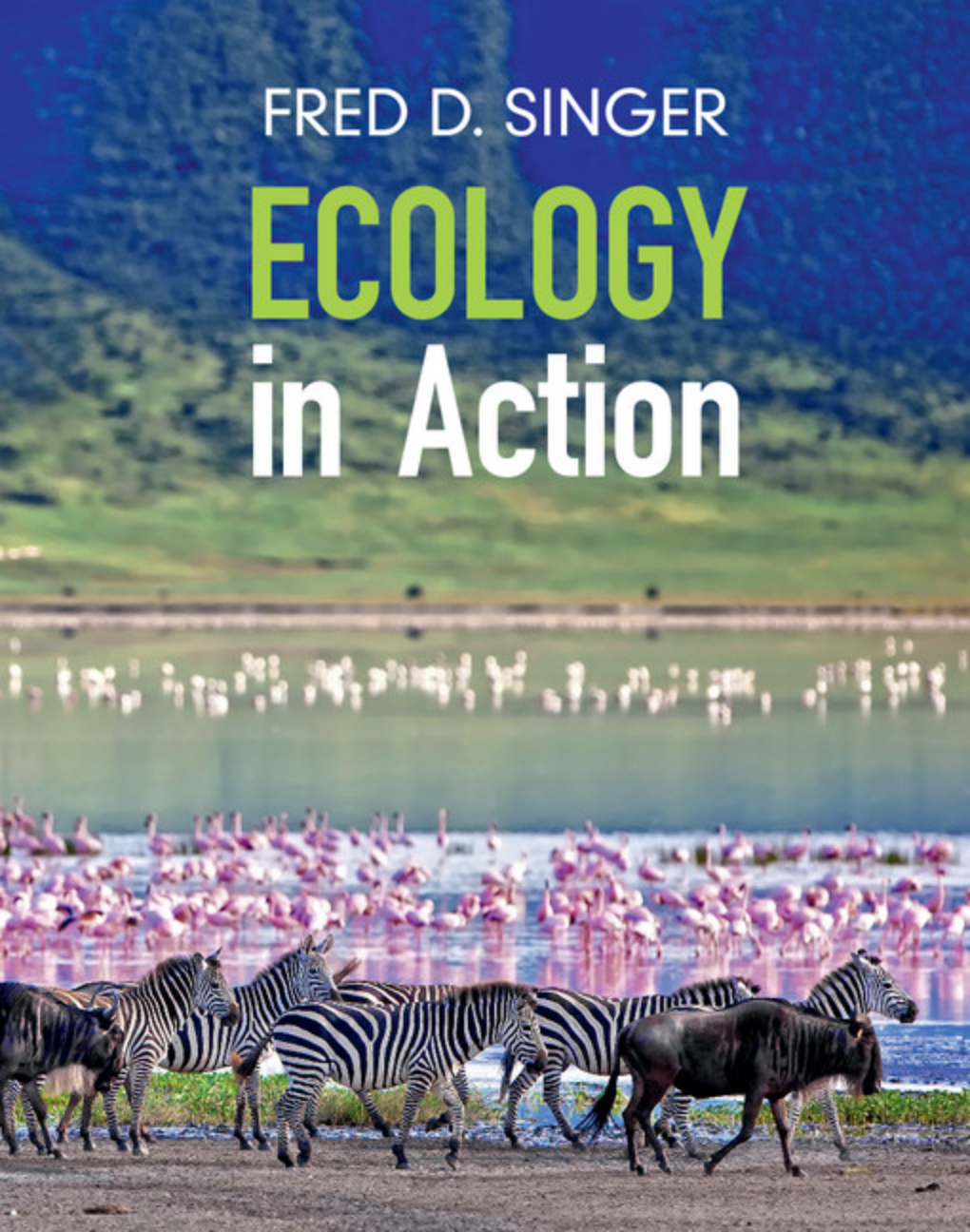
FRED D. SINGER

ECOLOGY in Action



Ecology in Action

Taking a fresh approach to integrating key concepts and research processes, this undergraduate textbook encourages students to develop an understanding of how ecologists raise and answer real-world questions. Four unique chapters describe the development and evolution of different research programs in each of ecology's core areas, showing students that research is undertaken by real people who are profoundly influenced by their social and political environments.

Beginning with a case study to capture student interest, each chapter emphasizes the linkage between observations, ideas, questions, hypotheses, predictions, results, and conclusions. Discussion questions, integrated within the text, encourage active participation and a range of end-of-chapter questions reinforce knowledge and encourage application of analytical and critical thinking skills to real ecological questions. Students are asked to analyse and interpret real data, with support from online tutorials that show them how to use the R programming language for statistical analysis.

Fred D. Singer is Professor Emeritus of Biology at Radford University, where he began teaching in 1989. A committed teacher, he developed research programs on the behavioral and community ecology of spiders, dragonflies, and zebrafish, while also collaborating with several colleagues to promote active learning as part of an ongoing research program on new approaches to teaching. In 2000, in recognition of his dual research programs, he was awarded the Radford Foundation Award for Creative Scholarship. He has taught approximately 20 different courses, including general ecology, field ecology, and climate change ecology, using the philosophy that the best learning occurs when students deal with real experiments and real data.

"In contrast to most other science textbooks, Singer's book... emphasizes the roles of curiosity and careful observation in discovering hypotheses that are worth testing. This will be an ideal ecology text for anyone who would like to help students appreciate the excitement of scientific creativity."

Robert Askins, Connecticut College, USA

"... an excellent resource for students and young professionals... Singer provides a detailed overview of the foundations of ecology while he seamlessly incorporates an illuminating insight into how ecology is done. This is a welcome perspective in an ecological textbook since many contemporary titles heavily focus on abstract ecological concepts."

Joris van der Ham, George Mason University, USA

"... written in a very student-friendly manner... Case studies incorporated into the text provide a much needed basis for the comprehension of difficult ecological concepts."

Troy Ladine, East Texas Baptist University, USA

"It is very refreshing to read a new textbook, rather than a new edition of an old textbook... The case studies bring the chapters to life, which contributes to making this a very interesting read."

Judith Lock, University of Southampton, UK

"... I'm excited by this book. It is refreshing and interesting with unique examples and clean artwork... The inclusion of an assortment of end of chapter questions... that run the gamut from application to data analysis will give students practice and insight into both critical thinking and quantitative skills that most books do not."

Lynn Mahaffy, University of Delaware, USA

"This book is a breath of fresh air. Singer has provided a clear and compelling text that will engage students at every level of knowledge."

Holly Porter-Morgan, City University of New York, USA

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Fred D. Singer
Radford University, Virginia

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To Cindy for true love and grace, to Jed and Alison who kept the questions coming
when they were young and have metamorphosed into awesome adults, and to my canine companions,
Maia, Sheik, and Cheyanne, who somehow knew when my face needed a good licking.

CONTENTS

PREFACE

I taught at a university where teaching is a professor's major action. Coming from a research background, I was somewhat surprised at this emphasis, but after immersing myself in teaching for 25 years, I decided that it was time to share my ideas. Over those years, I learned that students (and people in general) learn best when they are actively doing things. One of my goals in writing this text is to get students actively involved in what ecologists do, to learn where knowledge comes from, to learn how to ask questions, how to approach answering these questions, and to expect that the answer will be somewhat unsatisfactory and will generate a new series of stimulating questions. *Ecology in Action* is the title of this book but it is also a philosophy of learning, and a statement of hope for future times when scientifically sound ecological action will be essential.

Humans are natural ecologists. We are great observers of phenomena of all types, we develop expectations of what will happen under a set of conditions, and we recognize patterns. We also love to do experiments. Unfortunately, some of the experiments we are conducting today are very risky. We are increasing atmospheric carbon dioxide levels and collecting data on the effects of climate change. We have doubled the amount of fixed nitrogen in global systems and are collecting data on ecosystem response. We are breaking up large continuous habitat into small fragments and observing how populations of endangered species respond to their diminished habitat. The good news is that we are collecting at least some of the relevant data. My hope for the future is that everyone who reads this book will be able to interpret these data effectively, so they can take appropriate action as scientists or as private citizens.

MY GOALS FOR THE READER

I wrote this book for biology majors who have a year of introductory biology and at least one semester of general chemistry. Ecology is a young and growing science, and the informational content is increasing explosively.

After reading this book, students should be able to:

- understand the key concepts in ecology.
- learn how to learn, how to identify what is important, and how to go about finding answers to questions.
- understand how everything we know about ecology started as an idea and metamorphosed into knowledge; in other words, each reader will learn about ecological process. The approach throughout the book is to integrate content and process in a manner that promotes a much deeper understanding of core areas of ecology.
- appreciate how research can be an extension or reflection of an ecologist's personality, values, or social situation. The history of an idea is presented, so that students can follow the logical development of an ecological concept through time. Students learn how ecologists think of their questions, and students then become empowered to think of their own questions.
- recognize that the natural world is awesome and fascinating. Examples are carefully chosen to engage students, and introduce the reader to novel species from parts of the world that they may have never heard of. At the same time students learn that humans are influencing natural systems in many profound ways. Numerous explicit connections between ecological concepts and ecological applications are made, enabling students to use their knowledge to treat the world in a sustainable manner.

ORGANIZATION AND STRUCTURE OF THE BOOK

Ecology in Action has 24 chapters, beginning with an introductory part that presents major ecological questions and a discussion of the physical environment. Tony Sinclair's research in the Serengeti is highlighted in the first chapter, as the questions that he asks span the entire biological hierarchy, from molecules to global ecology. The remainder of the text is divided into four primary parts: organismal and evolutionary ecology, population ecology, community ecology, and ecosystem and global ecology. Each part has two major components. The bulk of each part (four or five major concepts chapters) presents students with the major concepts of each topic, and the supporting experimentation/observations related to each major concept. The final chapter of each part immerses the students in a research program of one individual or group of individuals that made important contributions to the field.

Major concepts chapters

Each major concepts chapter begins with an introduction that describes one element of a case study that will be discussed in some detail in the chapter. In addition, the introduction provides a roadmap of the major concepts that will be explored and concludes with a list of 3–5 key questions that will be addressed as the chapter's major focus. I gave preference to case studies that highlighted fascinating natural history, that taught an important ecological concept, that demonstrated important aspects of ecological process, and that showed how ideas changed over time. The main body of each chapter answers the initial 3–5 questions in the context of research studies, which were chosen based on three criteria: (1) Do they clearly demonstrate an important concept? (2) Are they classics that show where ideas or new methods originated? (3) Are they recent or ongoing? Recent

research is emphasized to convey the message that ecological knowledge is always evolving, that though we have just made a new discovery, there is now a new pressing question that needs to be addressed. At the end of each chapter is a *Revisit* section, which returns to the initial case study and address some of the issues it raises in light of what students have learned in the chapter.

All chapters have a strong emphasis on data analysis and interpretation. In my experience, the greatest challenge for many students is drawing reasonable conclusions from an experiment or observation. All chapters contain questions that prompt students to analyse data. These questions require certain analytic skills that students usually learn in an introductory statistics course, or in their science laboratories. To make sure all students can solve these problems, the text provides several opportunities to learn or review all of the necessary analytic approaches.

Research program chapters

One distinguishing feature of this text is the chapters that introduce students to research programs. Because we tend to do labs in 3 hour blocks of time, students gain a mistaken impression about how science is actually done. My goal with these research program chapters is to allow students to gain a deeper understanding of answers to the following questions:

1. How does a research program differ from a research project or question?
2. How do ecologists think of their questions?
3. How do ecologists and the scientific community decide what is important, and what is trivial?
4. How are research findings evaluated?
5. What factors determine a successful research program?
6. How is ecological research an extension or reflection of a scientist's personality?
7. How do ecologists work at different levels of the ecological hierarchy, and how do they collaborate with other ecologists and other scientists from different fields?

