in a particular way? Or a previous experiment may have raised new questions. What makes a scientist successful is the ability to recognize the worth of these casual observations, what-if thoughts, and new questions. From these sources, an ecologist constructs hypotheses and designs experiments to test them.

Experiments: The Heart of Research

A cornerstone of the scientific process is the **experiment**. Ecologists in particular use a wide variety of types of experiments. We use the term "experiment" here in its broadest sense: a test of an idea. Ecological experiments can be classified into three broad types: manipulative, natural, and observational. **Manipulative**, or **controlled**, **experiments** are what most of us think of as experiments: A person manipulates the world in some way and looks for a pattern in the response. For example, an ecologist might be interested in the effects of different amounts of nutrients on the growth of a particular plant species. She can grow several groups of plants, giving each of them a different nutrient treatment, and measure such things as their time to maturity and their final size. This experiment could be done in a controlled environment such as a growth chamber, in a greenhouse, in an experimental garden, or in a natural community in a field setting.

This range of potential settings for the experiment comes with a set of trade-offs. If the experiment is conducted in a laboratory or growth chamber, the ecologist is able to control most of the possible sources of variation so that the differences among treatments can be clearly attributed to the factors being studied in the experiment. These sorts of controlled experiments exemplify the scientific method as it was first laid out by Frances Bacon in the seventeenth century. Baconian experiments are the mainstay of most of molecular and cellular biology as well as the physical sciences. By working in a controlled environment, however, the ecologist sacrifices something. The controlled environment is highly artificial so that it compromises realism, and it is also narrow in scope (the results apply only to a limited range of conditions), sacrificing generality.

If an experiment is conducted in a field setting, it is more realistic or more natural, but now many factors may vary in an uncontrolled fashion. In a field experiment, the only factors that are controlled are the ones being studied. Instead of attempting to control all variation, variation due to factors other than the experimental ones is randomized among replicates, and conclusions are based on the use of statistical inference (see the Appendix). Such experiments can be carried out in many settings and are not restricted to the field. This sort of experiment was first developed by R. A. Fisher in the early twentieth century. Fisherian experiments are a mainstay of ecology and evolutionary biology as well as the social sciences. They are typically less narrowly defined than Baconian experiments, and thus their results may be more readily generalized. Where along this continuum of control versus realism the ecologist carries out her experiment depends on both her scientific goals and practical considerations.

Experiments are usually designed as tests of hypotheses. If the hypothesis is partially or wholly falsified, the scientist goes back, revises his ideas, and tries again. If the hypothesis is not falsified by the outcome of the experiment, the scientist gains confidence that his hypothesis might be correct. Sometimes, however, experiments are done without an explicit hypothesis in mind. These are "poke-at-it-and-see-what-happens" experiments designed to find out more about the world. Such experiments are common throughout the biological sciences, including ecology. Scientists have studied in detail only a few hundred of the quarter-million terrestrial plant species; of these, only a few [*Zea mays* (maize), *Arabidopsis thaliana,* and possibly *Oryza* spp. (rice)] approach being "thoroughly studied." An ecologist beginning the study of a new species, community, or ecosystem must do many of these general types of experiments. Of course, he is guided by his knowledge of other similar species and ecosystems. Each species or ecosystem is unique, however, which is why each study expands our ecological knowledge.

Manipulative experiments are powerful tools for two major reasons: first, because the scientist can control which parts of the natural world will be altered to study their effects, and second, because she can separate factors that typically occur together to test them individually. Such experiments have limitations, however. Sometimes manipulative experiments are plagued by artifacts—outcomes caused by a side effect of the experimental manipulation itself rather than being a response to the experimental treatment being tested. Good experiments avoid artifacts or take them into account in evaluating the results.

Another limitation is that of scale. Ecology is concerned with patterns and processes that occur across large scales of space and time—for example, the causes of differences in the numbers of species on different continents, or the responses of populations to climate change over the next two centuries. We cannot do

