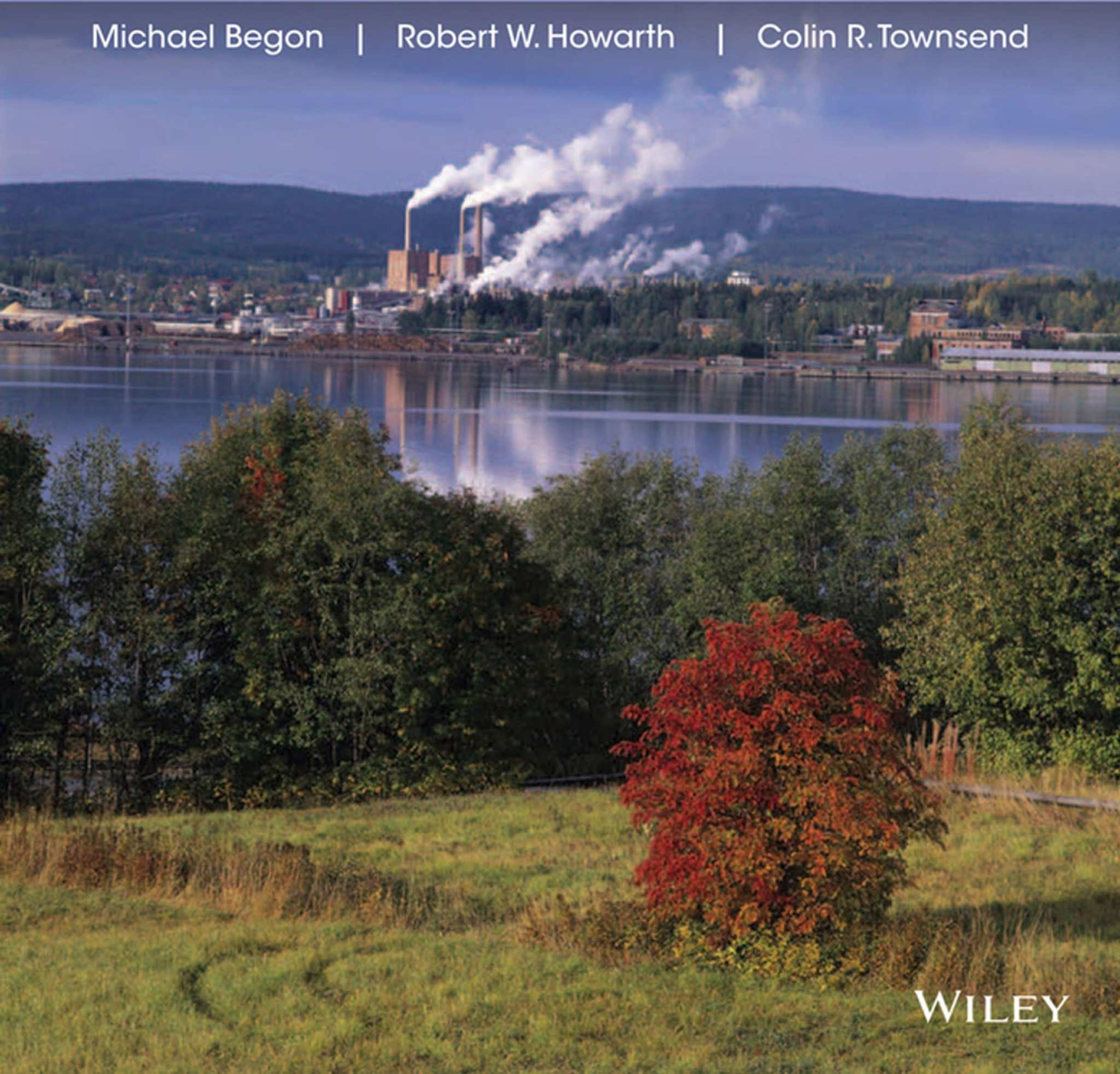
FOURTH EDITION

Essentials of ECOLOGY

Michael Begon | Robert W. Howarth | Colin R. Townsend



WILEY

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4TH EDITION

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(available online only: www.wiley.com/college/begon)

Preface

By writing this book we hope to share with you some of our wonder at the complexity of nature, but we must all also be aware that there is a darker side: the fear that we are destroying our natural environments and the services they provide. All of us need to be ecologically literate so that we can take part in political debate and contribute to solving the ecological problems that we carry with us in this new millennium. We hope our book will contribute to this objective.

The genesis of this book can be found in the more comprehensive treatment of ecology in our big book *Ecology: from Individuals to Ecosystems* (Begon, Townsend & Harper, 4th edn, 2006). This is used as an advanced university text around the world, but many of our colleagues have called for a more succinct treatment of the essence of the subject. Thus, we were spurred into action to produce a distinctively different book, written with clear objectives for a different audience—those taking a semester-long beginners course in the essentials of ecology. We hope that at least some readers will be excited enough to go on to sample the big book and the rich literature of ecology that it can lead into.

In this fourth edition of *Essentials of Ecology* we have continued to make the text, including mathematical topics, accessible while updating the material and expanding our coverage of ecosystem science and biogeochemistry. The fourth edition extensively covers both terrestrial and aquatic ecology, and we have strived to demonstrate how ecological principles apply equally to both types of environments. While we have expanded coverage on some topic areas in the fourth edition, we worked hard to not expand the size of the book. We want this text to be a readily accessible read.

Ecology is a vibrant subject and this is reflected by our inclusion of literally hundreds of new studies. Some readers will be engaged most by the fundamental principles of how ecological systems work. Others will be impatient to focus on the ecological problems caused by human activities. We place heavy emphasis on both fundamental and applied aspects of ecology: there is no clear boundary between the two. However, we have chosen to deal first in a systematic way with the fundamental side of the subject, and we have done this for a particular reason. An understanding of the scope of the problems facing us (the unsustainable use of ecological resources, pollution, extinctions and the erosion of natural biodiversity) and the means to counter and solve these problems depend absolutely on a proper grasp of ecological fundamentals.

The book is divided into five sections. In the introduction we deal with two foundations for the subject that are often neglected in texts. Chapter 1 aims to show not only what ecology is but also how ecologists do it—how ecological understanding is achieved, what we understand (and, just as important, what we do not yet understand) and how our understanding helps us predict and manage. We then introduce 'Ecology's evolutionary backdrop' and show that ecologists need a full understanding of the evolutionary biologist's discipline in order to make sense of patterns and processes in nature (Chapter 2).

What makes an environment habitable for particular species is that they can tolerate the physicochemical conditions there and find in it their essential resources. In the second section we deal with conditions and resources, both as they influence individual species (Chapter 3) and in terms of their consequences for the composition and distribution of multispecies communities and ecosystems, for example in deserts, rain forests, rivers, lakes and oceans (Chapter 4).

The third section (Chapters 5–8) deals systematically with the ecology of individual organisms and populations, with chapters on 'birth, death and movement' (Chapter 5), 'interspecific competition' (Chapter 6), and 'predation, grazing, and disease' (Chapter 7). This section also includes a chapter on 'Molecular and evolutionary ecology', added originally in the third edition and responding to the feelings of some readers that, although evolutionary ideas pervade the book, there was still not sufficient evolution for a book at this level.

In the fourth section (Chapters 9–11), we move up the hierarchical scale of ecology to consider communities consisting of many populations, and ecosystems, where we focus on the fluxes of energy and matter between and within systems.

Finally, armed with knowledge and understanding of the fundamentals, the book turns to the application of ecological science to some of the major environmental challenges of our time. Our goal in these final chapters is not to provide encyclopedic coverage to these environmental problems, but rather to illustrate how ecology contributes to understanding the problems, and can potentially help with their solution. In Chapter 12, we focus on global biogeochemical cycles, such as the global carbon dioxide cycle and how this has been dramatically changed by burning fossil fuels and other human activities. In 'conservation ecology' (Chapter 13), we develop an armory of approaches that may help us to save endangered species from extinction and conserve some of the biodiversity of nature for our descendants. The final chapter, 'the ecology of human population growth, disease, and food supply,' takes an ecological approach to examining the issues of the population problem, of human health, and of the sustainability of agriculture and fisheries.

A number of pedagogical features have been included to help you.