I present the research programs of four different ecologists or groups of ecologists who are major contributors to the discipline. Diversity of approach is important, so the following researchers are featured, in part because they used philosophically different approaches to ask and answer questions: organismal and evolutionary ecology – Bernd Heinrich; population ecology – Jane Goodall/Anne Pusey; community ecology – Dan Janzen/Winnie Hallwachs; ecosystem and global ecology – Jane Lubchenco. In addition to reading many of their papers and books, I conducted lengthy in-person interviews with each researcher, and also traveled with Anne Pusey to Tanzania to meet the famous chimpanzees of Gombe. On a personal level, it was awesome to meet these people (and chimpanzees) and to gain an understanding of why they are so successful.

PEDAGOGICAL FEATURES

Emphasis on ecological processes

Having read all of the books on the market (numerous times), I am quite confident that none explores ecological process as much as *Ecology in Action*. The four research program chapters have a heavy emphasis on ecological process, and this is carried on throughout the major concepts chapters to show students where ideas come from and how they develop over time. Through repeated exposure, students understand the relationship between a hypothesis and a prediction, how to analyse data, and how to draw logical conclusions.

Strong evolutionary foundation

Evolution is introduced early – initially in Chapter 1, and extensively in Chapter 3. Students learn skills that are rarely taught in ecology texts, for example, how to make and interpret an evolutionary tree and how to use molecular data to make evolutionary inferences. Having established a strong evolutionary foundation, students can then understand more advanced topics that are presented in almost every other chapter.

Historical perspective

People are natural storytellers and story listeners. The historical perspective used in the book immerses students in the history of an idea, so that they understand not only where an idea originated, but also how it changed over time and how it is related to other ideas that exist today. In the process, they also learn how to ask scientific questions and get considerable experience with how ecologists come up with their answers. Students learn that many answers are tentative, or only apply under restricted conditions.

Case studies

Engaging case studies begin each major concepts chapter and are revisited at the end of the chapter in light of the issues raised in the main text.

Key questions

Key questions are listed at the beginning of each chapter and provide a roadmap to help students prepare for and structure their learning. Summaries at the end of each chapter recap the key points.

Artwork

Illustrations are carefully designed to allow students to easily take away the key information they need and photographs help bring the subject to life.

Key terms

Key terms are highlighted in bold so that students can easily identify them. Definitions are provided in a comprehensive glossary at the end of the book.

Thinking ecologically questions

Each chapter has about three or four *Thinking ecologically* questions embedded in the text, allowing students to think about a problem while reading about it, rather than coming back to it at a later time. When I teach, I often require students to work on a *Thinking ecologically* question in class as soon as I finish the topic as a way of reinforcing the concept. These questions are usually open-ended; they develop a student's critical thinking skills and they can be easily read around without disrupting the flow of the narrative, which allows instructors to choose which questions to assign.

End-of-chapter questions

Review questions

About five or six review questions require students to review and summarize the major concepts, helping them retain what they have learned.

Synthesis and application questions

About 5–10 questions require students to use higher order thinking skills to apply what they've learned in the chapter. Students may be asked to design an experiment or a series of systematic observations to test a particular hypothesis, and to articulate predictions generated by the hypothesis. Alternatively, students may be asked to develop an analogy between what they just learned and a concept that they learned in a previous chapter; or students may be asked to apply a concept that they learned in the chapter to a different context.

Analyse the data

These end-of-chapter questions present students with real data sets (or occasionally graphs) and ask them to answer a question based on these data. In some cases the data were already presented in the text in a different context, while in other cases students are provided with new data sets to work from. Students are usually asked to interpret their findings in the context of a concept that was introduced in the chapter.

Dealing with data

To help students deal with data analysis a special embedded box feature, *Dealing with data*, is included primarily in the early chapters. *Dealing with data* boxes present analytic concepts such as extrapolation, error reduction, and data transformation, and applied statistical techniques beginning with calculating means and standard errors, branching into t-tests, one-way ANOVA, simple correlation and regression analysis, chi-square, and several other commonly used statistical approaches. There are also discipline-specific *Dealing with data* boxes that teach students how particular methodologies, such as molecular biology databases, geographic information systems, and stable isotope analyses, are used by ecologists to answer important questions.

Further reading

Each chapter concludes with 4–6 suggested readings that are a suitable basis for further discussion. These readings are mostly recent publications that present novel findings, but a few classics are also included to give students a sense of ecological history.

ONLINE RESOURCES

Supporting online resources for the book can be found at www.cambridge.org/ecologyinaction

For students and instructors

- All of the figures in jpeg (and PowerPoint) format
- Online glossary
- Statistics tutorial: an introduction to R.

One feature that distinguishes this text from some others is the *Analyse the data* feature that asks students to analyse real data sets and draw conclusions based on their analysis. To do so requires using elementary statistical analyses, so the website has a tutorial that, in conjunction with the *Dealing with data* feature, uses data sets in the text to teach the basics of statistics using the R programming language and software environment. R is free, and its use is expanding tremendously within the ecological community. Being able to use R will be a major boon to any ecology student moving forward. Much thanks to Dr Edd Hammill for developing a superb tutorial that integrates seamlessly with *Ecology in Action*.

For instructors only

- Solutions to questions.

The website provides answers to the *Analyse the data* questions.

Thinking ecologically and *Synthesis and application* questions are, for the most part, open-ended. As such, it is impossible to give an answer key, but some suggested approaches to dealing with each question are provided. I am also hoping to hear interesting ideas from students and instructors, for suggestions on the book and additional online resources that might be useful for teaching and learning.

ACKNOWLEDGMENTS

I'd like to thank ecologists around the world for doing the research that I've discussed, for doing so much more research that I could not discuss, and for persistently pushing the frontiers of our understanding of the natural world. Jane Goodall, Winnie Hallwachs, Bernd Heinrich, Dan Janzen, Jane Lubchenco, Anne Pusey and Tony Sinclair gave me large chunks of their time, so that I could hear their story and share it with you. I am very grateful to them.

My wife, Cindy Miller, carefully read the first draft and identified numerous mistakes, contradictions, omissions, and general cases of fuzziness before I passed the first draft to my development editor, Mary Catherine Hager. Mary Catherine further refined the first and second drafts, helping to me to write with a more consistent voice and coercing me to use a more linear approach in my writing. The folks at Cambridge University Press were awesome at every stage of the process. Dom Lewis adopted the project and has steadfastly encouraged me at every step. Claire Eudall coordinated my writing and research, and mostly kept me on schedule. Claire and Natasha Lewis sourced images and permissions, Charlie Howell co-ordinated the illustrations, text design and cover, and Jess Murphy and Rachel Cox managed the book through production with support from Megan Waddington.

Approaches to teaching don't develop within a vacuum; instead they are nurtured by experiences with students, colleagues, and even administrators. Edd Hamill of Utah State University wrote a spectacular tutorial that guides students through the R programming language and software environment. At Radford University, Joel Hagen, Chuck Kugler, and later Donna Boyd, Rich Murphy, Bob Sheehy, and about 5000 students taught me many things about teaching. One of those 5000 students, Daniel Metz, wrote out answers to many of the *Thinking ecologically* and *End-of-chapter questions*. Bud Bennett chased down hundreds of obscure articles and books through interlibrary loans. Matt Lee provided iconic help with some design issues. Lastly, Sam Minner, Orion Rogers, and Joe Scartelli provided financial support during sabbaticals and some summers.

When I was concerned about a particular chapter, I turned it over to other readers for help. These informal reviewers were David Blockstein, Judy Guinan, Joel Hagen, Chuck Kugler, and Mac Post. When I was puzzled about a study, I asked the study's lead author for help, and these researchers were almost universally delighted to provide clarification. Particularly helpful were Stanton Braude, Tim Brodribb, Jim Clark, William Cooper, Charlie Crisafulli, Jim Elser, Marc Fourrier, Jim Galloway, Philip Groom, Elizabeth Howard, Scott Kraus, William Laurance, Kim Mouritsem, Vojtech Novotny, Karen Oberhauser, Susan Riechert, Bill Ripple, W. H. Schlessinger, Rich Kliman, Paul Sherman, and Martin Wikelski.

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PART I

Introduction and the physical environment

Chapter 1

What is ecology in action?

INTRODUCTION

The Serengeti-Mara ecosystem in northern Tanzania and southern Kenya is a showcase of vertebrate life, home to over 650 species of birds and 79 species of large mammals. Equally impressive, many of the species are present in enormous quantities. In the early 1960s, there were approximately 250 000 wildebeest (*Connochaetes taurinus*), 200 000 zebras (*Equus burchelli*), 30 000 buffalo (*Syncerus caffer*), and 750 000 Thomson's gazelles (*Gazella thomsoni*) roaming through the ecosystem. Every year, the zebras, wildebeest, and gazelles spend the wet season in the southeast portion of the Serengeti, eating the grasses and herbaceous plants that grew during the wet season, which extends from November through May. These grasses have very high levels of nutrients, which are particularly important to pregnant females who give birth in the middle of the rainy season and begin the nutrient-demanding process of lactation. As rainfall diminishes in June, many of the zebras, wildebeest, and gazelles migrate to the northwest portion of the ecosystem, munching on taller but less nutritious grasses that grow in the much wetter northern and western plains. When the wet season returns in November, so do the large mammals that have survived the dry season, to begin the cycle anew.

Many researchers have converged on the Serengeti to answer important ecological questions. We will follow in their footsteps, using the Serengeti ecosystem to gain an understanding of what types of questions ecologists ask. We will then see how ecologists use the entire scientific toolbox to answer these questions, but that ecological questions, because they tend to be so broad, may require a researcher willing to tackle numerous levels of the biological hierarchy. Let's go back to the beginnings of ecosystem studies in the Serengeti.

KEY QUESTIONS

CASE STUDY: Birth of a research program

The western world was introduced to the Serengeti by a German father-and-son team, Bernhard and Michael Grzimek, who together created a movie, *Serengeti Shall not Die*, which was wildly popular around Europe. Tragically, in 1959, as Michael filmed from a low-flying airplane (Figure 1.1a), a griffon vulture flew into the plane, causing it to crash and killing him. Michael was buried atop Ngorongoro Crater, east of the Serengeti; his epitaph reads "He gave all he possessed including his life for the wild animals of Africa." His father joined him at the same site almost 30 years later (Figure 1.1b).

Though Michael gave his life for the Serengeti, he and his father gave birth to a growing global awareness of the beauty, drama, and potential plight of this vast ecosystem, and in particular they uncovered many features of the large mammal migrations. Bernhard, as director of the Frankfurt Zoological Garden, used proceeds from the movie to help fund Serengeti research. In addition, John Owen, then director of Tanzania National Park, used his position to establish the Serengeti Research Institute in 1961, which funded three scientists to continue working on the wildebeest migrations. Within a few years, several other researchers joined the Institute and began investigating other parts of the ecosystem.

Meanwhile, in England, Tony Sinclair was having some issues about what he was going to do for the rest of his life. His father, a New Zealander employed as a judge for the British government, was stationed primarily in Tanzania during the first 10 years of Sinclair's life. There, Tony spent much of his time outdoors hanging out with his friends, learning about the culture, becoming fluent in Swahili, and discovering the large diversity of non-human animals that lived in this ecoregion. At age 10, Tony was shipped off to England to continue his education. To him a career in biology meant medicine, and given his disdain for illnesses of all kinds, he entered a program in engineering, math, and physics. But these fields did not captivate him, and one day, at age 16, he just said, "What am I doing? I can do biology that's not medicine – I can do zoology."