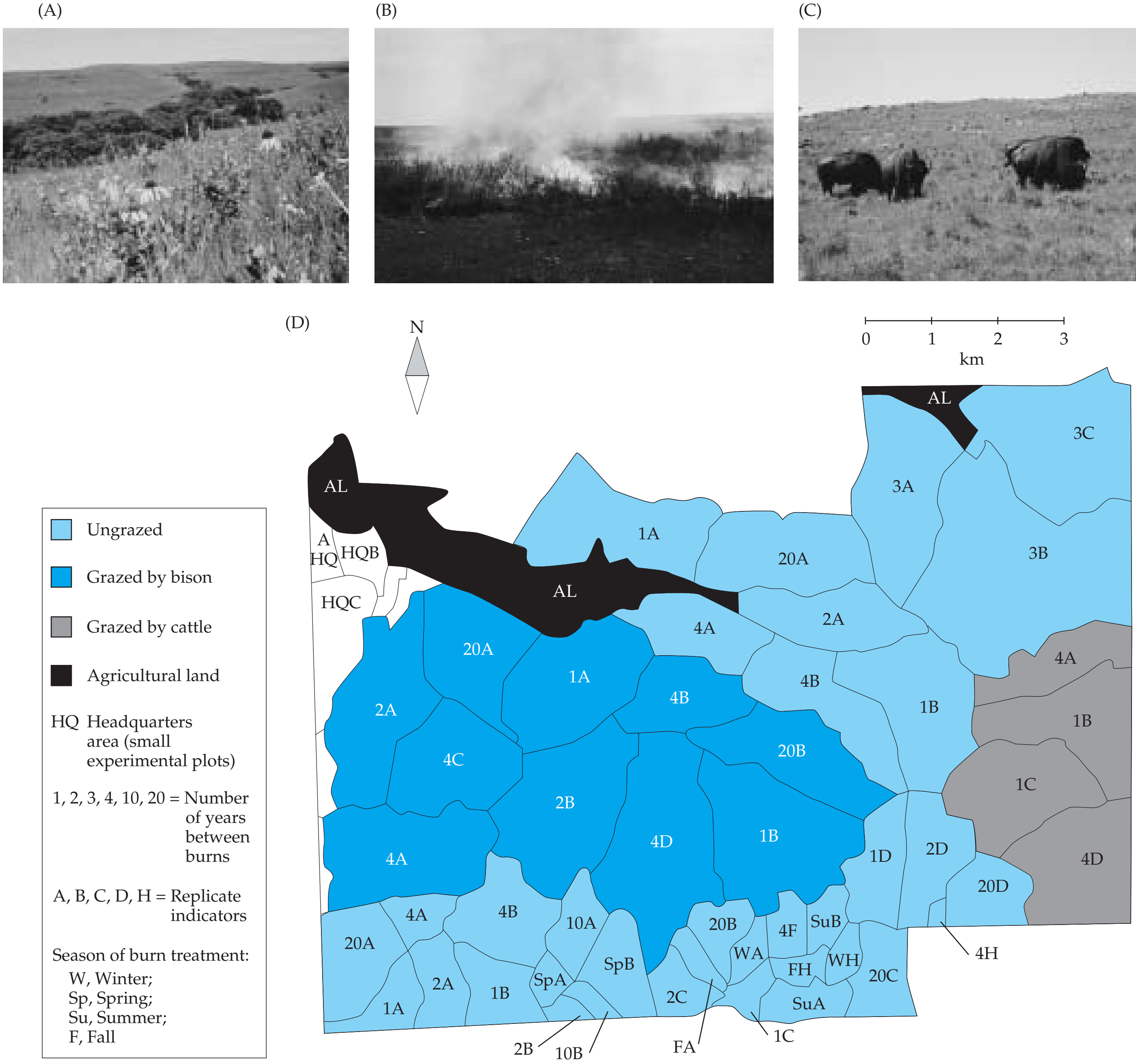

Figure 1.2
Large-scale manipulative experiments are being carried out at the Konza Prairie Research Natural Area (A). Prescribed burns (B) are done at various intervals to investigate the effects of fire and fire frequency on prairie communities. In addition, areas grazed by bison (C) are studied and compared with ungrazed areas and with plots subjected to cattle grazing. The experimental patches (D), which are watershed units, vary in size from approximately 3 to 200 hectares. In this map, each patch is designated by a code indicating the fire treatment. (After Knapp et al. 1998. Photographs courtesy of A. Knapp, Konza Prairie Biological Station, and S. Collins.)

manipulative experiments at these great scales of time and space. Ecologists are, however, increasingly making use of longer-term and larger-scale manipulative experiments (see Box 12C). One example of such a study is the long-term study of prairie ecology at the Konza Prairie Research Natural Area in Kansas, begun by Lloyd Hulbert in 1981 (Knapp et al. 1998). The reserve is divided into a series of large patches, which are subjected to different combinations of controlled burning at various time intervals and grazing by bison or cattle (Figure 1.2).

Large-scale manipulative experiments are often limited by the range of possible treatment, however; for example, at Konza Prairie, almost all of the controlled burning is carried out in the spring. Because we do not have firm data on prairie fire regimes prior to European settlement, we do not know how this spring-burning treatment compares to "natural" fire regimes.

Some types of manipulative experiments would be unethical to carry out. For example, we would not cause the extinction of a species just to study the effects of such an event. In such cases, ecologists must rely on two other types of studies. These are natural and observational studies, which may be thought of as different kinds of experiments.

Natural experiments are "manipulations" caused by some natural occurrence. For example, a species may go extinct in a region, a volcanic eruption may denude an area, or a flash flood may scour a streambed. Natural and manipulative experiments represent a trade-off between realism and precision, similar to the trade-off between laboratory and field experiments. Just as with a manipulative experiment, the ecologist compares the altered system either with the same system before the change or with a similar, unchanged system.

The major limitation of natural experiments is that there is never just a single difference before and after a change or between systems being compared. There are no guarantees, for instance, that the altered and unaltered systems were identical prior to the event. For example, if we are comparing areas burned in a major fire with others that remained unburned, the unburned areas might have been wetter, might have had a different site history or different vegetation before the fire, and so on. In other words, there are many other potential sources of difference besides the fire. Therefore, it can be difficult to determine the cause of any change.