- Each chapter begins with a set of key concepts that you should understand before proceeding to the next chapter.
- Marginal headings provide signposts of where you are on your journey through each chapter—these will also be useful revision aids.
- Each chapter concludes with a summary and a set of review questions, some of which are designated challenge questions.
- You will also find three categories of boxed text:
    - 'Historical landmarks' boxes emphasize some landmarks in the development of ecology.
    - 'Quantitative aspects' boxes set aside mathematical and quantitative aspects of ecology so they do not unduly interfere with the flow of the text and so you can consider them at leisure.
    - 'ECOncerns' boxes highlight some of the applied problems in ecology, particularly those where there is a social or political dimension (as there often is). In these, you will be challenged to consider some ethical questions related to the knowledge you are gaining.

An important further feature of the book is the companion web site, accessed through Wiley at www.wiley.com/college/begon. This provides an easy-to-use range of resources to aid study and enhance the content of the book. Features include self-assessment multiple choice questions for each chapter in the book, an interactive tutorial to help students to understand the use of mathematical modeling in ecology, and high-quality images of the figures in the book that teachers can use in preparing their lectures or lessons, as well as access to a Glossary of terms for use with this book and for ecology generally.

Acknowledgments

It is a pleasure to record our gratitude to the people who helped with the planning and writing of this book. Going back to the first edition, we thank Bob Campbell and Simon Rallison for getting the original enterprise off the ground and Nancy Whilton and Irene Herlihy for ably managing the project; and for the second edition, Nathan Brown (Blackwell, US) and Rosie Hayden (Blackwell, UK) for making it so easy for us to take this book from manuscript into print. For the third edition, we especially thank Nancy Whilton and Elizabeth Frank in Boston for persuading us to pick up our pens again (not literally) and Rosie Hayden, again, and Jane Andrew and Ward Cooper for seeing us through production. For this fourth edition, we thank Rachel Falk (Wiley, USA) for getting the ball rolling and for bringing in one of us (RWH) as a new author, Elisa Adams for her superb assistance with text editing, Chloe Moffett, Elizabeth Baird, MaryAnn Price and Lisa Torri (Precision Graphics) for their excellent overseeing of the final production, and the entire Wiley team for their dedicated efforts and cheerful "can-do" attitude.

We note with sadness the passing in 2009 of our long-time mentor and collaborator John Harper, author on the first three editions of this book. We owe him a special debt of gratitude that extends far beyond the past co-authorship of this book into all aspects of our lives as ecologists. He is sorely missed.

Colin Townsend, the lead author on the first three editions of *Essentials of Ecology*, has stepped from the treadmill of revisions and let us take the lead on this fourth edition. His imprint on the book remains strong, and we gratefully acknowledge his tremendous contribution to the series.

We are also grateful to the following colleagues who provided insightful reviews of early drafts of one or more chapters in this or earlier editions, or who gave us important advice and leads: William Ambrose (Bates College), Vickie Backus (Middlebury College), James Cahill (University of Alberta), Liane Cochrane-Stafira (Saint Xavier University), Mark Davis (Macalester College), Tim Crews (The Land Institute), Kevin Dixon (Arizona State University, West), Stephen Ellner (Cornell University), Alex Flecker (Cornell University), Bruce Grant (Widener University), Christy Goodale (Cornell University), Don Hall (Michigan State University), Jenny Hodgson, Greg Hurst (both University of Liverpool), William Kirk (Keele University, UK), Hans deKroon (University of Nijmegen), Zen Lewis (University of Liverpool), Sara Lindsay (Scripps Institute of Oceanography), James Maki (Marquette University), George Middendorf (Howard University), Paul Mitchell (Staffordshire University, UK), Tim Mousseau (University of South Carolina), Katie O'Reilly (University of Portland), Clayton Penniman (Central Connecticut State University), Tom Price (Univeristy of Liverpool), Jed Sparks (Cornell University), Catherine Toft (UC Davis), David Tonkyn (Clemson University), Saran Twombly (University of Rhode Island), Jake Weltzin (University of Tennessee at Knoxville), and Alan Wilmot (University of Derby, UK).

Last, and perhaps most, we are glad to thank our wives and families for continuing to support us, listen to us, and ignore us, precisely as required—thanks to Linda, and to Roxanne and Marina.

Michael Begon, Liverpool, UK and
Robert Howarth, Ithaca, NY USA

Part 1

Introduction

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Chapter 1

Ecology and how to do it

CHAPTER CONTENTS

KEY CONCEPTS

After reading this chapter you will be able to:

- explain how ecologists seek to describe and understand, and on the basis of their understanding, to predict, manage, mitigate, and control
- describe the variety of spatial and temporal scales on which ecological phenomena occur
- describe how ecologists use observations, field and laboratory experiments, and mathematical models to collect scientific evidence

Ecology today is a subject about which almost everyone has heard and most people consider to be important—even when they are unsure about the exact meaning of the term. There can be no doubt that it is important, but this makes it all the more critical that we understand what ecology is and how to do it.

1.1 WHAT IS ECOLOGY?

the earliest ecologists

We could answer the question 'What is ecology?' by examining various definitions that have been proposed and choosing one as the best (Box 1.1). But while definitions have conciseness and precision, and they are good at preparing you for an examination, they are not so good at capturing the flavor and excitement of ecology. There is a lot to be gained by replacing that single question about a definition with a series of more provocative ones: 'What do ecologists *do*?' 'What are ecologists *interested* in?' and 'Where did ecology emerge from in the first place?'

1.1 Historical Landmarks

Definitions of ecology

Ecology (originally in German, *Öekologie*) was first defined in 1866 by Ernst Haeckel, an enthusiastic and influential disciple of Charles Darwin. To him, ecology was 'the comprehensive science of the relationship of the organism to the environment.' The spirit of this definition is very clear in an early discussion of biological subdisciplines by Burdon-Sanderson (1893), in which ecology is 'the science which concerns itself with the external relations of plants and animals to each other and to the past and present conditions of their existence,' to be contrasted with physiology (internal relations) and morphology (structure).

In the years after Haeckel, plant ecology and animal ecology drifted apart. Influential works defined ecology as 'those relations of *plants*, with their surroundings and with one another, which depend directly upon differences of habitat among plants' (Tansley, 1904), or as the science 'chiefly concerned with what may be called the sociology and economics of *animals*, rather than with the structural and other adaptations possessed by them' (Elton, 1927). The plant ecologists and animal ecologist, though, have long since agreed that they belong together, and more recent definitions of ecology include all organisms, including bacteria, archaea, algae, and fungi in addition to plants and animals. Most modern definitions stress the relationships between and among organisms. For example, two textbooks from the 1970s defined ecology as 'the study of the natural environment, particularly the interrelationships between organisms and their surroundings' (Ricklefs, 1973) and as 'the scientific study of the *interactions* that determine the distribution and abundance of organisms' (Krebs, 1972).

Ecology certainly includes the investigation of organisms and their interactions, but to many ecologists, definitions that focus only on these interactions and on the distribution and abundance of organisms are too narrow. Ecologists also examine the interaction between life and the physical environment, for instance studying how organisms affect material fluxes in nature. The sequestration of carbon dioxide by a forest would be one example of this. Beginning in the mid-20th century, the American ecologist E. P. Odum (1953) pushed for a broader definition of ecology: 'the study of the structure and function of nature, which includes the living world.' Many have thought this definition overly broad, as geologists and meteorologists also study aspects of the structure and function of nature. In 1992, G. E. Likens stressed the need for the definition of ecology to include 'the interactions between organisms and the transformation and flux of energy and matter.' We agree, and in this text define ecology as:

> the scientific study of the distribution and abundance of organisms, the interactions that determine that distribution and abundance, and the relationships between organisms and the transformation and flux of energy and matter.