Having switched his career path, he knew he needed to get back to Africa, so when he entered the University of Oxford he immediately sought out Professor Arthur Cain, asking him, "How do I get to Africa?" Cain informed him of his plans to go there the following summer to study bird

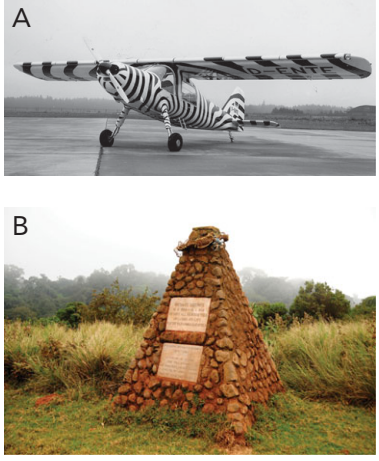


Figure 1.1 A. Michael Grzimek's airplane. B. Gravesite of Michael and Bernhard Grzimek atop Ngorongoro Crater.

migration (which Sinclair already knew something about), and Sinclair made enough of a nuisance of himself that he was invited to come along as a research assistant for the Serengeti Research Institute. That did it for Sinclair – he was hooked.

Recall that Sinclair was more experienced in surviving the Serengeti experience than most Oxford expatriates. He was fluent in Swahili, so if he needed help, he could explain his needs to the local people. He was also familiar with the wildlife and the environment, so that he knew where to find animals for observation, and also how to avoid getting eaten or gored by his subjects. After observing Sinclair's abilities to survive in the bush while collecting data under challenging circumstances, the researchers at the Institute presented him with a problem that was to be the focus of his PhD dissertation. They thought that the number of buffalo and wildebeest in the Serengeti-Mara ecosystem had been increasing in the past few years, but they did not know why. Could he come back and figure that out? He responded, "I can do anything you want – just get me there." And so was born a research program that has continued for over 40 years. We will use Sinclair's research in the Serengeti to help us understand what ecologists do, and how they do it.

1.1 WHAT ARE ECOLOGICAL QUESTIONS?

To get started on his project, Sinclair needed to answer two of the most basic questions addressed by population ecologists. The first question is: What is the abundance of a population? Or, how many individuals are there in the population? The second question is: What is the **distribution** of the population? Or, where are the individuals actually located in space and time? Later in this chapter, we will explore how Sinclair addressed a third important ecological question: How do interactions with the environment influence the distribution and abundance of organisms?

The buffalo challenge

The question of why the buffalo and wildebeest populations were increasing proved very challenging for several reasons. First, the buffalo were petrified of humans, because they had recently been targets of very heavy poaching. So anytime Sinclair got remotely close to a herd, they took off in terror – and motivated buffalo can run very quickly. Second, before discovering why buffalo abundance was increasing, Sinclair first needed to show that abundance was indeed higher than in previous years. Even if he could ultimately figure out how to count the current buffalo population, it would be challenging to go back in time to measure their abundance in previous years. Last, if he could show that buffalo were increasing, there were several potential causes of the increase. Each cause would be difficult to explore with any degree of rigor. We'll look at how Sinclair solved these problems sequentially, keeping in mind that he was actually working on all three problems at the same time.

Though his PhD research was on buffalo, Sinclair was also keeping track of the migrating wildebeest, in cooperation with other researchers at the Institute. Upon completing his dissertation research in 1970, Sinclair began working as a postdoctoral associate for the Institute, focusing on the wildebeest populations. Thus in the remainder of the chapter we will discuss research on buffalo, wildebeest, and other large Serengeti mammals.

Estimating buffalo and wildebeest abundance

Because buffalo were so afraid of humans, Sinclair's only option was to survey them from the air. Trained pilots and observers photographed the buffalo while flying about 200 m above the surface. Buffalo range almost exclusively in open woodlands, so there was no need for Sinclair to census areas that were exclusively grassland. As a result, all suitable habitats were screened in just a few days. Fortunately, buffalo are huge, but even from 200 m it was challenging, yet possible, to distinguish individual animals.

Wildebeest congregate in much larger herds than buffalo, and are much more tolerant of humans and their flying machines. Because wildebeest congregate so close together and are smaller than buffalo, the researchers needed a higher magnification on their telephoto lenses to see them, and thus only a small fraction of the herd could be photographed in one picture frame. One complete survey required 2770 frames and took 9 months to count.

Thinking ecologically 1.1

What types of problems might a researcher encounter when conducting aerial surveys? How might a researcher deal with these problems?

Estimating historical buffalo and wildebeest abundance

To estimate sizes of past populations, Sinclair did historical research on populations of both buffalo and wildebeest. Some of his information came from interviews with people who had lived in the Serengeti, but most came from books, articles, travelogues, and especially photographs taken in previous decades. As one example, Sinclair knew that Martin and Osa Johnson had written a travelogue called *Safari* back in the 1920s, which described their experiences in Africa. He knew

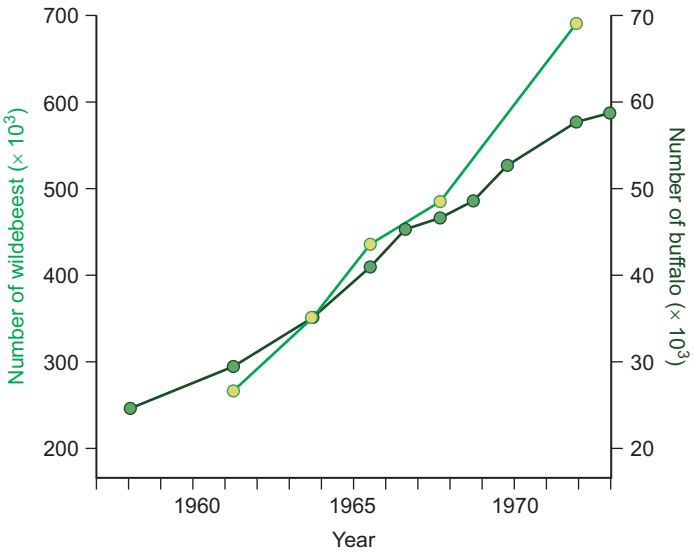


Figure 1.2 Increases in populations of buffalo (dark green) and wildebeest (light green) in 1958–1972.

that for every book there are thousands of journal writings, pictures, and stories that don't make it into the book, and in 1981 Sinclair discovered the Martin and Osa Johnson Museum in Chanute, Kansas, Osa's hometown. It was a repository for much of the Johnsons' travel documents and pictures, and Sinclair was able to convince the curator to grant him access to all of their materials. In return, he organized the collection, so the curator and future patrons would know which materials were from the Serengeti.

Because he knew the Serengeti so well, Sinclair could identify exactly where many of the photographs were from. So he now had historical records of the vegetation from 1926, 1928, and 1933. One set of aerial photographs included a series of contiguous pictures that encompassed the entire wildebeest migration, which allowed Sinclair to estimate an abundance of approximately 90 000 animals. He was not so fortunate with historical research on buffalo, so we have no good early estimates of buffalo abundance.

More recent estimates of buffalo and wildebeest populations, beginning in the late 1950s, are more accurate, though they have a margin of error as well. Based on estimates by previous researchers, and Sinclair's more refined techniques in the late 1960s, the buffalo and wildebeest populations more than doubled in the 1960s, and continued to increase through the mid-1970s (Figure 1.2).

Having established that his colleagues at the Serengeti Research Institute were correct about a sudden increase in the buffalo and wildebeest herds, Sinclair's next task was to figure out why this was happening. He considered several hypotheses to explain why population sizes were increasing. We will use this question to explore how ecologists use hypotheses and predictions to answer questions.

1.2 HOW DO ECOLOGISTS TEST HYPOTHESES ABOUT ECOLOGICAL PROCESSES?

To answer questions about biological processes, ecologists test hypotheses that are provisional explanations for their observations. To be worthy of study, hypotheses must be plausible and generate testable predictions. Predictions are logical outcomes that are likely to be true if the hypothesis is true. Philosophers of science have extensive and sometimes passionate discussions about the relationship between hypotheses and predictions, which we will not delve into. Rather, we will simply point out that if a prediction is shown to be true, we feel somewhat more inclined to accept the hypothesis, but if we are good scientists, we will continue testing the hypothesis by exploring other predictions it generates. If the prediction is shown to be false, the hypothesis, as stated, is very unlikely to be true, unless there is something wrong in the methods we used to test the prediction.

This relationship between hypotheses and predictions will become clearer as we consider three hypotheses for why buffalo and wildebeest populations increased so sharply in the 1960s and 1970s. Sinclair's research also brings home the point that, ideally, researchers will consider all hypotheses when attempting to understand a biological process.

The food availability hypothesis

Perhaps herbivore populations were increasing because their food was becoming better in quality, or more abundant. If this hypothesis was correct, Sinclair predicted that food quality and abundance would have increased sharply in the early 1960s and remained high during that entire decade.

Sinclair and his colleagues suspected that the amount of rainfall would profoundly influence grass production – the amount of grass that was available to the grazers. To test this hypothesis, the researchers established a series of fenced areas, or exclosures, that prevented grazers from accessing the vegetation within the fences. They periodically harvested the vegetation, and measured the amount of grass that had grown in relation to the amount of rainfall that had recently fallen in the area. They predicted that there would be a positive **correlation** between rainfall and grass production (see Dealing with data 1.1 for a discussion of correlation). The results were striking – as rainfall increased, grass production also increased (Figure 1.3). The researchers concluded that rainfall has a significant positive effect on grass availability (Sinclair 1975).

This strong correlation between rainfall and food availability allowed Sinclair to use rainfall as an index of food availability. Sinclair did not begin his buffalo research until 1966, so he relied on measures of rainfall as his indication of grass availability during the early and middle 1960s. If increased food availability was causing the increase in buffalo and wildebeest abundance, he

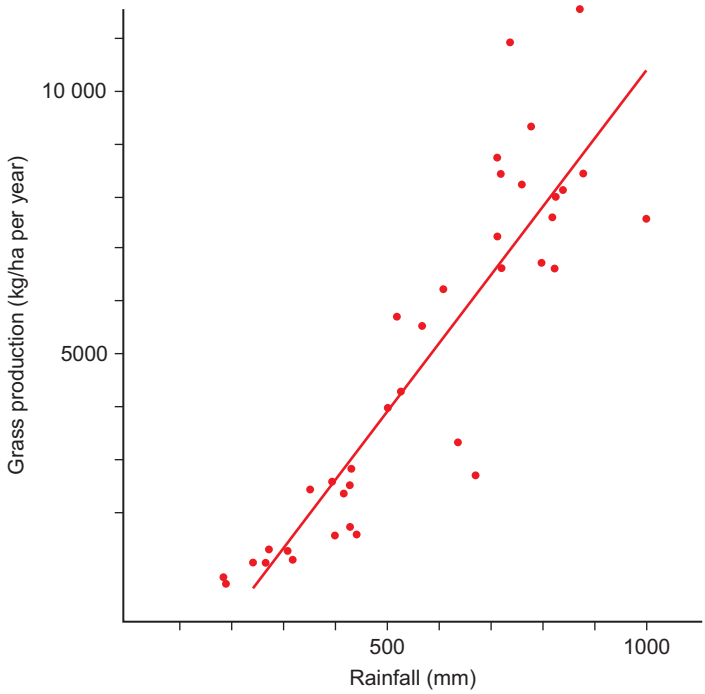


Figure 1.3 Relationship between rainfall and grass production.

Thinking ecologically 1.2

Draw a scatterplot showing how rainfall in the Serengeti varied over time. Year should be the *x*-axis label, and mean monthly rainfall (mm) should be the *y*-axis label. Is this a strong or weak correlation? Is this a positive or negative correlation?