The best natural experiments are ones that repeat themselves in space or time. If an ecologist finds similar changes each time, then she gains confidence about the causes of those changes. Another approach is to combine natural experiments with manipulative experiments. For example, the patches subjected to grazing and fire treatments at Konza Prairie are being compared with patches elsewhere that are not subjected to experimental manipulation.

Observational experiments consist of the systematic study of natural variation. Such observations or measurements are experiments if an ecologist starts with one or more hypotheses (predictions) to test. For example, one could measure patterns of species diversity across a continent to test hypotheses about the relationship between the number of plant species number and productivity (see Chapter 20). Again, the limitation of this type of experiment is the potential for multiple factors to vary together. If several factors are tightly correlated, it becomes difficult to determine which factor is the cause of the observed pattern. For example, if the number of herbivores is also observed to increase as the number and productivity of plant species increases, the ecologist cannot tell for sure whether the increase in herbivores is a result of increased plant numbers and productivity, or whether the increased productivity is a result of increased herbivory.

As with natural experiments, observational experiments repeated in space or time add confidence to our conclusions (Figure 1.3). Other sciences, notably geology and astronomy, also rely largely or exclusively on observational experiments because of the spatial or temporal scales of their studies or because direct manipulation is impossible.

Ecological knowledge comes from combining information gained from many different sources and many different kinds of experiments. The ecologist's use of this complex variety of information makes ecology a challenging and exciting science.

Testing Theories

The testing of scientific theories, especially ecological ones, is a more subtle, nuanced, and complicated endeavor than nonscientists often realize. The popular image of the scientific method portrays it as a process of falsifying hypotheses. This approach was codified by the German philosopher of science Karl Popper (1959). In this framework, we are taught that we can never prove a scientific hypothesis or theory. Rather, we propose a hypothesis and test it; the outcome of the test either falsifies or fails to falsify the hypothesis. While hypothesis testing and falsification is an important part of theory testing, it is not the whole story, for two reasons.

First, this approach fails to recognize knowledge accumulation. In a strict Popperian framework, all theories are held to be potentially false. We never *prove* anything to be true; we merely *disprove* ideas that are false. This assumption goes against our own experience and the history of the accumulation of scientific understanding. Today we know that the Earth revolves around the sun, even though this was once just a hypothesis. We know that the universe is approximately 15 billion years old (give or take a few billion) and began with the Big Bang, even if we still do not know the details of that event. We know that life began and assumed its present shape through the process of evolution. We know that many diseases are caused by microbial infections, not by "humours," and that hereditary traits are conveyed by DNA, not by blood. While we may acknowledge that all of this knowledge has not, in a strictly philosophical sense, been proved to be true, but has only failed thus far to be falsified, we also recognize that some knowledge is so firmly established and bolstered by so many facts that the chance that we are wrong is very much less than the chance of winning the lottery several times in a row. The school of philosophy of science called realism recognizes this progressive accumulation of knowledge (Mayo 1996).