Ecology can lay claim to being the oldest science, as the most primitive humans must have been ecologists of sorts, driven by the need to understand where and when their food and their (nonhuman) enemies were to be found. The earliest agriculturalists needed to be even more sophisticated, with knowledge of how to manage their domesticated sources of food. These early ecologists, then, were *applied* ecologists, seeking to understand the distribution, abundance, and productivity of organisms in order to apply that knowledge for their own benefit. Applied ecologists today still have many of the same interests: how to optimize the rate at which food is collected from natural environments in a sustainable way; how domesticated plants and animals can best be managed so as to maximize rates of return; how food organisms can be protected from their own natural enemies; and how to control the populations of pathogens and parasites that live on us.

a pure and applied science

In the last century or so, however, since ecologists have been self-conscious enough to give themselves a name, ecology has consistently covered not only applied but also fundamental, 'pure' science. A.G. Tansley was one of the founding fathers of ecology. He was concerned especially to understand, for understanding's sake, the processes responsible for determining the structure and composition of different plant communities. When, in 1904, he wrote from Britain about 'The problems of ecology' he was particularly worried by a tendency for too much ecology to remain at the descriptive and unsystematic stage (such as accumulating descriptions of communities without knowing whether they were typical, temporary, or whatever), too rarely moving on to experimental or systematically planned, or what we might call a *scientific* analysis.

Tansley's worries were echoed in the United States by another of ecology's founders, F. E. Clements, who in 1905 in his *Research Methods in Ecology* complained:

> The bane of the recent development popularly known as ecology has been a widespread feeling that anyone can do ecological work, regardless of preparation. There is nothing . . . more erroneous than this feeling.

On the other hand, the need for *applied* ecology to be based on its *pure* counterpart was clear in the introduction to Charles Elton's (1927) *Animal Ecology* (Figure 1.1):

> Ecology is destined for a great future . . . The tropical entomologist or mycologist or weed-controller will only be fulfilling his functions properly if he is first and foremost an ecologist.

In the intervening years, the coexistence of these pure and applied threads has been maintained and built upon. Many applied sciences such as forestry, agronomy, and fisheries biology have contributed to the development of ecology and have seen their own

courtesy Robert Elton

FIGURE 1.1 One of the great founders of ecology: Charles Elton (1900–1991). *Animal Ecology* (1927) was his first book but *The Ecology of Invasions by Animals and Plants* (1958) was equally influential. (After Breznak, 1975.)

development enhanced by ecological ideas and approaches. All aspects of food and fiber gathering, production, and protection have been involved. The biological control of pests (the use of pests' natural enemies to control them) has a history going back at least to the ancient Chinese but has seen a resurgence of ecological interest since the shortcomings of chemical pesticides began to be widely apparent in the 1950s. The ecology of pollution has been a growing concern from around the same time and expanded further in the 1980s and 1990s from local to regional and global issues. The last few decades have also seen expansions in both public interest and ecological input into the conservation of endangered species and the biodiversity of whole areas, the control of disease in humans as well as many other species, and the potential consequences of profound human-caused changes to the global environment.

unanswered questions

And yet, at the same time, many fundamental problems of ecology remain unanswered. To what extent does competition for food determine which species can coexist in a habitat? What role does disease play in the dynamics of populations? Why are there more species in the tropics than at the poles? What is the relationship between soil productivity and plant community structure? Why are some species more vulnerable to extinction than others? Are wetlands net sources or sinks of greenhouse gas emission to the atmosphere? And so on. Of course, unanswered questions—if they are *focused* questions—are a symptom of the health, not the weakness, of any science. But ecology is not an easy science, and it has particular subtlety and complexity, in part because ecology is peculiarly confronted by 'uniqueness': millions of different species, countless billions of genetically distinct individuals, all living and interacting in a varied and ever-changing world. The beauty of ecology is that it challenges us to develop an understanding of very basic and apparent problems—in a way that recognizes the uniqueness and complexity of all aspects of nature – but seeks patterns and predictions within this complexity rather than being swamped by it.

understanding, description, prediction, and control

Let's come back to the question of what ecologists do. First and foremost ecology is a science, and ecologists therefore try to *explain* and *understand*. Explanation can be either 'proximate' or 'ultimate,' and ecologists are interested in both. For example, the present distribution and abundance of a particular species of bird may be 'explained' in terms of the physical environment that the bird tolerates, the food that it eats, and the parasites and predators that attack it. This is a *proximate* explanation – an explanation in terms of what is going on 'here and now.' We can also ask how this bird came to have these properties that now govern its life. This question has to be answered by an explanation in evolutionary terms; the *ultimate* explanation of the present distribution and abundance of this bird lies in the ecological experiences of its ancestors (see Chapter 2).

In order to understand something, of course, we must first have a description of whatever it is we wish to understand. Ecologists must therefore *describe* before they explain. On the other hand, the most valuable descriptions are those carried out with a particular problem or 'need for understanding' in mind. Undirected description, carried out merely for its own sake, is often later found to have selected the wrong things and has little place in ecology—or any other science.

Ecologists also often try to *predict*. For example, how will global warming affect the sequestration (storage) of carbon in natural ecosystems? Will warming reduce this storage, and therefore result in even more global warming since less carbon dioxide will be removed from the atmosphere? Often, ecologists are interested in what will happen to a population of organisms under a particular set of circumstances, and on the basis of these predictions to control, exploit or conserve the population. We try to minimize the effects of locust plagues by predicting when they are likely to occur and taking appropriate action. We try to exploit crops most effectively by predicting when conditions will be favorable to the crop and unfavorable to its enemies. We try to preserve rare species by predicting the conservation policy that will enable us to do so. Some prediction and control can be carried out without deep explanation or understanding: it is not difficult to predict that the destruction of a woodland will eliminate woodland birds. But what if the woodland is not destroyed, but rather fragmented into distinct parts with suburbs or agricultural fields between them? What effect may this have on the woodland birds? Insightful predictions, precise predictions, and predictions of what will happen in unusual circumstances can be made only when we can also explain and understand what is going on.

This book is therefore about:

1 How ecological understanding is achieved.

2 What we do understand, and what we do not.

3 How ecological understanding can help us predict, manage, mitigate, and control.

1.2 SCALES, DIVERSITY OF APPROACHES, AND RIGOR

Ecology is a diverse discipline, and ecologists use a vast array or tools and approaches. Later in this chapter, we briefly give some examples of this diversity, but first we elaborate on three general points:

- ecological phenomena occur at a variety of scales;
- ecological evidence comes from a variety of different sources;
- ecology relies on truly scientific evidence.

Questions of scale

Ecology operates at a range of scales: time scales, spatial scales, and 'biological' scales. It is important to appreciate the breadth of these and how they relate to one another.

the 'biological' scale

Life is studied at a variety of hierarchical levels, with much of biology focused on levels from molecules, to organelles, cells, tissues, organs, and whole organisms. Ecologists study levels from individual organisms, to populations, communities, ecosystems, and the global biosphere (Figure 1.2).

- Populations are functioning groups of individual organisms of the same species in a defined location.
- Communities consist of all the species populations present in a defined location.
- Ecosystems include both the community of organisms and the physical environment in which they exist.
- The biosphere is the totality of all of life interacting with the physical environment at the scale of the entire planet.

At the level of the organism, ecology deals primarily with how individuals are affected by their environment and with their physiological and behavioral responses to the environment. **Population ecology** stresses the trends and fluctuations in the number of individual of a particular species at a particular time and place, as determined by the interactions of birth and death rates and the interactions between the populations themselves (such as predators and prey). **Community ecology** focuses on questions such as what controls the diversity of species of in a given area. **Ecosystem ecology** strives to understand the functioning of entire lakes, forests, wetlands, or other portions of the Earth in terms of energy and material inputs and outputs. Across all scales of biological hierarchy—including these ecological ones—three generalities emerge.

1. The properties observed at a particular level arise out of the functioning of parts at the level below. For example, how a tissue functions is the result of the functioning of the cells in that tissue, and how an ecosystem functions is the result of the functioning of the communities within it interacting with the physical environment.
2. In order to understand the mechanistic reasons that a particular property is observed at any level of biological organization, a scientist needs to look at the next lowest level of organization. To understand dysfunction in an individual organism, we must look at the functioning of the organs in that organism; and to understand the controls on birth rate in a population, we must look at reproduction in individual organisms.
3. However, properties observed at a given level of organization may be predicted without fully understanding the functioning at lower levels. This third generality may seem to contradict the other two, but it does not. Consider an analogy from the physical sciences. As early as 1662, Boyle knew that when the pressure of a gas is doubled, its volume is halved, if temperature remains constant. This behavior of the gas as a whole is the result of the interactions of the gas molecules, yet Boyle's law provided valuable predictive power for centuries, long before the concept of the molecule was developed. Today, physical chemists can indeed explain gas behavior based on understanding of the behavior of individual molecules, but the explanation is complex, and not even taught to most undergraduate college students. Similarly, ecologists can predict patterns in ecosystems without understanding all of the details of the dynamics of constituent populations, and can predict patterns in populations without understanding all of the details of the responses of individual organisms.

a range of spatial scales

Within the living world, there is no arena too small nor one so large that it does not have an ecology. Even the popular press talk increasingly about the 'global ecosystem', and there is no question that several ecological problems can be examined only at this very large scale. These include the relationships between ocean currents and fisheries, or between climate patterns and the distribution of deserts and tropical rain forests, or between elevated carbon dioxide in the atmosphere (from burning fossil fuels) and global climate change.