Dealing with data 1.1 Correlation analysis

When both variables are numeric or continuous (have values that can be counted or measured), we can use a correlation analysis to evaluate the relationship between the two variables. In the exclosure example described previously, Sinclair and his colleagues predicted a positive correlation between the amount of rainfall and grass production. The researchers found

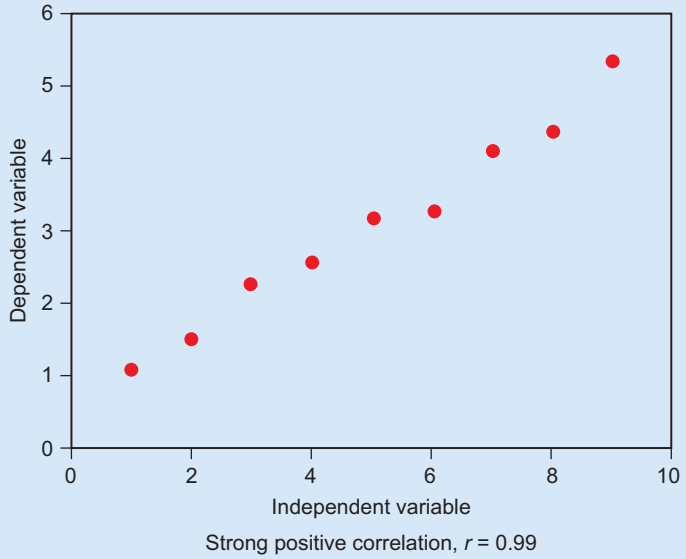
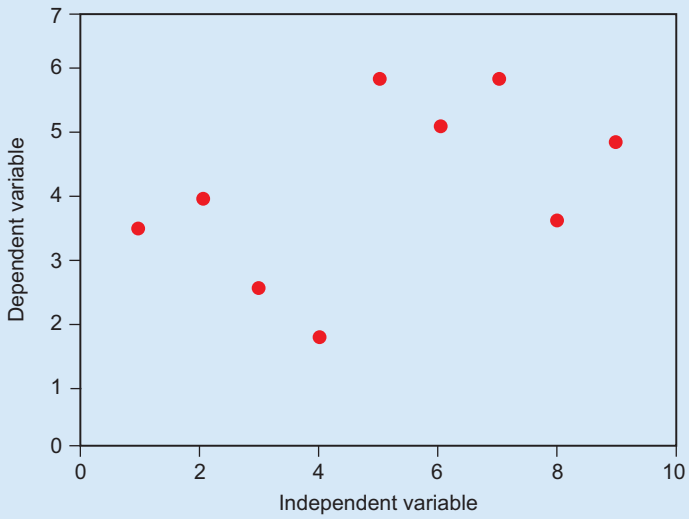


Figure D1.1.1

a strong positive correlation, which means that as rainfall increased, so did grass production. Figures D1.1.1 and D1.1.2 are examples of strong and weaker positive correlations.

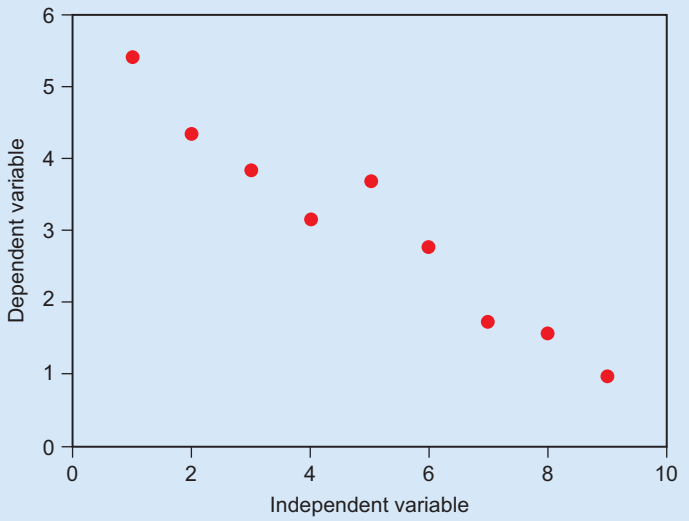
Statisticians use the **correlation coefficient (*r*)** to describe the strength of the correlation. If *r* is equal to 1.0, then all the data points will line up perfectly together to make a straight line. If *r* is less than 1.0, there will be a general upward trend. The closer *r* is to 1.0, the less scatter there is in the data (the closer the data points are to forming a line). The closer *r* is to 0, the more scatter there is in the data. If $r = 0$, there is no correlation between the two variables. A graph showing this type of relationship is often called a scatterplot or scattergram. For Figure 1.3, $r = 0.96$, which indicates a strong positive relationship between rainfall and grass production.

Many relationships between numeric variables have negative correlations. These are sometimes called inverse correlations. In this case, as one variable increases, the other variable decreases. As one example, Figure 1.10 illustrates a negative correlation between wildebeest abundance and the percentage of burned area. The exact same rules apply as for a positive correlation: As *r* approaches −1.0, the negative correlation grows stronger, and there is less scatter among the points. Figures D1.1.3 and D1.1.4 show strong and weak negative correlations. We will not discuss the mathematical formulas that calculate *r*, but you can refer to Gotelli and Ellison (2004) to learn how this is done. You will be expected to use simple statistical software packages for all statistical analyses in this text. These packages will do the work for you – in this case they will generate an *r*-value.



Weak positive correlation, $r = 0.46$

Figure D1.1.2



Strong negative correlation, $r = -0.97$

Figure D1.1.3

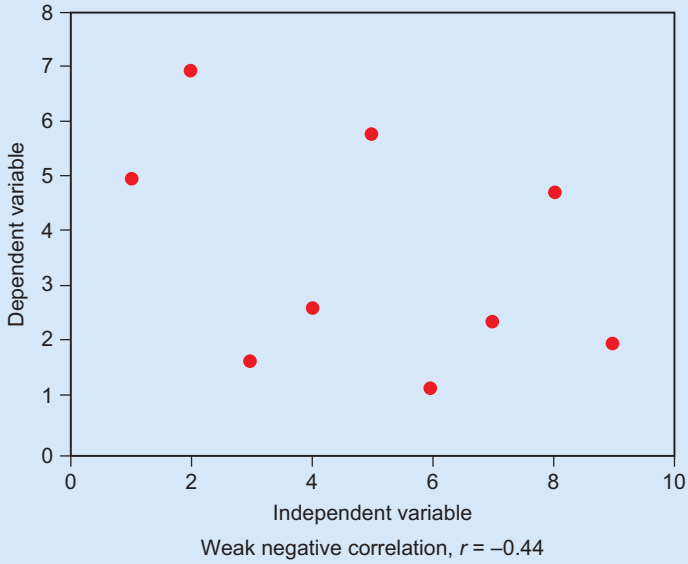


Figure D1.1.4

Cautionary note: A strong correlation does not necessarily mean that one variable caused a change in the other variable. Correlation analyses simply measure the strength of association between two variables.

predicted that there would have been higher than average rainfall during that decade.

Historically, dry-season rainfall in the central and northern Serengeti woodlands has averaged 37.5 mm per month. Table 1.1 gives rainfall data for 1962–1969. Restricting ourselves to the 1960s, you can see that average monthly dry-season rainfall during the 1960s – 36.96 mm – was very close to the historical average. Sinclair concluded that the abundance of buffalo and wildebeest was increasing for reasons other than increased food availability.

Given the lack of support for the food availability hypothesis, Sinclair considered an alternative hypothesis.

The predator release hypothesis

Perhaps herbivore populations increased during the 1960s because there was a reduction or release from high levels of predation. If this hypothesis was correct, Sinclair predicted that the abundance of **predators** capable of killing buffalo and wildebeest would have declined during the 1960s.

Unfortunately, the data on the abundance of predators in the Serengeti is a bit spotty, but all indications are that predator numbers actually increased during the 1960s and into the late 1970s. Lions and hyenas are the two most important predators in the Serengeti. Jeannette Hanby and David Bygott (1979) surveyed all of the lions in the Serengeti in 1974–7, and compared their numbers to George Schaller's surveys conducted in 1966–8 (Schaller 1972). Hanby and Bygott showed that the number of lion groups or prides increased from 18 to 24 between the mid-1960s and the mid-1970s. In addition, the mean number of lions per pride increased from about 15 to 19. Hanby and Bygott also surveyed the number of hyenas in the mid-1970s, and estimated 3391 hyenas in 1977 in comparison to Hans Kruuk's estimate of 2117 for the same area in 1964–8 (Kruuk 1972). In contrast to the prediction of the reduction in predation pressure hypothesis, the number of lions and hyenas was actually increasing during the same time period that wildebeest and buffalo populations were increasing rapidly.

A final hypothesis focused on the complicated effects of a disease – rinderpest – on buffalo and wildebeest populations.

Table 1.1 Estimated abundance of wildebeest and mean monthly dry-season rainfall for the central and northern Serengeti woodland in 1962–1969.

	1962	1963	1964	1965	1966	1967	1968	1969
Wildebeest abundance	309 743	*	397 624	439 124	461 208	483 292	535 663	588 034
Mean monthly rainfall (mm)	38.75	*	54.25	32.50	38.00	29.25	33.50	32.50

*There were no measurements in 1963.

The rinderpest release hypothesis

Having rejected two important hypotheses as explanations for the increase in buffalo and wildebeest populations during the 1960s and early 1970s, Sinclair was left with one other option to consider. Rinderpest is a measles-like virus that attacks and kills cattle and other *ruminants*. Ruminants are mammals, such as buffalo and wildebeest, that digest plant-based food by initially softening it within their rumen, where it ferments with the help of microorganisms that live there. They then regurgitate the semi-digested mass, chew it, and swallow it again. Sinclair knew that the Great Rinderpest Plague of 1890 originated in Europe and killed about 95% of the cattle in southern and eastern Africa. He also knew that several other waves of rinderpest had caused serious damage to the African ruminant populations in the early and mid-twentieth century. He reasoned that perhaps the increase in wildebeest and buffalo populations in the 1960s resulted from a reduction or release from high levels of rinderpest infection. Perhaps rinderpest infection had been keeping the populations of buffalo and wildebeest unnaturally low during the 1950s, and that somehow, the animals were no longer being infected by rinderpest in the early 1960s. Sinclair's task was to test the predictions of the rinderpest release hypothesis.

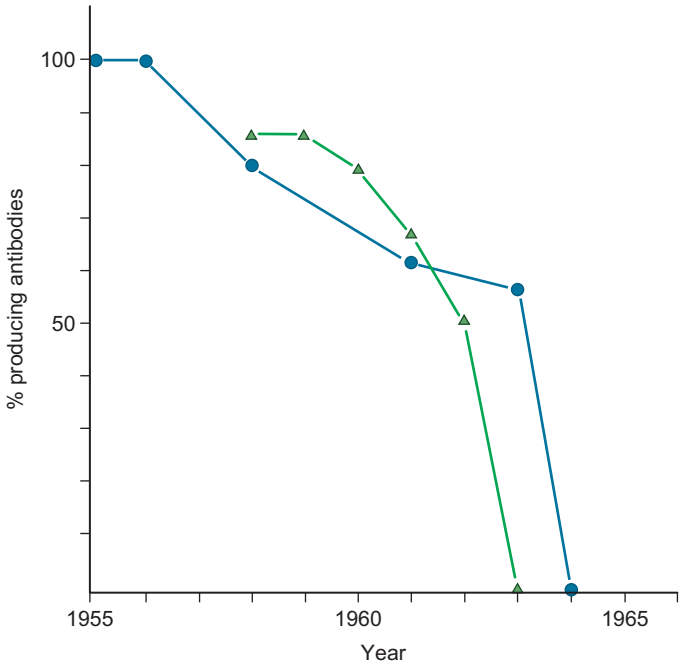


Figure 1.4 Percentage of buffalo (circles) and wildebeest (triangles) producing antibodies to rinderpest from 1955–1964.