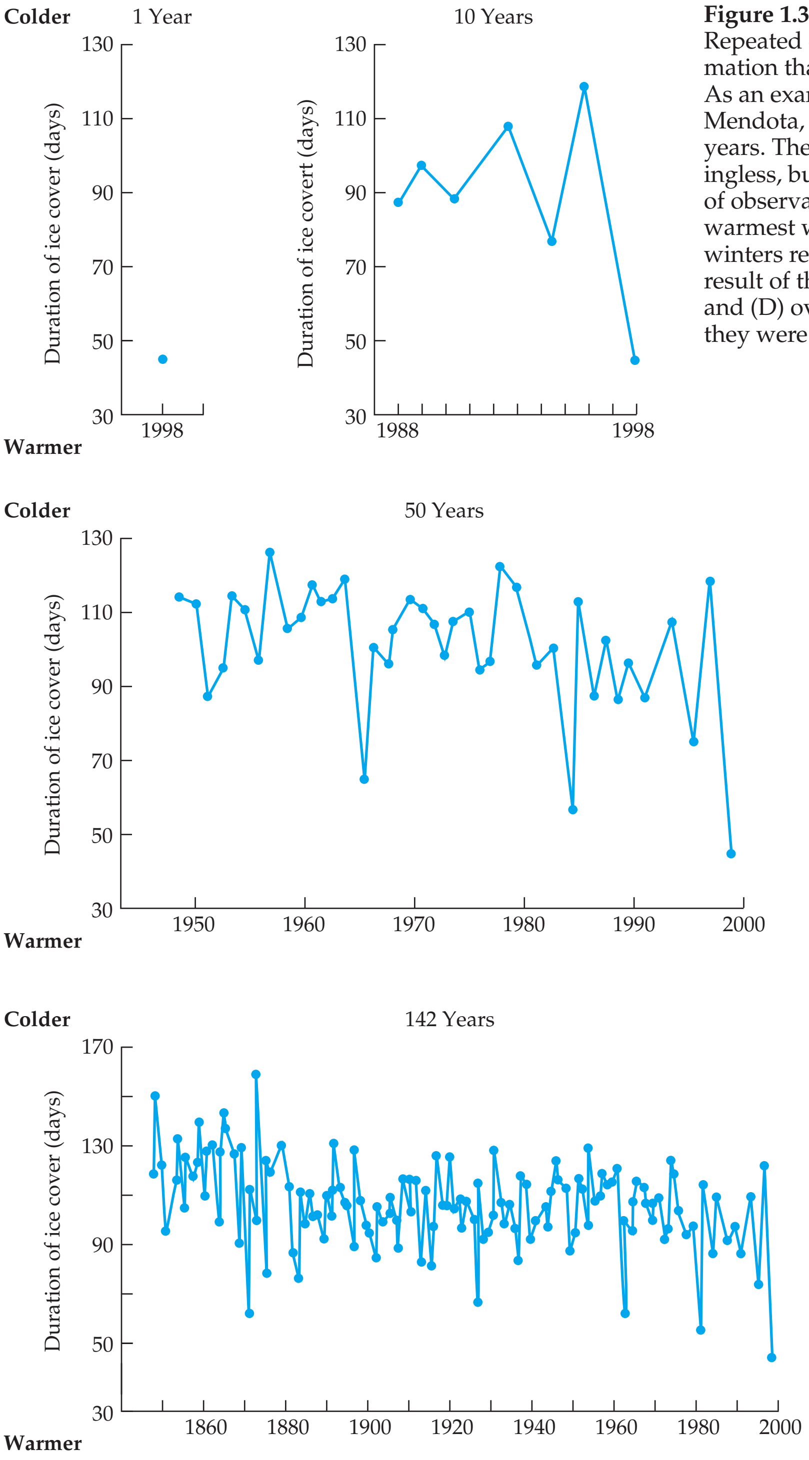

Figure 1.3
Repeated observations over space or time can reveal information that is not apparent from one or a few observations. As an example, records of the duration of ice cover on Lake Mendota, Wisconsin, have been kept for more than 142 years. The information for a single year (A) is fairly meaningless, but expanding the context with increasing numbers of observations over time shows that (B) 1998 was the warmest winter in 10 years; (C) there is a cycle of warmer winters recurring every few years (now known to be the result of the El Niño Southern Oscillation; see Chapter 18); and (D) overall, winters in Wisconsin are warmer now than they were 142 years ago. (After Magnuson et al. 2001.)

Second, and more importantly, the Popperian framework fails to account for a second type of question that we very commonly ask in ecology. Often the issue is not one of falsifying a hypothesis. Rather, we ask about the relative importance of different processes. When we examine the structure of a plant community, we do not ask, "Is it true or false that competition is occurring?" Instead, we ask, "How much, and in what ways, do the processes of competition and herbivory each contribute to shaping this community?" So, when we are building our theories about plant community structure, our activities are more akin to assembling a complex model than to falsifying a set of propositions.

Falsification does play a role in science, but a more limited one than Popper envisaged. Theory construction is like assembling a jigsaw puzzle from a pile of pieces from more than one box. We can ask whether a particular piece belongs in this spot, yes or no, by erecting a hypothesis and falsifying it. We may even conclude that this particular piece does not belong in this puzzle. Less often are we attempting to completely throw away the piece, saying that it does not belong to any puzzle.

Controversy also plays an important part in ecology, as it does in all scientific fields. During the process of amassing evidence regarding the validity of a theory, different interpretations of experimental data, and different weight given to different pieces of evidence, will lead different scientists to differing opinions. These opinions may be passionately held and forcefully argued, and discussion can sometimes become heated. As the evidence supporting a theory accumulates, some scientists will be willing to accept it sooner, while others will wait until the bulk of the evidence is greater.

If the issue under debate has political or economic implications, nonscientists will also contribute to the debate and may be able to offer valuable insight, judgment, and perspective to the discussion. But when the evidence in favor of a scientific theory becomes overwhelming and the vast majority of scientists knowledgeable in that field are convinced of its validity, then the matter becomes settled (unless startling new evidence or a new, broader theory forces a reevaluation). Ultimately, it is the judgment of scientists that must decide the answers to scientific questions. When a scientific consensus has been reached on a scientific theory, it is unreasonable to consider that theory to be just another guess or opinion and to hold that everyone's opinion is equally valid. That may work for the democratic process, but not in science. Opinions not supported by evidence are not the same as those supported by the weight of a great deal of evidence; giving them equal weight would be contrary to the way science works.

This does not mean that scientists should decide issues of public policy. For example, if scientists are in strong agreement about something—say, that if more than x% of its remaining habitat is lost, then plant species Y has a 90% chance of extinction within the next 20 years—that does not necessarily dictate any particular public policy. Policy decisions depend on how important people think it is to save species Y, and on what costs they are willing to pay to do so. While we personally hope this would never happen, we recognize that someone who wanted (for whatever reason) to exterminate species Y could use the scientific conclusions for their own ends, just as we could use those same scientific conclusions to promote conservation.