At the opposite extreme, an individual cell may be the stage on which two populations of pathogens

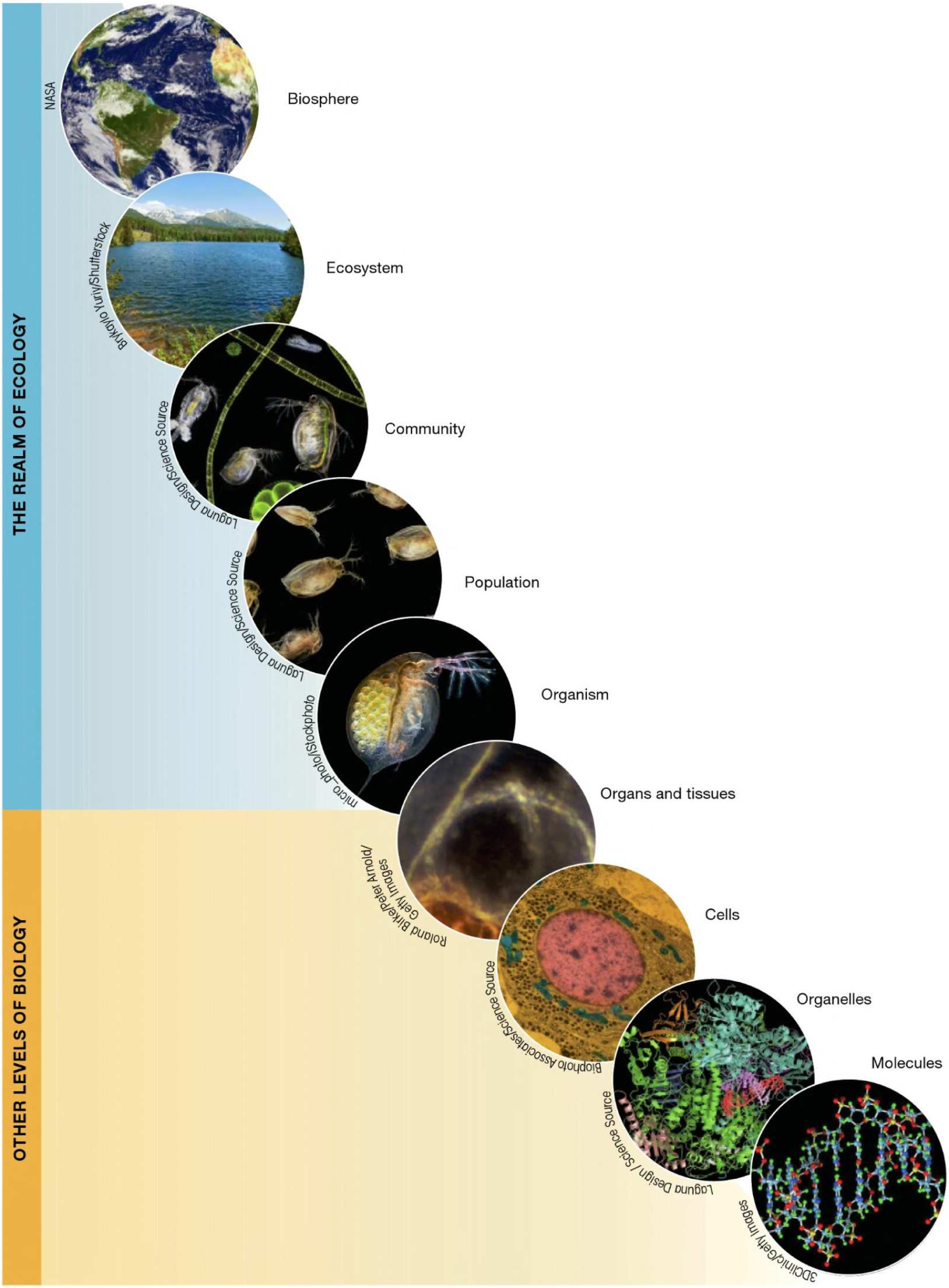

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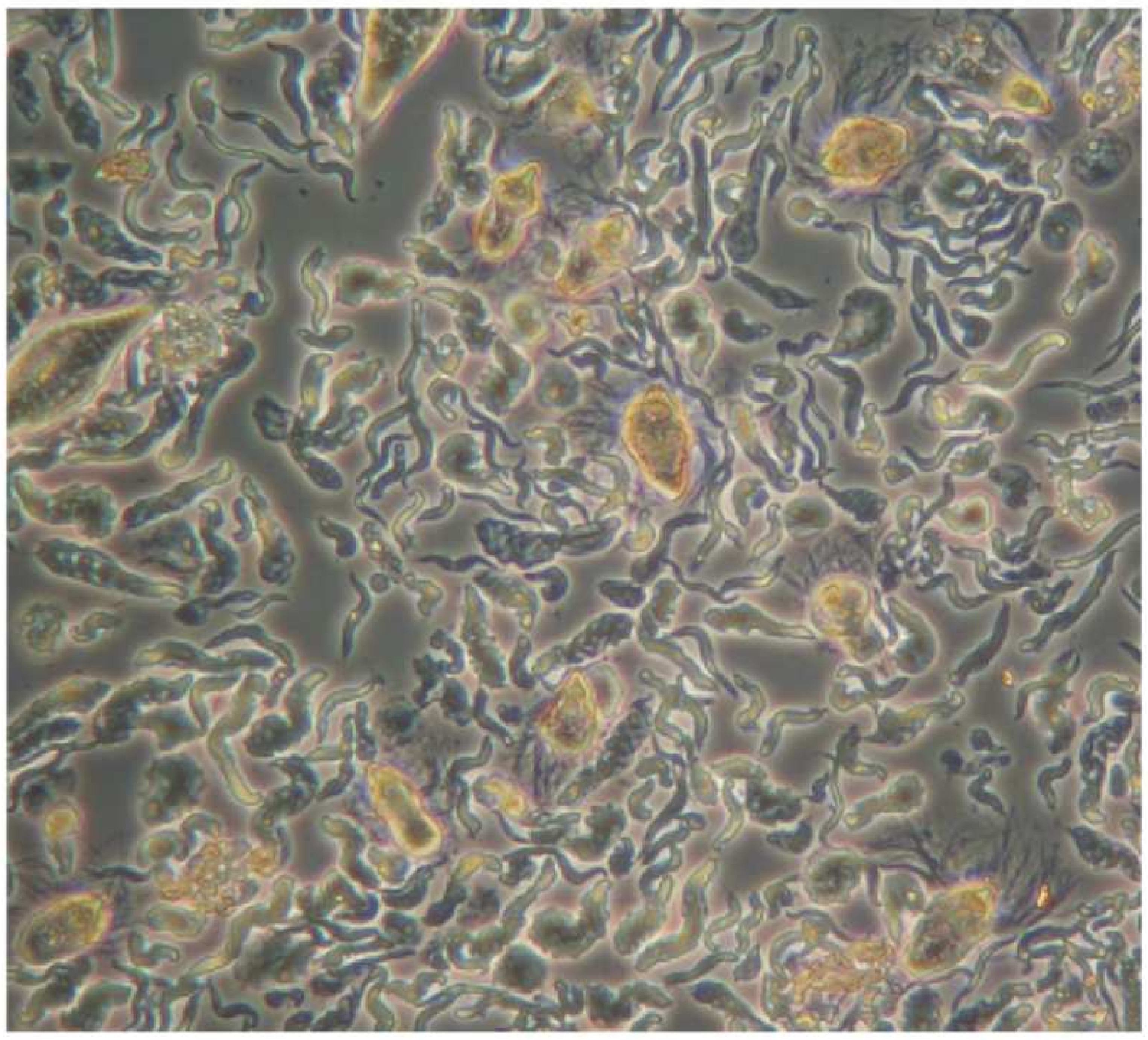
FIGURE 1.2 Ecology is studied at many hierarchical levels.