Prediction 1: A negative correlation between rinderpest infection and ruminant abundance

One prediction of the rinderpest release hypothesis is that rinderpest infection should have declined substantially in association with an increase in the abundance of buffalo and wildebeest. If this was true, then blood from animals born in the early and mid-1960s, when the populations began increasing, should have fewer antibodies to the rinderpest virus than blood from animals born in the 1950s, when the populations were more stable.

Veterinarians were very interested in rinderpest because it killed cattle owned by local tribesmen and devastated the local economy. Walter Plowright, a veterinarian working for the East African Veterinary Research Organization, helped develop a vaccine against rinderpest, and began inoculating cattle in East Africa in 1956. He knew that wildebeest also contracted the disease, so he carried out a wildebeest-monitoring program in the early 1960s. He discovered that juvenile wildebeest received passive immunity from their mother's milk, but by 7 months of age were highly susceptible to infection. He discovered that wildebeest from Tanzania showed no evidence of rinderpest antibodies in 1962, in contrast to an infection rate of about 70% in 1959–61 (Plowright and McCulloch 1967).

Though Plowright moved back to England in 1964, his paper indicates that there was no evidence of major rinderpest infection in wildebeest from 1963 to 1967. But Plowright was a veterinarian interested in eradicating rinderpest, and he was not working on the question of why the wildebeest and buffalo populations were increasing. He was delighted that rinderpest was no longer present in the population but warned that it was likely to return, as it had several times in the past.

In contrast, Tony Sinclair was profoundly interested in the correlation between rinderpest release in wildebeest and population growth. But he also knew that a simple correlation between rinderpest release and population growth did not mean that wildebeests were increasing because they were no longer being infected by rinderpest. He needed more confirmation of the rinderpest release hypothesis.

One of Sinclair's first actions was to work with other veterinarians to measure rinderpest levels in the buffalo. The rinderpest release hypothesis predicts that rinderpest should also have disappeared in buffalo in the early 1960s. Fortunately, veterinarians had supplies of buffalo blood in the freezer, and they also knew (much to Sinclair's delight) the age of each animal that had provided the sample. The results of their analysis showed that rinderpest had completely disappeared from the buffalo population by 1964 (Figure 1.4).

Prediction 2: No correlation between rinderpest infection and non-ruminant abundance

Encouraged, Sinclair proceeded to test other predictions of the rinderpest hypothesis. He argued that Serengeti mammals that were not susceptible to rinderpest (animals that were not ruminants) would not show a trend of population growth over the 1960s, because rinderpest release would, of course, not affect them in any significant way. Zebra were the only large non-ruminant for which there were good survey data and, as predicted, there was no trend for zebra populations to increase over the 1960s (Figure 1.5).

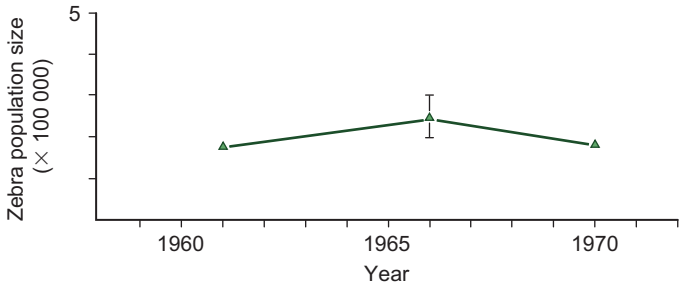


Figure 1.5 Estimates of zebra abundance in the 1960s.

Prediction 3: Increased survival rate in juvenile ruminants

Sinclair also knew that rinderpest had historically killed juveniles after the passive immunity from their mother's milk wore off. If rinderpest release was responsible for the population increase, he predicted an increase in the survival rate of juveniles. One way of measuring juvenile survival is using aerial surveys to measure what percentage of the population is made up of 1-year-old juveniles. An early survey of wildebeest indicated that juveniles made up 8% of the population (Talbot and Talbot 1963). After 1963, that percentage was much higher, usually between 14 and 17% (Sinclair 1977b).

Recall that Sinclair considered two other hypotheses – the food availability and the predator release hypotheses – to explain the increase in buffalo and wildebeest abundance, but the data did not support the predictions of these two alternative hypotheses. When Sinclair came up with the rinderpest release hypothesis, he systematically tested each prediction generated by the hypothesis and was able to support each prediction with data based on observations, models, and experimentation. As each prediction was confirmed, Sinclair's confidence in the rinderpest release hypothesis increased. As Sinclair's experiences reflect, ecology is no different than any other science, in that observation, modeling, and experimentation lie at its heart.

1.3 HOW DO ECOLOGISTS USE OBSERVATION, MODELING, AND EXPERIMENTATION?

In some ways, ecology is a very complex science because it happens in the real world, where controlling variables is difficult, and where replication may be impossible. Sinclair's question of why the buffalo and wildebeest were increasing was especially challenging, because it was an event that happened only once and sample sizes of one are very difficult to test with any degree of certainty. Working under this handicap, a successful ecologist must be a keen observer, able to pick up on small nuances of patterns, and able to extract small amounts of information from a large amount of background noise.

Observations

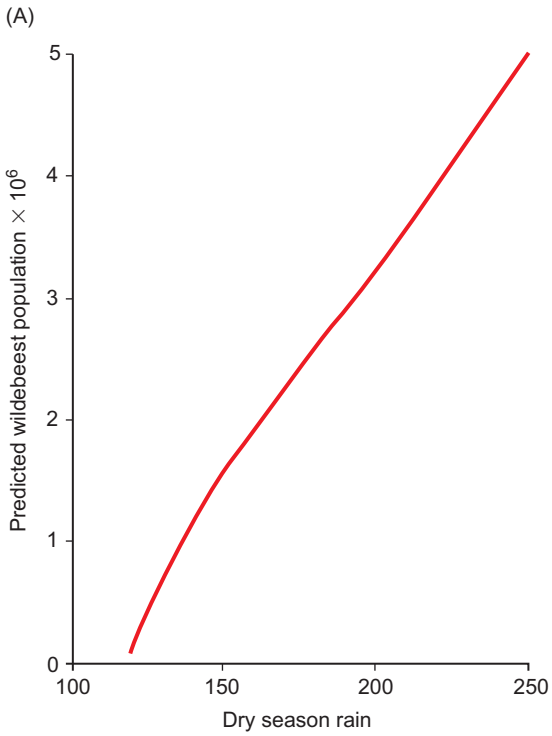
Scientists use three types of observations. First, they observe actual processes with their senses, or with devices that are extensions of their senses. To estimate abundance and proportions of juveniles, Sinclair used airplanes and cameras. Second, scientists observe and learn from the published literature, which was essential for Sinclair's knowledge of abundance levels prior to his study, in the 1950s and early 1960s. Last, they observe from what other people are doing or saying. Sinclair's ability to speak Swahili helped with his historical research into wildebeest abundance, and his social skills enabled him to establish a rapport with the veterinarians and collaborate with them on the buffalo antibody analyses. Perhaps most importantly, Sinclair got to hang out with a dozen or so senior researchers at the Serengeti Research Institute, bounce ideas off of them, and benefit from their many years of accumulated knowledge. Sinclair states that one of his golden rules is: "If you want to conserve and manage an ecosystem, you need to know all there is to know about it." Much of this knowledge comes from these three types of observations described above. These observations can also be used to construct scientific models.

Scientific models

There are many types of models with very different goals, and you will learn – and hopefully master – some of them as you work through this text. Models seek to describe a system, or to predict what the system will do in the future. All models are simplifications of reality, but ideally each model contains the essential attributes of what it seeks to describe or predict. For example, a map has some of the essential attributes of a landscape, while a global climate model has some of the essential attributes of the world's climatic conditions. But both are simplifications of reality. And both aspire to have enough of the essential attributes to accomplish their goal. In the case of the map, the goal is primarily descriptive, so that the user will be able to make good decisions when on an unfamiliar route. In the case of a global climate model, the goal is primarily predictive, so that citizens can understand the repercussions of their actions and make informed decisions.

Sinclair's research used many models of population growth and of ecosystem function. Sinclair hypothesized that with rinderpest release, buffalo and wildebeest abundance would continue to increase until the populations were limited by grass availability during the dry season. At that point, the populations would begin to level off. One of the problems of making this prediction is that rainfall is highly variable; for example, dry-season rainfall increased sharply in the early and mid-1970s from a mean of about 150 mm to about 250 mm. Based on the correlation between rainfall and food availability (Figure 1.3), and making certain assumptions about predation rates, Ray Hillborn and Sinclair (1979) created a simple mathematical model that predicted wildebeest abundance in relation to dry-season rainfall (Figure 1.6A).

Based on this model, wildebeest abundance could exceed 4 million if dry-season rainfall remained above 250 mm. However, Hillborn and Sinclair issue three warnings in association with this model. First, it would take several decades for the population to reach equilibrium. Second, rainfall levels were



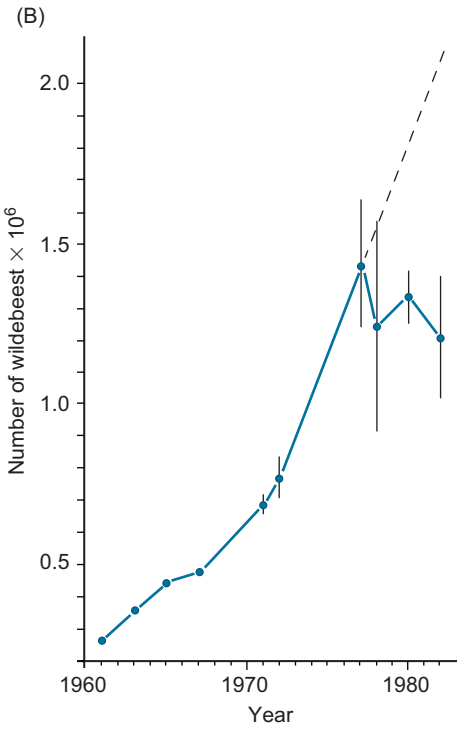


Figure 1.6 A. Graph generated by Hilborn and Sinclair's mathematical model predicting the number of wildebeest in relation to dry-season rainfall. B. Wildebeest abundance through the early 1980s. Dotted line shows predicted abundance if rainfall stayed at 250 mm.

unusually high in the early 1970s, and would likely be lower in the future. Third, this model was an oversimplification – in their paper the authors explicitly state, "We will be wrong in some places, but we invite criticism because this is the most rapid means of improving our understanding of Serengeti dynamics."

How well has this model withstood the test of time? As it turns out, dry-season rainfall in 1977–82 dropped to a mean of 149 mm – almost exactly its historical average during the 1960s. According to the model, the population, under these rainfall conditions, should stabilize at about 1.3 to 1.4 million. Figure 1.6B shows that the population increase of the early and mid-1970s did level out abruptly in association with the decrease in dry-season rainfall (Sinclair *et al*. 1985).

Many observational studies designed to test models will run into problems of getting a large enough sample. Also, just because the prediction of a model is validated does not mean that the model will be correct the next time it is tested. Scientific experiments are designed to get around this problem by controlling as many variables as possible. However, you should recognize that even well-designed experiments are subject to numerous sources of error.

Designing and conducting experiments

Scientists do not control all the variables in a controlled experiment. The simplest experiments attempt to keep all of the variables at similar levels, excepting the one variable or factor the experiment is designed to test. More complex experiments can evaluate the effects of more than one factor at a time, but these are more difficult to design and interpret.