Specific Results versus General Understanding

Because ecologists work at such a variety of scales and on such a diversity of organisms and systems, the question arises as to how far one can extend the conclusions of a particular study to other organisms or places. In the fields of chemistry or physics, the results of an experiment are considered to be absolutely true for all times and places: an atom of helium is made up of two protons and two neutrons, which in turn are made up of quarks, with no qualifications needed. This is the popular image of scientific theories.

Ecology is different. Do the results of a field experiment on competition between two plant species extend to other seasons or locations, or to other pairs of species within the same families or functional groups? Experiments involving helium deal with a universal entity, the helium atom. In contrast, in experiments on plant competition, the exact composition of the entities changes (e.g., the individual plants used each time are not genetically identical), and the surroundings change as well (e.g., the weather is different this year than last year). For this reason, extremely cautious scientists take the position that no conclusion can be extended beyond the particular conditions that existed when the experiment was conducted. If that were so, however, there would be no value and no point in doing any experiments, because they would tell us nothing beyond something of such limited scope as to be worthless.

The truth is somewhere between these two extremes, creating a constant and dynamic tension in ecology. One approach to resolving this tension is to see how the outcome of a particular experiment fits into the workings of existing models, and whether it supports or rejects the predictions of those models. Another approach is to use methods for the quantitative synthesis of the results of independent experiments. These methods, known collectively as **meta-analysis**, can be used to evaluate where the outcome of a particular experiment fits in with—or differs from—the results of other similar experiments conducted on different organisms at different places and times. This approach has been used to evaluate the broad body of experimental evidence for a number of important ecological questions in recent years (Gurevitch et al. 2001).

Scale and Heterogeneity

A great deal of recent interest in ecology has been generated by consideration of how ecological patterns and processes vary as a function of the scale at which they operate and are studied (Figure 1.4). The same phenomenon can be seen very differently when studied within a small local area and at the scale of a landscape or region—that is, at different spatial scales. Likewise, one's perspective can change dramatically when studying an ecological process over a single growing season of a few months or over a period of decades or centuries (see Figure 1.3). Different kinds of things may be going on at different scales, and expanding one's focus to more than one scale can be richly rewarding. In a study of a local community, for example, we might see that competitive interactions keep individual plants of a particular species at a distance from one another. At a larger scale, we might notice that the plants are grouped together across the landscape because individuals that are too far apart from any others never become pollinated, and fail to leave descendents; or because the seeds have limited ability to disperse. At a regional or continental scale, the plants may exist in several large but separated enclaves, determined by patterns of glaciation and species migration thousands of years in the past.

We often refer to these scale changes in terms of a hierarchy, and one can move up and down many different kinds of hierarchies in ecology. For instance, one can move from the level of molecules to tissues to organs to entire organisms. A different kind of hierarchy could expand from individual organisms to populations to communities to ecosystems and up to entire biomes; an alternative hierarchy might move from things that occur at the level of organisms to those that function at a scale of habitats, landscapes, watersheds, regions, and so on up to global-scale phenomena. These levels are not necessarily congruent: one might study the individual adaptations of plants over a range of different environments across an entire landscape or even a region, for instance,

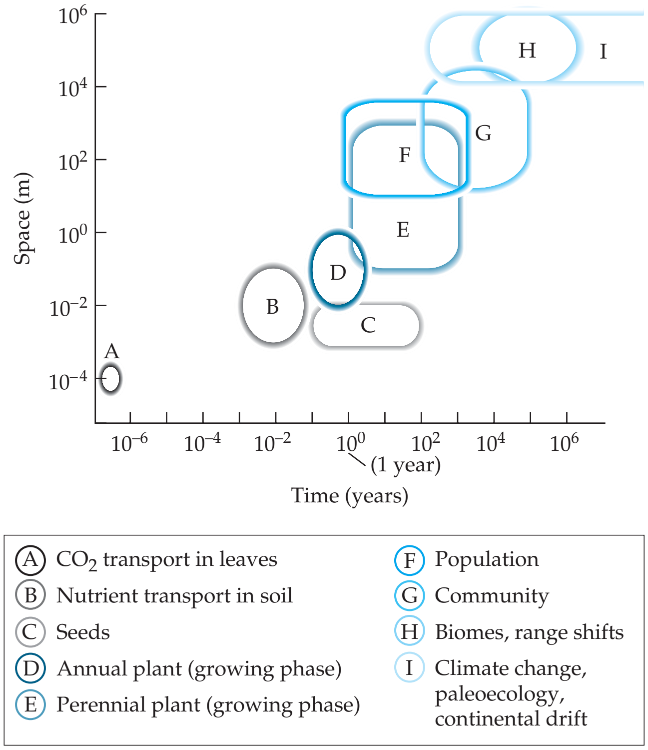

Figure 1.4
Ecologists study patterns and processes across a wide range of scales in space and time. The processes of plant physiology, such as the diffusion of CO_2 molecules in a leaf, occur over the shortest distances (10^{-4} m) and times (10^{-7} years). Moving up the hierarchy, the domain of the whole plant and its birth, growth, reproduction, and death encompasses slightly longer distances (10^0 m) and times (10^0 years). At yet larger scales (10^1–10^2 m and 10^1–10^2 years), we enter the realm of populations and communities and their changes over the course of years and decades. Finally, ecologists study patterns that stretch across the entire globe (10^5 m) and thousands or even millions of years (10^3–10^6 or more years).