Shigeharu Moriya

FIGURE 1.3 The diverse community of a termite's gut. Termites can break down lignin and cellulose from wood because of their mutualistic relationships (see Chapter 8) with a diversity of microbes that live in their guts.

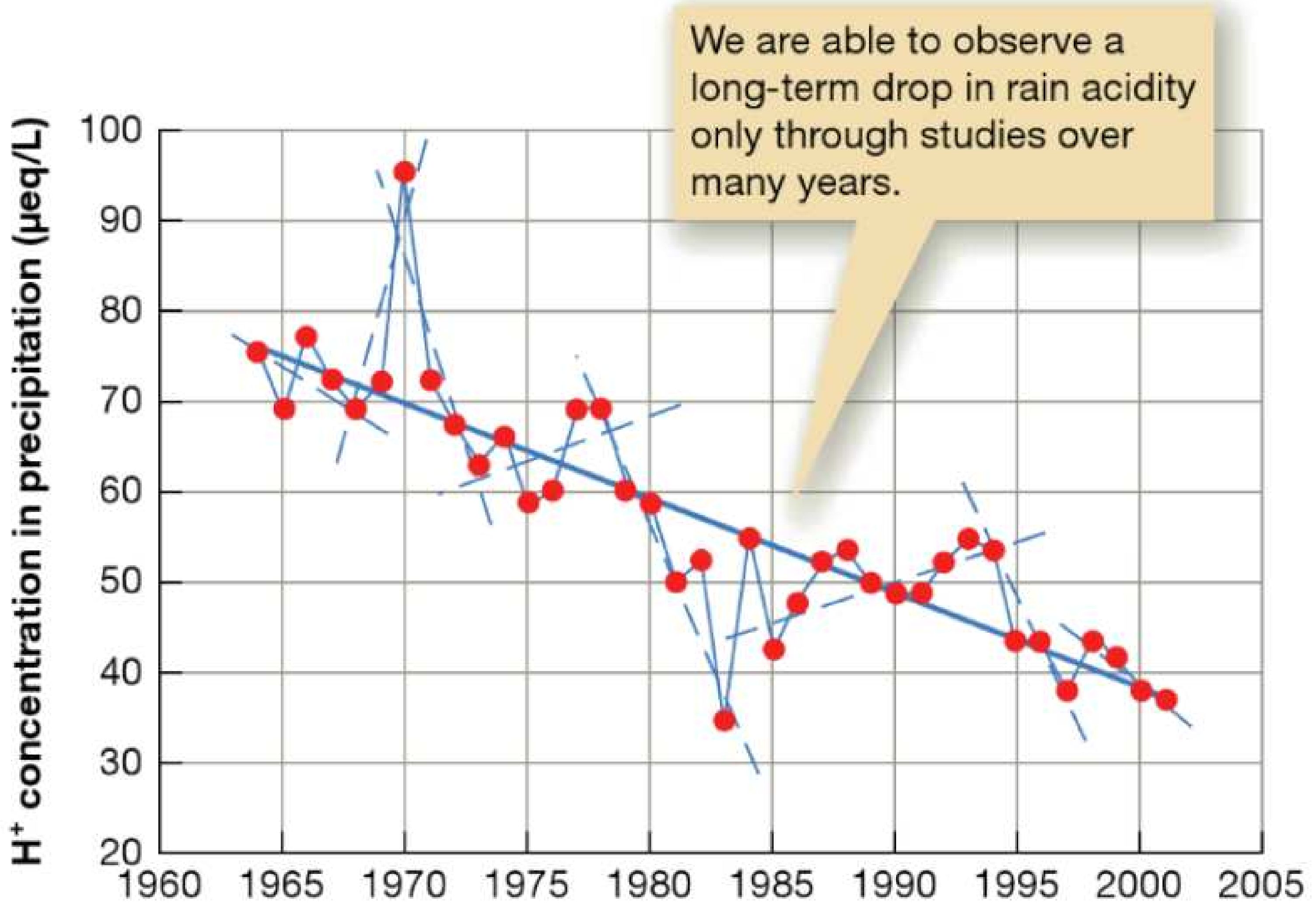
compete with one another for the resources that the cell provides. At a slightly larger spatial scale, a termite's gut is the habitat for bacteria, protozoans, and other species (Figure 1.3) – a community whose diversity is comparable to that of a tropical rain forest in terms of the richness of organisms living there, the variety of interactions in which they take part, and indeed the extent to which we remain ignorant about the species identity of many of the participants. Between these extremes, different ecologists, or the same ecologist at different times, may study the inhabitants of pools that form in small tree-holes, the temporary watering holes of the savannas, or the great lakes and oceans; others may examine the diversity of fleas on different species of birds, the diversity of birds in different sized patches of woodland, or the diversity of woodlands at different altitudes.

a range of time scales

To some extent related to this range of spatial scales, and to the levels in the biological hierarchy, ecologists also work on a variety of time scales. **Ecological succession** – the successive and continuous colonization of a site by certain species populations, accompanied by the local extinction of others – may be studied over a period from the deposition of a lump of sheep dung to its decomposition (a matter of weeks), from the abandonment of a patch of tropical rain forest cleared for slash-and-burn agriculture (years to decades), or from the development of a new forest on land wiped clean to bedrock by the retreat of a glacier in the arctic or high mountains (centuries). Migration may be studied in butterflies over the course of days, or in the forest trees that are still (slowly) migrating into deglaciated areas following the last ice age.

the need for long-term studies

The appropriate time scale for ecological investigation varies with the question to be answered. However, many ecological studies end up being shorter than appropriate for the question, due to human frailties. Longer studies cost more and require greater dedication and stamina. The often short-term nature of funding, an impatient scientific community, and the requirement for concrete evidence of activity for career progression all put pressure on ecologists (and all scientists) to publish their work sooner rather than later. Why are long-term studies potentially of such value? The reduction over a few years in the numbers of a particular species of wild flower, or bird, or butterfly might be a cause for conservation concern—but one or more decades of study may be needed to be sure that the decline is more than just an expression of the random ups and downs of 'normal' population dynamics. One of the longest, continuously run ecological studies is at the Hubbard Brook Experiment Forest in the White Mountains of New Hampshire. Among other measures, Gene Liken and other scientists there have monitored the acidity of rain since the early 1960s. In the 1960s, the rain was quite acidic (low pH: high hydrogen ion concentrations), and this was in fact one of the earliest discoveries anywhere of the phenomenon of acid rain. The long-term trend, though, has been for precipitation to become less acidic over subsequent decades (Figure 1.4); but we can observe this only



We are able to observe a long-term drop in rain acidity only through studies over many years.

FIGURE 1.4 Hydrogen ion concentration in precipitation at the Hubbard Brook Experimental Forest over time. Note the long-term trend of decreasing concentration, indicating that the pH has been rising, and the rain has become less acidic over time. However, analysis of periods of only a few years in duration can show sharp increases or decreases in the hydrogen ion concentration, and are quite misleading with regard to the long-term trend (After Likens 2004).

because we have that long-term record. Observations over periods of even 5 to 10 years at a time would be very misleading.

This does not mean that all ecological studies need to last for 20 years – nor that every time an ecological study is extended the answer changes. But it does emphasize the great value to ecology of the small number of long-term investigations that have been carried out or are ongoing.

The diversity of ecological evidence

Ecological evidence comes from a variety of different sources and approaches. The principal tools are:

- *Observations*, often of changes in abundance or system functioning over either time or space, and often involving comparisons across and between different areas or systems.
- *Experiments*, including both those in the lab and in the field.
- *Mathematical models* that capture some component of ecological interactions, function, and structure.