Ecologists make liberal use of carefully designed experiments, both in the laboratory and in the field. As one example, Sinclair wanted to know whether buffalo had preferences for certain

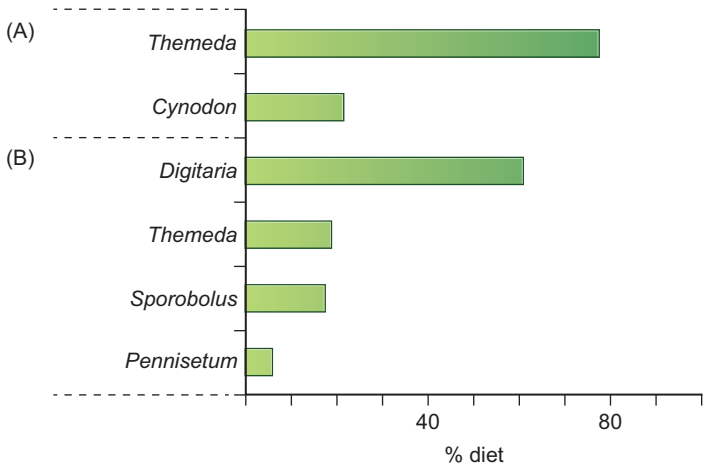


Figure 1.7 Percentage of food eaten when a choice of grass species was presented to tame buffalo: when buffalo were given a choice of two grass species (A); when buffalo were given a choice of four grass species (B).

types of grasses, reasoning that such preferences, if they existed, would be important for buffalo survival, and could help with conservation efforts. Presumably, buffalo would tend to prefer the most nutritious foods, and evaluation of habitat quality by conservation ecologists should be based on how much nutritious food was available to the buffalo.

Sinclair maintained a herd of 10 tame buffalo to test for food preferences. In one series of experiments, he put individual buffalo in a 10-m-diameter enclosure, and gave them a choice of two different species of grasses that were available to them in their natural habitat, *Themeda triandra* and *Cynodon plectostachyus*. The buffalo ate much more *Themeda* than *Cynodon* (Figure 1.7A). In a second series of experiments, the buffalo were given a choice of four grasses,

including *Themeda* and three other species. In this case, *Digitaria*, a species that Sinclair knew from circumstantial evidence was heavily grazed by buffalo, was the clear choice (Figure 1.7B). A third series of experiments had to be prematurely terminated because lions broke into the enclosure and seriously damaged the subjects.

The results of this experiment were important, because they showed that food quality is important to the buffalo, and suggested that buffalo survival may depend on their having the correct type of food in the environment. Sinclair's research has shown that dry-season food quality can drop to such a low level that the food-digesting bacteria within the rumen die, at which point the buffalo begin to starve, even while surrounded by an ocean of grass (Sinclair 1977a).

All of the sciences use observation, modeling, and experimentation. All biologists, including ecologists, borrow liberally from the tool bags developed by the other sciences, including chemistry, geology, physics, and mathematics. But ecologists differ from many other biologists, in that their research addresses issues that span and tie together many different levels of the biological hierarchy.

1.4 HOW DO ECOLOGISTS ASK QUESTIONS THAT LINK DIFFERENT LEVELS OF THE BIOLOGICAL HIERARCHY

Biologists study life on all size scales, from subatomic interactions that influence the function of the nervous system, to climatic changes occurring on a global scale. Because ecologists focus their attention on interactions, ecologists must be able to understand processes from all levels of the biological hierarchy. However, ecologists generally devote most of their attention to processes occurring on the level of the organism and above, up to the level of the biosphere. We can use the Serengeti ecosystem to understand the types of questions that can be asked at different levels of the biological hierarchy.

Processes occurring at or above the level of the organism

At the level of the **organism**, we can ask how an individual buffalo forages in a way that meets its daily needs for energy and nutrients. As we have already seen, buffalo have food preferences, and these preferences are tied to underlying physiological requirements. At a higher level, we can explore questions about the distribution and abundance of populations of a species at a particular location. How many individuals are there, what is their distribution, and how are both abundance and distribution changing over time? Questions about the vast migrations of wildebeest, zebra, and Thompson's gazelles are all addressed at the level of the populations.

But of course these populations interact with each other, and form biological communities. Samuel McNaughton (1976) showed that wildebeest grazing actually benefited Thomson's gazelles by stimulating the regrowth of succulent grasses and herbaceous plants, which were then eaten by gazelles who followed in wildebeest footsteps. This interaction among wildebeest, gazelles, grasses, and herbaceous plants is an example of a community-level interaction. Linkages extend, of course, beyond the living organisms, and include the nonliving, or abiotic elements of the environment. This brings us into a discussion of the Serengeti **ecosystem**, which includes both the community of organisms and the abiotic (nonliving) features that interact with the community. Thus the nutrients in the soil determine the grasses that grow there, which influence the distribution of the mammalian community. Conversely, the mammals return nutrients, which are broken down by the burying beetles, to the soil and thus the nutrients can be reused by the next year's population of grasses. These are examples of linkages that occur at the ecosystem level (Figure 1.8A). We will explore some of these linkages in more detail.

At a still higher level, ecologists explore landscapes, groups of interacting, and usually spatially connected, ecosystems. As one example, just to the west of the Serengeti is an ecosystem dominated by agriculture. The human population there is increasing at a minimum of 3% per year (about three times the global growth rate), with the result that humans supplement their resources by hunting elephants, wildebeest, and other ungulates that move in during the dry season (Sinclair *et al*. 2008). Landscape ecologists want to understand how different elements of the landscape, in this case savanna in the Serengeti, and cropland to its west, influence interactions across ecosystems (Figure 1.8B). However, landscapes are parts of larger geographical regions that experience a common set of environmental and evolutionary influences. Thus regional ecologists might ask why large mammal abundance and **species richness** (the number of species) are so high in the East African region, in comparison to similar regions in North America or Australia (Figure 1.8C).

The highest level is the **biosphere** itself – the part of the world that supports life. Studies of microorganisms are revealing that the biosphere is almost as large as the globe itself, and extends many kilometers below and above the surface (see Chapter 2). One recurring issue is how global climate change – a biosphere-level process – will influence the functioning of ecosystems such as the Serengeti. Given all the linkages that occur among biotic and abiotic components of the Serengeti ecosystem, there is profound concern that disrupting these linkages could negatively affect its conservation. Let's explore some of those linkages in more detail.

Serengeti abiotic linkages

The three primary abiotic factors that have been studied in the Serengeti are nutrients, fire, and rain, which, as you might imagine, are tightly linked to each other. Nutrient levels are highest in the southeastern plain, as nearby volcanoes have recently erupted and blanketed the region with inorganic minerals. However, rainfall levels are lowest there.

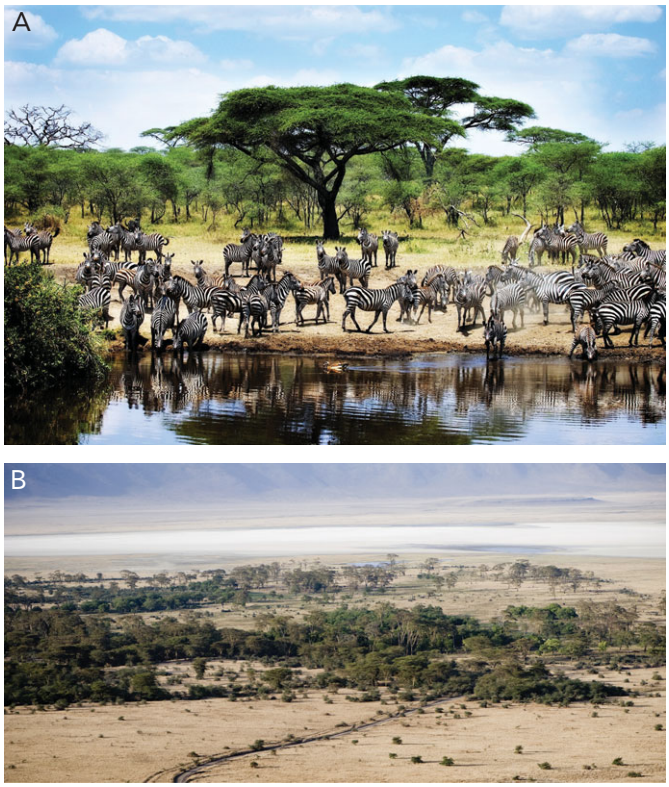


Figure 1.8 A. Serengeti ecosystem. B. Diversity of Serengeti landscape. C. East African region – satellite view.

Nutrient levels are lowest in the northwest, but rainfall levels are highest there. As a result of these differences, migratory wildebeest, zebras, and gazelles tend to spend the wettest months in the southeast, then migrate to the northwest, where there is still some forage available, even during the dry season. Thus the distribution of rainfall and nutrients influences the distribution and abundance of the organisms (Figure 1.9).

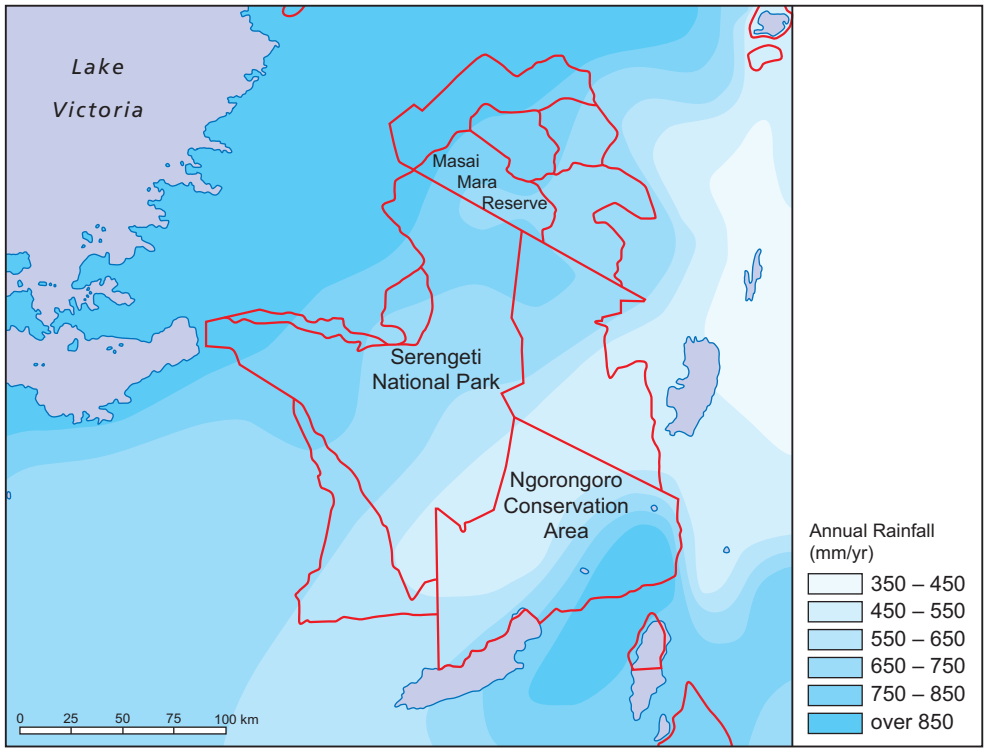


Figure 1.9 Mean annual rainfall (mm) in Serengeti and surrounding ecosystems.

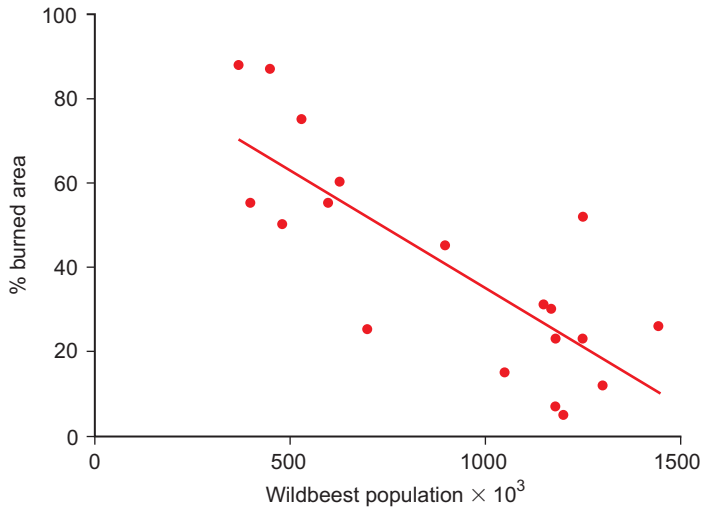


Figure 1.10 Relationship between wildebeest abundance and percentage of the Serengeti that is burned annually. ($r = -0.793$ $P = 0.00005$).