or how population interactions at very local scales contribute to the global range limitations of a species. Likewise, one's interpretation of data collected over a short time period may be completely upended when the same data are examined for trends over longer periods of time.

One of the reasons that scale is now recognized as being so important is that the world is a very heterogeneous place. Even over very small distances, conditions can change in ways that may be very important to living organisms. Environmental conditions are a particular concern in plant ecology because plants cannot move. Or, at least, mature terrestrial plants generally are firmly rooted in place, although their offspring may be dispersed some distance away. So, the environment immediately surrounding an individual plant is overwhelmingly important to its survival, growth and reproduction.

The **habitat** of a population or species is the kind of environment it generally inhabits and includes the set of **biotic** (living) and **abiotic** (nonliving) factors that influence it in the places one usually finds it. But the conditions in the immediate surroundings of an individual plant—its **microhabitat**—may differ considerably from the average conditions in the general habitat (Figure 1.5). Factors operating to distinguish a microhabitat from others around it include the composition of the soil, the microclimate of the immediate area, the presence, size, and identity of neighboring plants, and other organisms in the immediate surroundings (grazers, pollinators, seed eaters or dispersers, and mutualistic or pathogenic fungi or bacteria).

Similarly, the environment varies from moment to moment. There are no specific ecological terms for the components of temporal heterogeneity, but it also exists at many scales and has major effects on plants. Variations in conditions from day to night, summer to winter, across periods of wet years, cold years, or snowy years, and at a longer scale as climate changes over thousands of years all have important influences on plants. Depending on the ecological process being studied and the organisms involved, it may be the small-scale, moment-to-moment variation that matters most (such as fluctuations in light levels in a small forest gap on a partially cloudy day), or it may be large-scale, long-term average conditions (such as CO_2 concentration in the atmosphere), or it may be the interplay between processes occurring at different scales (such as CO_2 flux in a forest canopy over the course of a day or a season).

Groups of organisms, such as populations and species, sometimes average these sorts of microenvironmental influences over larger areas and over generations of organisms' lives. This averaging acts to counter the effects of heterogeneity, particularly over evolutionary time. At even larger scales, heterogeneity again becomes critical. As continents are carried apart on tectonic plates and climates are altered, organisms must either respond to changing conditions by evolving or by changing their distributions, or else become extinct.

The Structure and History of Plant Ecology

Ecology is a very synthetic subject. By that we do not mean that it is unnatural or artificial, but that it brings together a very wide range of other fields of science, perhaps to a greater extent than does any other subject. Some of the fields that ecology encompasses or overlaps with include geology, geography, climatology, soil science, evolutionary biology, genetics, statistics and other branches of mathematics, systematics, behavior, physiology, developmental biology, molecular biology, and