Ecologists often combine two or more of these approaches. For instance, they may use models or inferences from comparative observations across systems to inform experiments, or they may use experiments and observations to calibrate models.

observations and field experiments

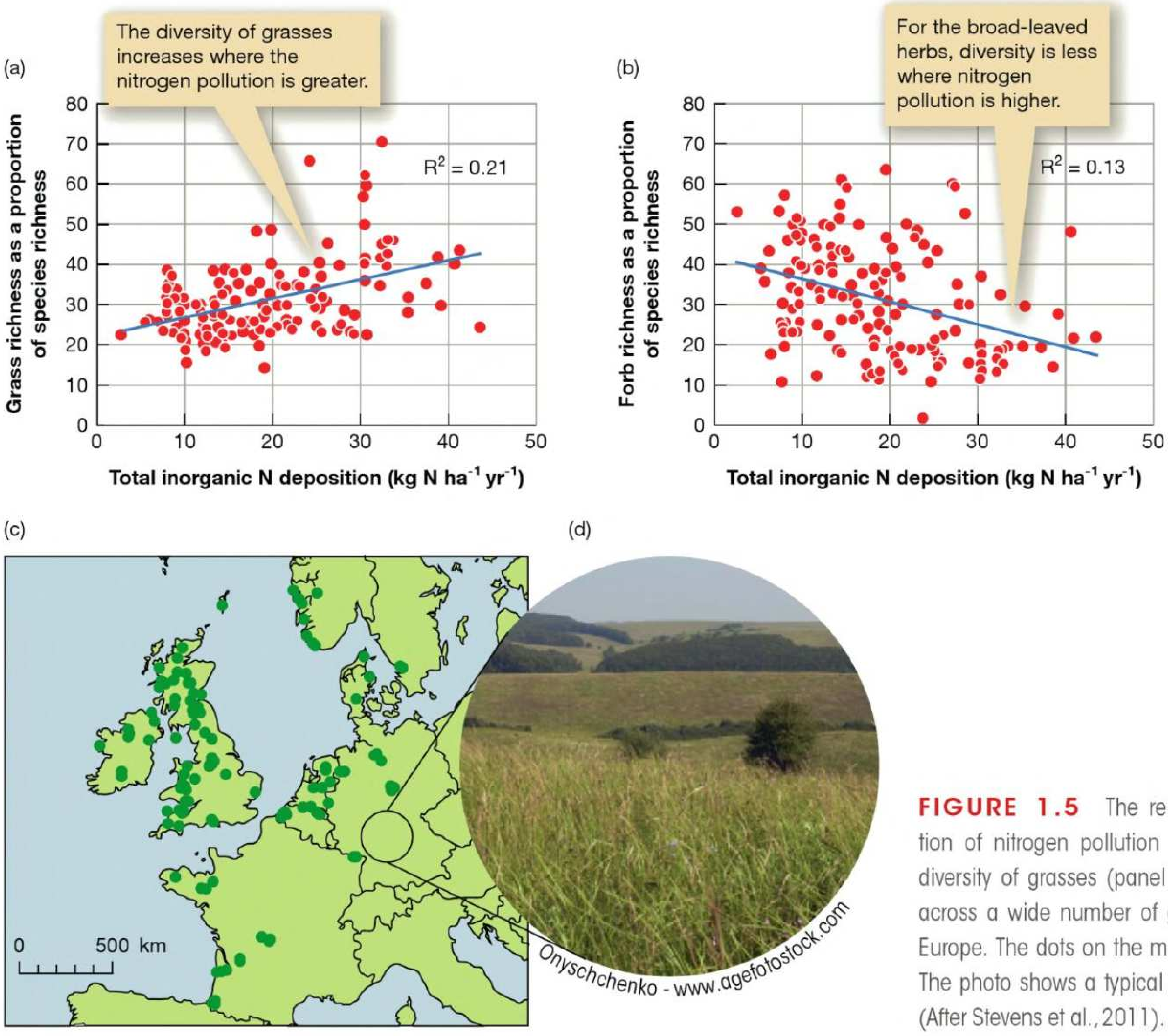
Many ecological studies include careful observation and monitoring in the natural environment, for instance, of the changing abundance of one or more species over time, or over space, or both. In this way, ecologists may establish patterns, for example, that red grouse (birds shot for 'sport') exhibit regular cycles in abundance peaking every 4 or 5 years. Documenting the pattern does not provide explanation for the cause of the cycle, but it is a start toward understanding. A next step might be to development one or more hypotheses to explain the pattern: for instance, perhaps the 4- to 5-year cycle is caused by a gradual accumulation of parasitic worms in the grouse populations over this period of time. A **manipulative field experiment** is one approach to test such a hypothesis, in this case by ridding the grouse of the parasites and monitoring whether the 4- to 5-year population cycle persists. Treating the grouse for their parasites strongly dampens the population cycle, giving strong support to this hypothesis (Hudson, Dobson, & Newborn, 1998).

We can also use **comparative field observations** to test hypotheses. That is, we explicitly compare the same sort of data from many different sites. Consider the question whether the amount of nitrogen pollution deposited onto the landscape in rain, snow, dust, and gases affects the biodiversity of grassland communities (nitrogen is a major component of acid rain). The extent of this nitrogen pollution varies greatly over the landscape of Europe, so we can test the hypothesis that more nitrogen pollution lowers biodiversity by comparing diversity in different grasslands receiving different inputs of nitrogen pollution from the atmosphere (Figure 1.5). The diversity of forbs (broad-leaved herbs) is indeed lower when nitrogen pollution is greater, but the diversity of grasses increases with increasing nitrogen pollution. The scatter in the relationships is great, but the relationships are nonetheless significant. (We will discuss what we mean by "significant" later in this chapter.) The scatter is undoubtedly the result of other factors across the landscape – in addition to the nitrogen pollution – that might also affect diversity, such as types of soil, differences in precipitation and other climate variables, and other types of pollution and disturbance.

observations can test hypotheses

Rather than relying on this comparative observational approach, we could conduct a manipulative field experiment to test the hypothesis that nitrogen pollution affects biodiversity. The result of one such experiment shows a very tight and pronounced effect of increasing nitrogen supply on biodiversity (expressed as species richness, the number of species) after just 4 years of nitrogen addition (Figures 1.6). This experiment has an advantage over the comparative observational study, in that other confounding variables – soil type, climate, disturbance history – are held constant between treatments and hence eliminated, and this probably explains the tighter relationship between nitrogen and diversity. On the other hand, the experiment is conducted on just one type of soil, with one type of climate and disturbance history, and over a fairly limited period of time (4 years in this case), and so the result may not fully apply to other areas and to longer time scales. Both manipulative experiments and observations are critical to ecology, and ecologists gain confidence in their understanding of nature when the two approaches lead to similar conclusions.

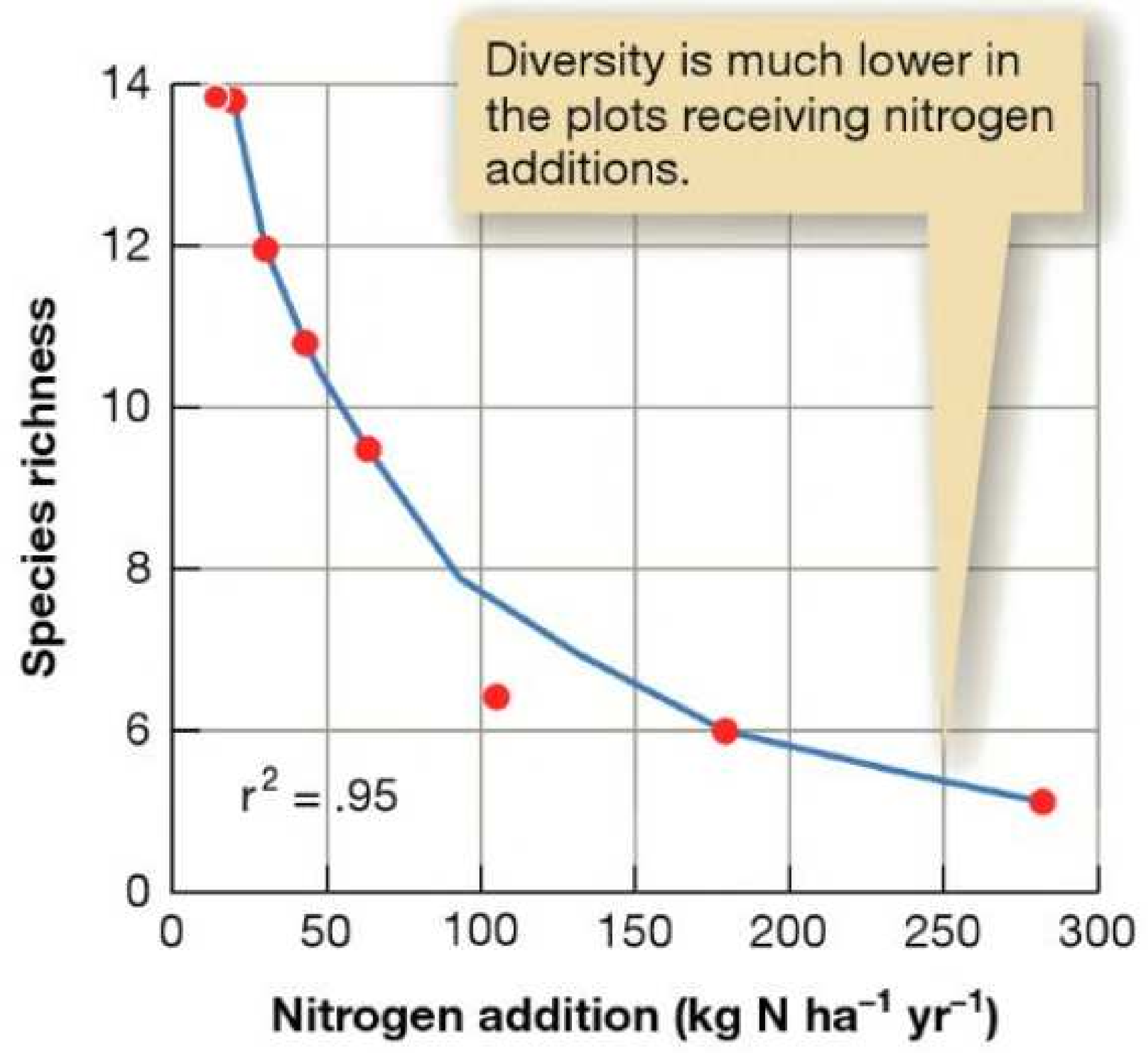
Why might nitrogen affect plant biodiversity? One hypothesis is that the effect is one of fertilization, with plants growing more as the nitrogen supply increases, and this leading to less diversity as species that grow particularly well come to dominate the community and shade out other plants. A creative experiment gave some