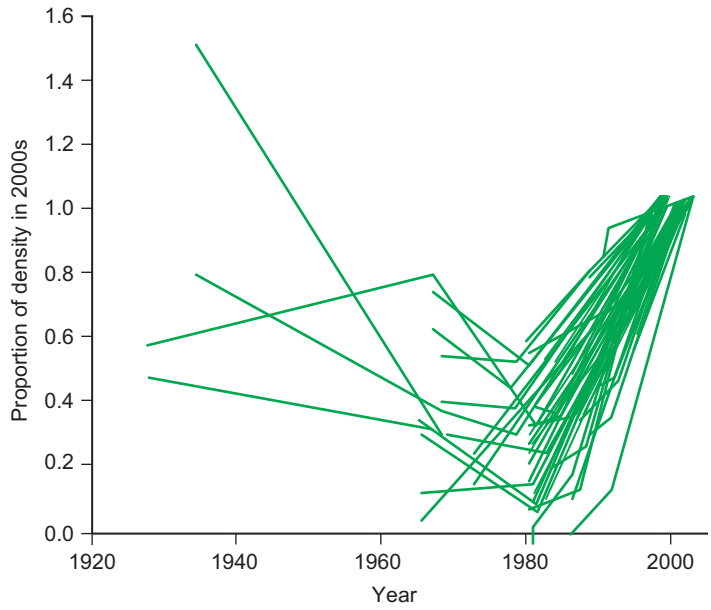


Figure 1.11 Changes in tree density over time as a proportion of tree density values measured in 2000–2003. Each line represents one study site.

The story with fire is a bit more complex. Almost all of the Serengeti fires are started by humans. Some fires are set to improve grazing pastures, others are set by Serengeti National Park employees under park management plans, and others are started by honey hunters smoking out bees from their hives. Fires only occur during the dry season, and require fuel (dried grass) to burn substantial areas. Michael Norton-Griffiths (1979) showed that fires were actually more common in wetter areas of the park, because wet areas grow more grass and hence provide more dry-season fuel. As wildebeest populations have increased since 1960, there has been a sharp reduction in the percentage of the Serengeti that burns annually (Figure 1.10), because the wildebeest have removed much of the fuel. This is an unusual example of a biotic process (grazing by wildebeest) profoundly influencing an abiotic process. This type of relationship can be analysed through correlation or regression analysis (see Dealing with data 1.2).

Sinclair emphasizes that many of the Serengeti linkages are between different biotic components of the ecosystem. We will explore some of these and consider the evidence supporting them.

Serengeti biotic linkages

We've discussed the differences in grass quality in the Serengeti, but we have not mentioned that much of the western and northern portion of the ecosystem is open woodland, primarily *Acacia* species, with **canopy cover** – the percentage of the ground shaded by the tree canopy – varying between 2% and 30%. Because the woodland is so open, abundant grass grows between the trees, and the shade and cover harbor large numbers of herbivores and carnivores.

Sinclair used historical data from photographs to assess the density of trees in the Serengeti over time. The data are sparse for early years (until about 1962), but there was a trend of high tree density in the 1920s and 1930s, with declining density in the 1960s and 1970s, followed by a sharp increase in the 1980s until 2003 (Figure 1.11). Sinclair and his fellow Serengeti researchers suspected that fire played a role in changing tree density.

Fire is lethal for young trees, but once trees become more mature, they can survive a grass fire. Michael Norton-Griffiths (1979) developed a simple mathematical model that predicted that tree density within the Serengeti would stop declining when the annual percentage burned declined below 30%. This level was reached in 1972. His model predicted that if burning levels remained below 30%, tree density would begin to increase. However, Norton-Griffiths also cautioned that high numbers of giraffes or elephants could also kill trees, and that no data were yet available on whether elephants or giraffes ate very small trees.

Despite Norton-Griffiths' predictions, the woodlands in the Serengeti, and in the Masai Mara National Reserve in Kenya, continued to decline into the 1980s, but then the two adjacent parks diverged. Tanzania went through a period of political turmoil, the economy and authority of the Serengeti National Park Service were undermined, and poachers killed off most of the elephants in the Serengeti. Many of the remaining elephants migrated across the border (which was closed to humans but not to elephants) to the Masai Mara Reserve in Kenya. Thus the Serengeti lost most of its elephant population and the Masai Mara's population of elephants climbed (Figure 1.12). The co-occurrence in the 1980s of the decline in the Serengeti's elephant

Dealing with data 1.2 Variables, regression analyses, and *P*-values

For this text, I will adopt a suggestion by Gotelli and Ellison (2004) that correlation analysis and **regression analysis** are functionally equivalent. These analyses look for associations between two continuous variables, and construct a *regression line* – a line of best fit – that highlights that relationship.

In the example above, Sinclair argues that high wildebeest abundance reduces the frequency of fire. In this case, wildebeest abundance is the **independent variable** because Sinclair proposes that wildebeest abundance influences the value of the percentage of burned area. Conversely, percentage of burned area is the **dependent variable**, because Sinclair proposes that its value is influenced by wildebeest abundance (the independent variable). Usually the dependent variable is graphed on the *y*-axis and the independent variable is graphed on the *x*-axis. The data appear to show an impressively negative correlation between wildebeest abundance and fire frequency.

Qualitatively, the regression line is drawn through the data points in a way that minimizes the total distance between the points and the line. The regression line, like all lines, has a formula that can be described as $Y = \beta_0 + \beta_1 X$, where β_0 is the *y*-intercept, and β_1 is the slope of the regression line. The regression line is determined mathematically, but the mathematical description is beyond the scope of this book. Fortunately, spreadsheet graphics and statistical programs will draw regression lines for you, if you provide the data in the appropriate format. For Figure 1.10, the regression formula is $y = 91.1 - 0.0561x$. This formula tells us that with each increase of one on the *x*-axis (and remember that a value of 1 represents 1000 wildebeest), the percentage of burned area decreases by 0.0561%. Usually, researchers also cite the coefficient of determination (R^2), which measures the proportion of the variance of the data explained by the line of best fit in a regression analysis. R^2 ranges between 0 and 1 – higher R^2 values indicate closer fit between the observed data and the regression.

The hypothesis we wish to test is called the research hypothesis (H_R). In this case H_R states that there truly is a negative correlation between wildebeest abundance and fire frequency. To establish some credibility for the research hypothesis, we first define a null hypothesis (H_0) that directly opposes H_R. In this case H_0 states that if we collected more data, we would find that there is no relationship between the two variables.

To test correlations, we test the H_R that the slope of the regression line is significantly different from 0 (Figure D1.2.1). This opposes H_0 that the slope of the regression line = 0. The *P*-value in this case is 0.00005. *P* stands for probability. In essence, the ***P*-value** is telling us what the probability is that H_0 is actually true. Based on these data, there is very low probability (0.00005 or 5 in 100 000) that, if we sampled more years or more wildebeest densities (in other words, if we had a larger data set), β_1 would ultimately equal zero.

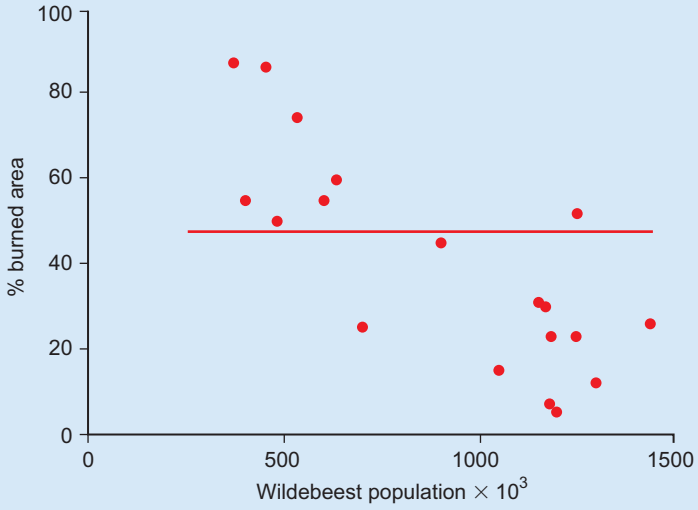


Figure D1.2.1 Regression line with $\beta_1 = 0$. Notice how some of the data points are very far from the regression line, which makes this hypothesis (H_0) very unlikely.

P-values are used in many of the statistical analyses in this text, and in ecology and most other sciences in general. Very low (small) *P*-values indicate that there is a very small probability that H_0 is correct. The question then arises, how confident do we need to be that H_0 is false, before we have support for H_R? It is up to the researcher to decide how unlikely H_0 must be before it can be rejected. This is known as the critical value (α). The most common α is 0.05. But I emphasize that you need to be very careful about interpreting *P*-values, there is nothing magical about $P = 0.05$. So if you find $P = 0.07$, you should suspect that there may be a correlation between two variables, but your confidence level for this relationship would be low. And, in contrast, if $P = 0.0001$, then you can be much more certain that there is a correlation between the two variables.

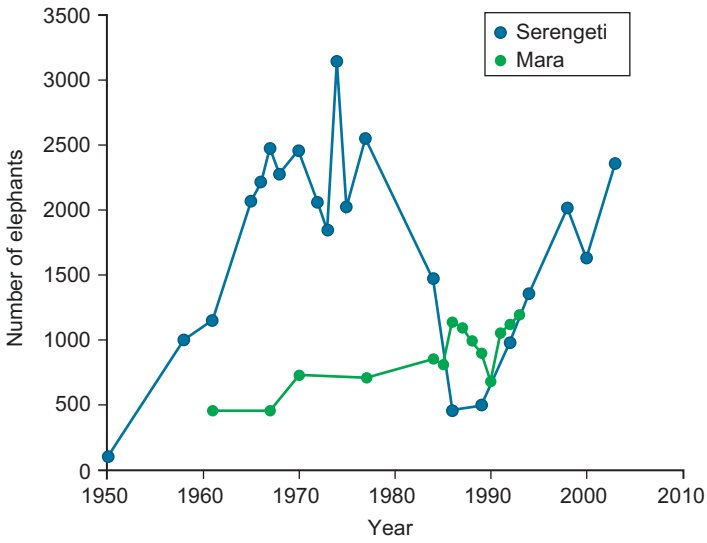


Figure 1.12 Elephant population abundance in the Serengeti woodlands and in the Masai Mara Reserve. Remember that the Masai Mara is much smaller than the Serengeti.

population and the increase in the Masai Mara Reserve elephant population can be seen more clearly if we transform the data (Dealing with data 1.3).

Holly Dublin (1995) reported that the woodlands in the Mara preserve continued to decline during the 1980s and 1990s. In contrast, woodland abundance in the Serengeti began to rebound sharply, so that, at present, woodlands are back to their estimated levels from the 1930s. By carefully watching elephant feeding behavior, Dublin was able to demonstrate that elephants at the Mara ate large numbers of small trees. Dublin and her colleagues (1990) argued that ecosystems such as the Serengeti have two stable states. In the case of the Serengeti–Mara ecosystem, there can be either grassland or open woodland. To change a woodland to a grassland, there must be both high fire and abundant elephants. To change a grassland to a woodland, there must be both low fire and sparse elephants. Thus once an ecosystem is in one state, it remains there unless it is disturbed by a profound change in both fire conditions and browsing by elephants.