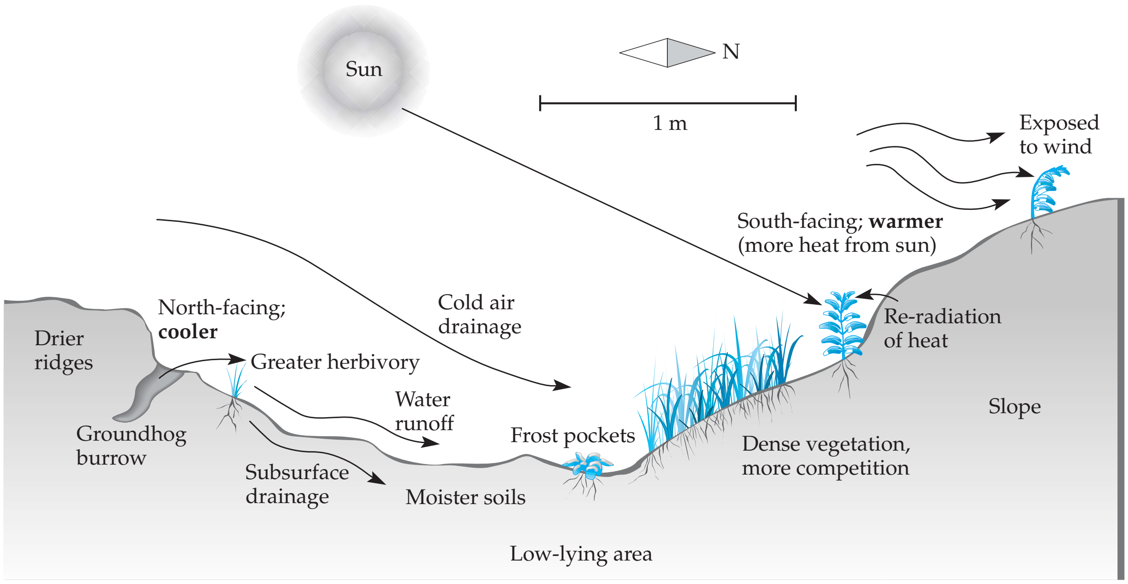

Figure 1.5
The environment in a particular microhabitat can differ in a number of ways from conditions in the surrounding area. Individual plants experience the conditions in their immediate microhabitat, not the average conditions in the general area. The grass on the north-facing slope at the left of the diagram experiences cooler temperatures, and perhaps greater herbivory due to its proximity to the groundhog burrow. The plants in the low-lying area may experience frost sooner in the fall and later in the spring than the surrounding areas due to cold air drainage; here, the soils are moister, and competition for light and soil moisture may be more intense, than on the ridges. Other potential effects of a microclimate are also illustrated.

biochemistry. We touch on many of these fields throughout this book, showing you how they fit into the toolkit of an ecologist and how familiarity with them affects the ways in which ecologists think about and study organisms in nature.

This is not the place to present a detailed and definitive history of plant ecology. Instead, we sketch some of the major milestones, with an admitted bias toward the English-speaking scientific community. Other historical details are scattered throughout the book as we discuss particular topics and subfields. While no single definitive history of plant ecology exists, several books and papers describe parts of its history (McIntosh 1985; Westman and Peet 1985; Nicholson 1990; Allen et al. 1993).

The roots of plant ecology go back to prehistoric times, when people's health and survival depended on their abilities to understand many aspects of the ecology of plants with great accuracy. Ecology as a science began with the Greeks, most notably Aristotle, in the fourth and fifth centuries B.C.E. The modern science of plant ecology began as the study of natural history in the eighteenth and nineteenth centuries, carried out by professional and amateur naturalists in Europe and North America and in their travels throughout the world. Ships on journeys of discovery and colonization often carried a ship's naturalist who cataloged the remarkable range of organisms and environments they encountered. Charles Darwin was one such ship's naturalist, and the story of his five-year voyage was published as his *Voyage of the* Beagle (Figure 1.6). Ecology as a recognized discipline coalesced in the latter half of the nineteenth century. The German biologist Ernst Haeckel coined the term "oecology" in 1866, and by early in the twentieth century the Ecological Society of America had formed.

Plant ecology as a discipline is made up of a number of different subdisciplines, some of which have quite distinct traditions and histories. Some early plant ecologists and botanists focused on whole communities, while others focused on single species and the properties of individuals. The older (now largely archaic) terms for these two subfields are **synecology** and **autecology**. Plant community ecologists, in particular, were active in the origins of ecology as a discipline in the last part of the nineteenth century and dominated plant ecology during the first half of the twentieth century. A more detailed discussion of the history of plant community ecology and some of the key figures in that history is given in Chapters 12 and 13.

Early studies in plant autecology were especially concerned with understanding unique plant adaptations

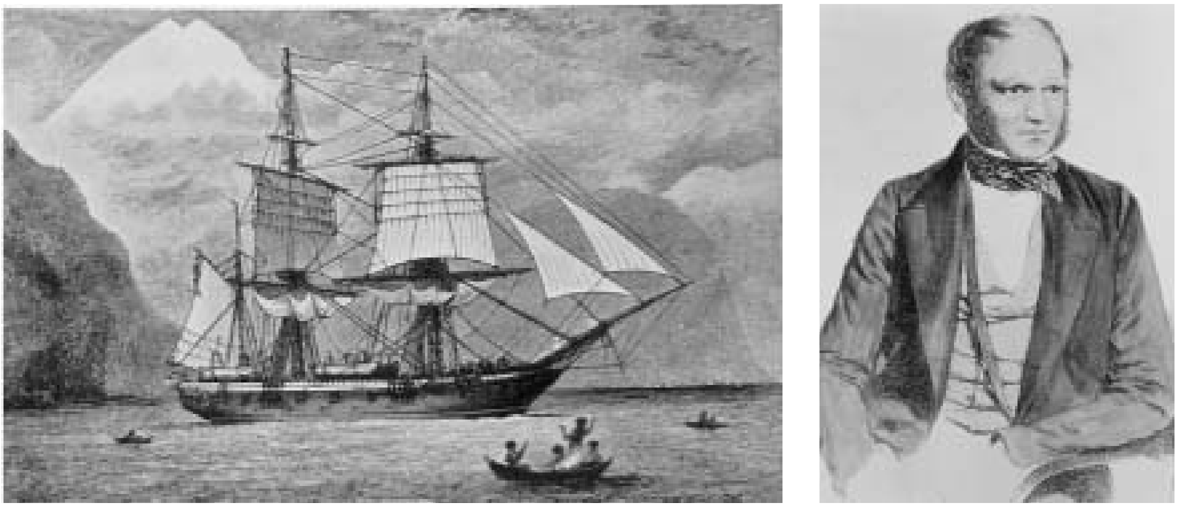

Figure 1.6
H.M.S. Beagle sailed from England December 27, 1831 on a 5-year mission to chart the oceans and collect biological information from around the world. Charles Darwin sailed with the *Beagle* as ship's naturalist; he is pictured here at the age of 24, shortly after completing the voyage. Darwin collected vast numbers of plant and animal specimens and recorded copious scientific observations that were instrumental in the creation of his most famous work, *On the Origin of Species.* (Images from Science Photo Library/Photo Researchers, Inc.)