The diversity of grasses increases where the nitrogen pollution is greater.

For the broad-leaved herbs, diversity is less where nitrogen pollution is higher.

FIGURE 1.5 The relationship between deposition of nitrogen pollution from the atmosphere and diversity of grasses (panel "a") and forbs (panel "b") across a wide number of grasslands on acid soils in Europe. The dots on the map show the sites sampled. The photo shows a typical grassland from the Ukraine (After Stevens et al., 2011).



Diversity is much lower in the plots receiving nitrogen additions.

FIGURE 1.6 Experimental addition of nitrogen to a grassland in Minnesota reduces species diversity. Reprinted from Huston (1997), based on data in Tilman (1996).

preliminary support for this hypothesis: when artificial light was supplied to the shaded plants of the understory in nitrogen fertilized plots, biodiversity was maintained despite the higher nitrogen (Hautier et al., 2009).

laboratory experiments and mathematical models

Perhaps less obviously, ecologists also often turn to laboratory systems or to mathematical models designed to capture ecological processes. These have played a crucial role in the development of ecology, and they are certain to continue to do so. Field experiments are almost inevitably costly and difficult to carry out. Moreover, even if time and expense were not issues, natural field systems may simply be too complex to allow us to tease apart the consequences of the many different processes that may be going on. Are the intestinal worms actually capable of having an effect on reproduction or mortality of individual grouse? How do light and nitrogen interact to regulate the growth rate of the various species in a grassland ecosystem? Controlled laboratory experiments are often the best way to provide answers to specific questions that are key parts of an overall explanation of the complex situation in the field.

Of course, the complexity of natural ecological communities may simply make it inappropriate for an simple laboratory systems . . .

ecologist to dive straight into them in search of understanding. We may wish to explain the structure and dynamics of a particular community of 20 animal and plant species comprising various competitors, predators, parasites, and so on (relatively speaking, a community of remarkable simplicity). But we have little hope of doing so unless we already have some basic understanding of even simpler communities of just one predator and one prey species, or two competitors, or (especially ambitious) two competitors that also share a common predator. For this, it is usually most appropriate to construct, for our own convenience, simple laboratory systems that can act as benchmarks or jumping-off points in our search for understanding.

. . . and mathematical models

What is more, you have only to ask anyone who has tried to rear caterpillar eggs, or take a cohort of shrub cuttings through to maturity, to discover that even the simplest ecological communities may not be easy to maintain or keep free of unwanted pathogens, predators, or competitors. Nor is it necessarily possible to construct precisely the particular, simple, artificial community that interests you; nor to subject it to precisely the conditions or the perturbation of interest. In many cases, therefore, there is much to be gained from the analysis of mathematical models of ecological communities: constructed and manipulated according to the ecologist's design.

On the other hand, although a major aim of science is to simplify, and thereby make it easier to understand the complexity of the real world, ultimately it is the real world that we are interested in. The worth of models and simple laboratory experiments must always be judged in terms of the light they throw on the working of more natural systems. They are a means to an end—never an end in themselves. Like all scientists, ecologists need to 'seek simplicity, but distrust it' (Whitehead, 1953).

Statistics and scientific rigor

For a scientist to take offense at some popular phrase or saying is to invite accusations of a lack of a sense of humor. But it is difficult to remain calm in the face of phrases such as 'There are lies, damn lies and statistics' or 'You can prove anything with statistics.' Statistics *are* regularly misused, but more often in the public media and by those who may seek to manipulate popular opinion, and rarely if ever in the scientific literature. You should not mistrust statistics. Rather, you should understand their strengths and limitations. An essential point: you cannot *prove* anything with statistics. Rather, statistical analysis allows us to attach a level of confidence to our conclusions. Ecology, like all science, is a search not for statements that have been 'proved to be true' but for conclusions in which we can be confident.

ecology: a search for conclusions in which we can be confident

What distinguishes science – what makes science rigorous – is that it is based not simply on assertions, but rather on conclusions resulting from investigations that test specific hypotheses, and to which we can attach a level of confidence, measured on an agreed-upon scale.

ecologists must think ahead

Statistical analyses are carried out after data have been collected, and they help us to interpret those data. Really good science, though, requires forethought. Ecologists, like all scientists, must know what they are doing, and why they are doing it, *while* they are doing it. Ecologists must plan, so as to be confident that they will collect the right kind of data, and a sufficient amount of data, to address the question they hope to answer. As discussed in Box 1.2, more data are required to obtain statistically significant results when the relationship being tested is a weak one, or when the relationship is confounded by other factors, as is likely the case for the relationship between nitrogen deposition and diversity illustrated in Figure 1.5.

replication in experiments

Many ecological field experiments rely on a large number of replicates for each treatment, and this increases the likelihood of obtaining statistically significant results. For example, ecologists experimentally testing the effect of nitrogen deposition on plant diversity in grasslands might have 8 different levels of nitrogen inputs, with 10 different plots for each treatment (a total of 80 plots). However, replication can be expensive and time consuming, particularly if the ecologists include in the responses they monitor processes that are difficult to measure. Determining the biomass of the plants at the end of the experiment is relatively simple (cutting, drying, and weighing); characterizing the diversity of the community is more difficult, particularly if the diversity is high with many species potentially present; measuring the rate at which each species is assimilating nitrogen is far, far more difficult and time consuming. Most experimentalists feel a constant tug between having a large number of replicates and keeping their experiments doable.

replication in whole-ecosystem experiments

As noted by David Schindler (1998), experiments can often involve a trade-off between realism and replication. Smaller scale experiments – such as small plots of grassland, or

1.2 Quantitative Aspects

Interpreting probabilities

Ecologists need to know, as do any scientists dealing with sets of data, what conclusions can be drawn from those data. Imagine we are interested in determining whether high abundances of a pest insect in summer are associated with high temperatures the previous spring, and imagine we have data on summer insect abundances and mean spring temperatures for each of a number of years. How do we use statistical analysis to conclude, with a stated degree of confidence, either than there is or is not a relationship between the spring temperature and summer insect numbers?

Null hypotheses and *P*-values

To carry out a statistical test we first need a *null hypothesis*, which simply means in this case that there is *no* association; that is, no association between insect abundance and temperature. The statistical test (stated simply) then generates a probability (a *P*-value) of getting a data set like ours if the null hypothesis is correct.

Suppose the data were like those in Figure 1.7a. The probability generated by a statistical test of association on these data is $P = 0.5$ (equivalently 50%). This means that, if the null hypothesis really was correct (no association), then 50% of studies like ours should generate just such a data set, or one even further from the null hypothesis. We therefore could have no confidence in any claim that there *was* an association.

Suppose, however, that the data were like those in Figure 1.7b, where the *P*-value is 0.001 (0.1%). This would mean that such a data set (or one even further from the null hypothesis) could be expected in only 0.1% of similar studies if there was really no association. In other words, either something very improbable has occurred, or there *was* an association between insect abundance and spring temperature. Thus, since we do not expect highly improbable events to occur, we can have a high degree of confidence in the claim that there *was* an association between abundance and temperature.

Significance testing

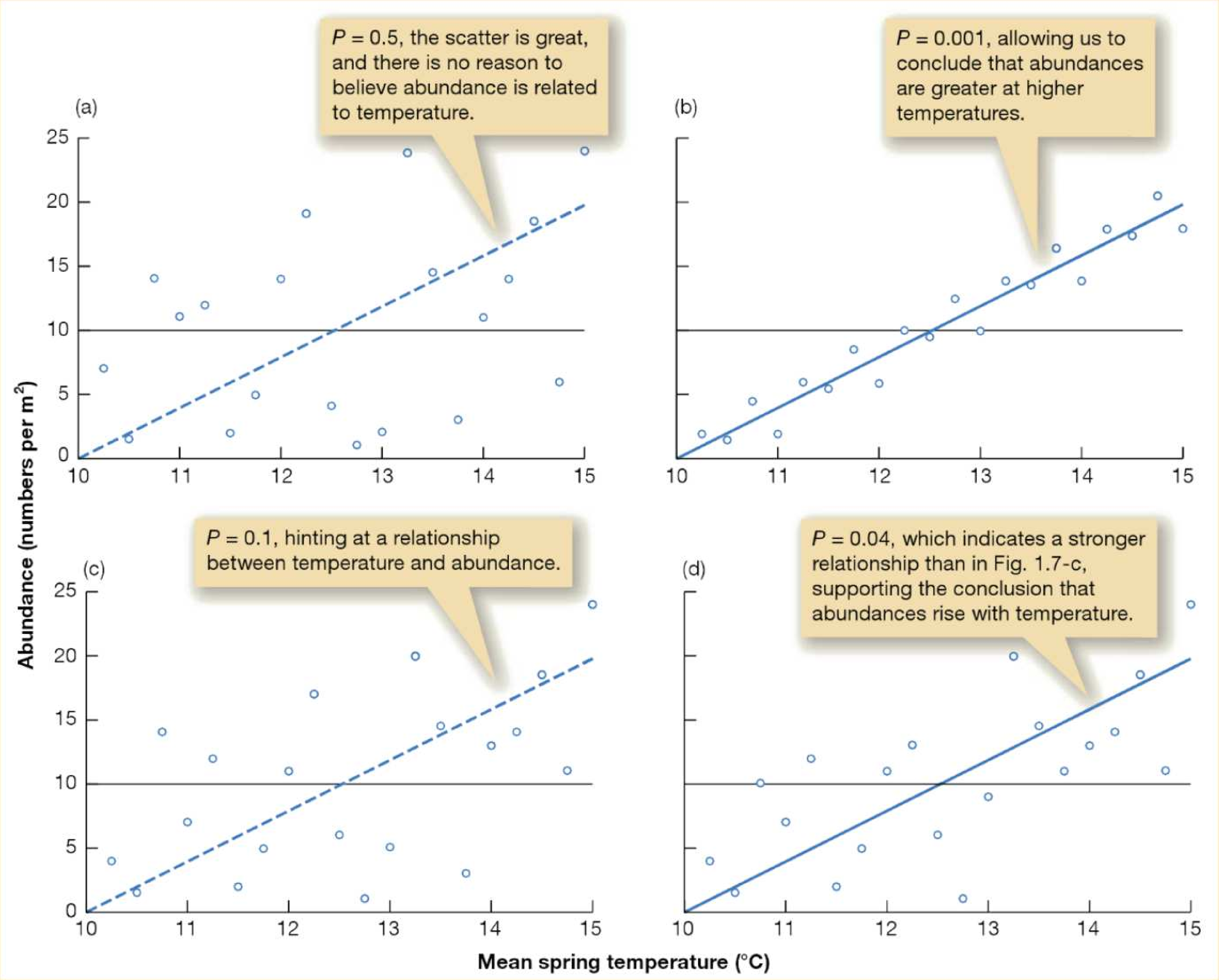
Both 50% and 0.01%, though, make things easy for us. Where, between the two, do we draw the line? There is no absolute answer to this, but scientists and statisticians have established a convention in *significance testing*, which says that if *P* is less than 0.05 (5%), written $P < 0.05$ (e.g., Figure 1.7d), then results are described as 'statistically significant' and confidence can be placed in the effect being examined; whereas if $P > 0.05$, then there is no statistical foundation for claiming the effect exists (e.g., Figure 1.7c). A further elaboration of the convention often describes results with $P < 0.01$ as 'highly significant.'

'Insignificant' results?

Some effects are naturally strong (there is a powerful association between people's weight and their height) and others are weak (the association between people's weight and their risk of heart disease is real but weak, since weight is only one of many important factors). More data are needed to establish support for a weak effect than for a strong one. Hence a *P*-value of greater than 0.05 (lack of statistical significance) may mean one of two things in an ecological study:

1. There really is no effect of ecological importance.
2. The data are simply not good enough, or there are not enough of them, to support the effect even though it exists, possibly because the effect itself is real but weak.

Throughout this book, then, studies of a wide range of types are described, and their results often have *P*-values attached to them. Remember that statements like $P < 0.05$ and $P < 0.01$ mean that these are studies where: (i) sufficient data have been collected to establish a conclusion in which we can be confident; (ii) that confidence has been established by agreed means (statistical testing); and (iii) confidence is being measured on an agreed and interpretable scale.



P = 0.5, the scatter is great, and there is no reason to believe abundance is related to temperature.

P = 0.001, allowing us to conclude that abundances are greater at higher temperatures.

P = 0.1, hinting at a relationship between temperature and abundance.

P = 0.04, which indicates a stronger relationship than in Fig. 1.7-c, supporting the conclusion that abundances rise with temperature.

FIGURE 1.7 The results from four hypothetical studies of the relationship between insect pest abundance in summer and mean temperature the previous spring. In each case, the points are the data actually collected. Horizontal lines represent the *null hypothesis* – that there is no association between abundance and temperature, and thus the best estimate of expected insect abundance, irrespective of spring temperature, is the mean insect abundance overall. The second line is the *line of best fit* to the data, which in each case offers some suggestion that abundance rises as temperature rises. However, whether we can be confident in concluding that abundance does rise with temperature depends, as explained in the text, on statistical tests applied to the data sets. (a) The suggestion of a relationship is weak ($P = 0.5$). There are no good grounds for concluding that the true relationship differs from that supposed by the null hypothesis and no grounds for concluding that abundance is related to temperature. (b) The relationship is strong ($P = 0.001$) and we can be confident in concluding that abundance increases with temperature. (c) The results are suggestive ($P = 0.1$) but it would not be safe to conclude from them that abundance rises with temperature. (d) The results are not vastly different from those in (c) but are powerful enough ($P = 0.04$, i.e., $P < 0.05$) for the conclusion that abundance rises with temperature to be considered safe.

Standard errors and confidence intervals

Another way in which our confidence in results is assessed is through reference to 'standard errors,' which statistical tests often allow to be attached either to mean values calculated from a set of observations or to slopes of lines like those in Figure 1.7. These mean values and slopes can only ever be estimates of the 'true' mean value or slope, because they are calculated from data that are only a sample of all the imaginable items of data that could be collected. The standard error, then, sets a band around the estimated value within which the true value can be expected to lie, with a given, stated probability. In particular, there is a 95% probability that the true mean lies within roughly two standard errors (2 SE) of the estimated mean; we call this the *95% confidence interval*.

Large standard errors (little confidence in the estimated value) can arise when data are, for whatever reason, highly variable; but they may also be due to only a small data set having been collected. Standard errors are smaller, and confidence in estimates greater, *both* when data are more consistent (less variable) *and* when there are more data.