to extreme environments, such as deserts, and a number of famous studies were concerned with plant performance in the field. Although some major insights were gained, technological limitations severely hampered the development of the field. As instrumentation and methodology became more sophisticated, plant physiologists began to carry out most of their research in controlled laboratory environments.

Beginning in the middle of the twentieth century, further advances in technology made it possible for physiological studies to come out of the greenhouse and into nature, eventually leading to the creation of the fields of plant physiological and functional ecology. At about the same time, autecology began to fission into subfields that focused on single individuals and on populations. Plant population ecology as a recognizable subdiscipline had its origins in Great Britain in the 1960s, particularly with John Harper and his students. It then spread to North America in the 1970s. This is necessarily a very simplified and limited description of events; for instance, a number of individuals in many countries around the world were carrying out studies that today we would label as plant physiological ecology or plant population ecology as far back as the nineteenth century.

For the most part, plant ecology for the first three-quarters of the twentieth century developed independently of animal ecology. Animal community ecology has a long history parallel to that of plant community ecology (Mitman 1992). Substantial work in animal population ecology extends back to at least the 1920s (for example, with the work of Gause, Pearl, Lotka, and others). Plant population ecology drew on these ideas and theories as it was developing, as well as other ideas that originated among plant ecologists. Eventually new theories were needed as discoveries about the unique nature of plants made it obvious they could no longer be shoehorned into many of the theories constructed for animals.

Conversely, physiological ecology advanced earlier and more rapidly among plant ecologists than it did among animal ecologists. Undoubtedly this was because the characteristics of plants are much easier to measure, and their environments easier to characterize, than those of animals (for most purposes, one does not have to catch plants!). On the other hand, in the 1980s, animal physiological ecology joined with evolutionary biology to create the field of evolutionary physiology (Feder et al. 1987), a move that plant biologists have not yet clearly made.

The gap between the fields of plant and animal ecology was bridged in the 1970s, although distinct subfields continue to this day. Two related developments were responsible. The first was the rise of studies of plant-animal interactions, especially pollination (see Chapter 8) and herbivory (see Chapter 11). The second development was the burgeoning interest in the evolutionary aspects of ecology in the 1970s and 1980s, which transcended the traditional separation of the studies of plants and animals.

The most recent changes in the field of plant ecology have been the rise of landscape ecology and conservation ecology as recognized disciplines in the late 1980s. Landscape ecologists began their careers from various different directions, including fields as diverse as plant community ecology and remote sensing. Conservation ecologists likewise created their field from backgrounds in mathematical modeling and population, community, and ecosystem ecology. Other fields within plant ecology have seen major shifts in emphasis. Plant community ecology has seen such a shift in the past quarter century. Previously it was dominated by questions about whole-community patterns and processes; now, its main focus has shifted to questions closer to population ecology, about interactions within and among species.

A major trend in contemporary ecology, including plant ecology, is toward larger, more integrated research projects that involve many collaborators and examine phenomena across large scales of space and time or across levels of organization. Except in the subdiscipline of ecosystem ecology, which was undertaking projects with large teams of scientists in the 1970s, such multi-investigator studies were very rare in ecology until recent years. These studies may cover a range from molecular genetics up through ecosystems and social systems, and are erasing many of the traditional boundaries among subdisciplines. Plant ecology is experiencing exciting times, and we hope you will sense that excitement in this book.

Additional Readings

Classic References

Platt, J. R. 1964. Strong inference. *Science* 146 : 347–353.

Popper, K. R. 1959. *The Logic of Scientific Discovery*. Hutchinson & Co., London.

Salt, G. W. 1983. Roles: Their limits and responsibilities in ecological and evolutionary research. *Am. Nat.* 122: 697–705.

Contemporary Research

Hull, D. L. 1988. *Science as a Process*. University of Chicago Press, Chicago, IL.

Mayo, D. G. 1996. *Error and the Growth of Experimental Knowledge*. University of Chicago Press, Chicago, IL.

Nicholson, M. 1990. Henry Allan Gleason and the individualistic hypothesis: The structure of a botanist's career. *Bot. Rev.* 56:91–161.

Additional Resources

McIntosh, R. P. 1985. *The Background of Ecology*. Cambridge University Press, Cambridge.

Pickett, S. T. A., J. Kolasa and C. G. Jones. 1994. *Ecological Understanding*. Academic Press, San Diego, CA.