Recent Serengeti studies and unexpected biotic and abiotic linkages

Sinclair and his colleagues (2013) have recently turned up a new series of biotic and abiotic linkages. During his early years in the Serengeti, Sinclair noticed that the abundance of the Natal multimammate rat, *Mastomys natalensis*, oscillated over time. Sometimes populations were very low, and other times they were much higher. As he was not initially studying rats, Sinclair's first observations were not systematic; he simply wrote down in his field notes that he came across some rats on a particular date.

However, Sinclair was somewhat more systematic about noting the presence of an important rat predator – the black-winged kite, *Elanus caeruleus*. These predators move into areas of high rat density, and can reproduce very quickly when rat abundance climbs to high levels. Recall that Sinclair's first visit to the Serengeti involved studying bird migrations, which led him into the habit of keeping records of all the common birds he observed. Thus he has a record of black-winged kite density dating back to 1965.

Sinclair and his colleagues were not surprised to discover a linkage between natal multimammate rat and black-winged kite abundance (Figure 1.13). It seemed logical that an increase in rat abundance would be closely followed by an increase in the abundance of its predator. But there were two puzzling aspects about this system. First, why did the rats explode in population approximately every 5 years? Second, why were some other species in the ecosystem also showing variation in survival on a 5-year time schedule? For example, wildebeest showed variable juvenile survival rates, which also peaked approximately every 5 years, but on a different schedule from peaks in rat abundance.

The researchers wanted to know whether there was a linkage between rats and wildebeest, or whether, alternatively, a previously unidentified factor was influencing both species in opposing directions. Fortunately, researchers at the Serengeti have been keeping monthly rainfall data since 1937. By combining rainfall and temperature data with the surveys of rats, kites, and wildebeest, the researchers were able to show that rat populations exploded following unusually heavy rains in November

Dealing with data 1.3 Data transformations

When comparing two variables – for example, elephant abundance in the Serengeti over time versus elephant abundance in the Mara over time – it is sometimes helpful to transform the data so they can be compared more meaningfully. In the case of Figure 1.12, it might make more sense to redraw the graph with the *y*-axis being the relative number of elephants in each ecosystem. Eyeballing the graph, you can see that the maximum number of elephants in the Serengeti was about 3200 in 1973. Based on that estimate, we can redraw the Serengeti curve so that 1973 has a relative number of elephants of 1.0. In 1950, the relative number would be about 100/3200 = 0.03, while in 1958, the relative number would have climbed to 1000/3200 = 0.31.

We can then repeat the process for the Mara ecosystem, noting that the maximum abundance is about 1200 elephants in 1993. Thus the value for 1993 has a relative number of 1.0. In 1961, the first Mara elephant census has a relative number of 450/1200 = 0.38. Figure D1.3.1 shows the completed transformation of the data for both curves. What relationships are easier to visualize when the data are transformed in this way?

There are many types of data transformations you will encounter is this book. Some transformations make the data more visually understandable, while others prepare the data for a particular type of analytical test.

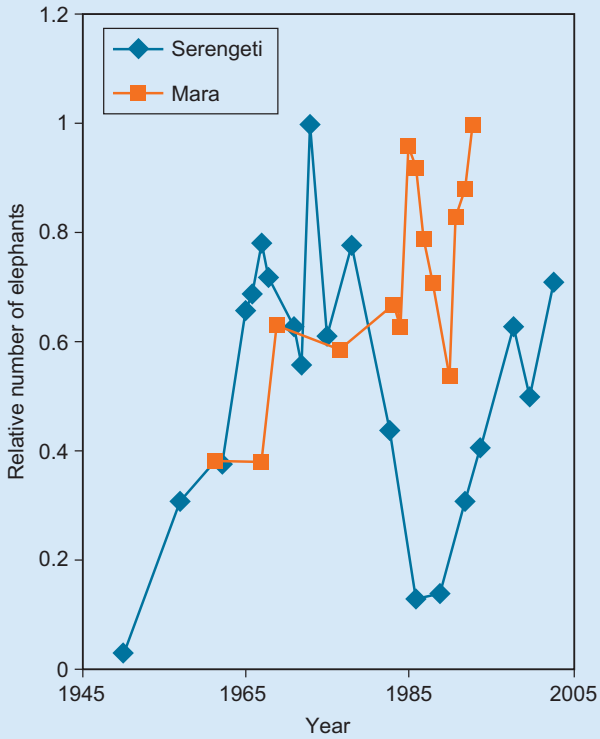


Figure D1.3.1

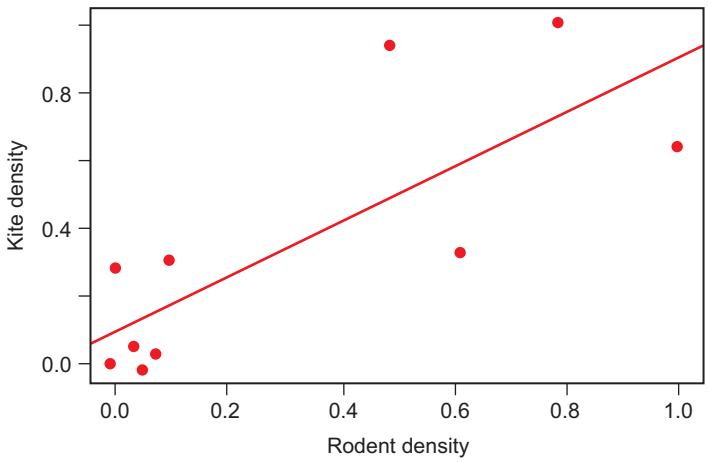


Figure 1.13 Relationship between the density of the Natal multimammate rat and the black-shouldered kite. Data are normalized so that a value of 1.0 represents the greatest value of kite and rodent density observed in the years of the surveys.

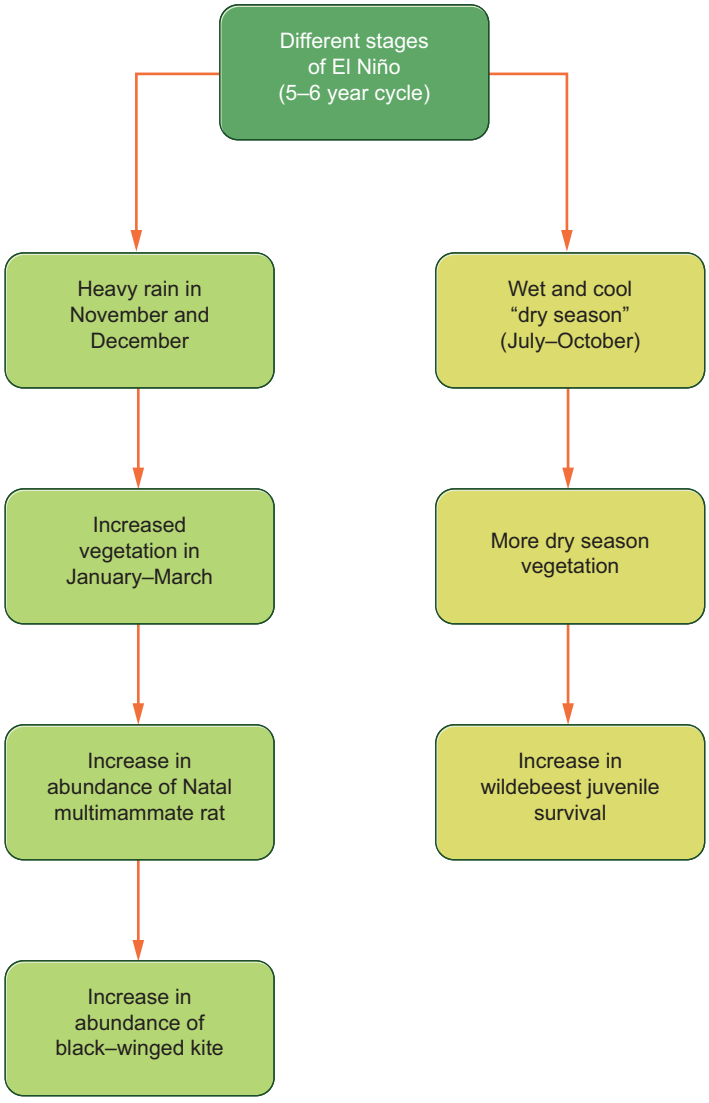


Figure 1.14 Abiotic and biotic linkages in the Serengeti.

and December of the previous year, presumably because this provided more vegetation for rats to eat during a time of year when food availability usually limited their survival and reproduction. In contrast, wildebeest juvenile survival was greatest when the dry season (July through October) was unusually wet and cool, because grass production was greater under those conditions.

In the Serengeti, fluctuations in weather are influenced by the **El Niño Southern Oscillation (ENSO)**, a large-scale atmospheric system that affects climate worldwide. Over the course of about 5 years, the air pressure and sea surface temperatures across the south Pacific and Indian oceans oscillate in a somewhat predictable fashion. During one phase of ENSO, the sea surface temperature increases and atmospheric temperature decreases near the west coast of South America, spawning heavy rains across much of the Americas and Western Europe, and drought in Africa and Australia. In the opposing phase (La Niña), the sea surface temperature decreases and atmospheric temperature increases near the west coast of South America, bringing drought to much of the Americas and Western Europe, and heavy rains to Africa and Australia. The upshot is that about every 5 years there are heavy rains in the Serengeti during November and December, which is, in part, responsible for an explosion in the population of *M. natalensis*. At a different stage of ENSO, there is unusually heavy dry-season rainfall, which increases grass production, and leads to very high juvenile wildebeest survival (Figure 1.14)

REVISIT: The Serengeti narrative

The Serengeti is home to a diverse community of species that respond differently to the wide variety of factors that may influence survival and reproductive success. By studying these processes over a span of several decades, researchers are beginning to uncover some of these interactions. Though Sinclair has recently retired, many other researchers in the Serengeti continue to uncover and deepen our understanding of the ecological linkages.

We began this discussion of Sinclair's research by considering his basic work that estimated the distribution and abundance of two species – wildebeest and buffalo – within the Serengeti ecosystem. But Sinclair wanted to know how these abundances were changing over time, and what factors were causing them to change. This search required Sinclair to consider interactions among these two species and both biotic and abiotic elements of the environment. His most recent work shows that periodic variation in an abiotic factor (rainfall) causes changes in an abiotic factor (grass abundance), which has a cascading influence on a variety of other species. Like a great detective or mystery story, uncovering these linkages provides clues to general patterns of past and present species distribution and abundance, as viewed from different levels of the biological hierarchy. Perhaps most important, understanding these linkages allows ecologists to make predictions about what will happen to species in the future, which is particularly important in a rapidly changing environment.

SUMMARY

Over the years, the Serengeti has been a model ecosystem for answering basic ecological questions about the distribution and abundance of organisms, populations, and species, and about how different species interact with each other and with their environment. Tony Sinclair and many other researchers have addressed some of these questions, and continue to work on understanding important biotic and abiotic linkages that influence ecosystem functioning.

In common with all types of scientific inquiry, ecologists use predictions to test hypotheses about ecological processes; this approach is highlighted by Sinclair's research that explored why buffalo and wildebeest populations were rapidly expanding. Like other scientists, ecologists use observation, modeling, and experimentation to generate and test hypotheses. However, in contrast with much biological inquiry, ecologists ask questions that link numerous levels of the biological hierarchy, from molecular to global ecology.

FURTHER READING

Goulson, D. 2014. Pesticides linked to bird declines. *Nature* 511: 295–296.

A short understandable summary on the effect of a commonly used class of pesticides on ecosystems. A great opportunity to gain familiarity with different biotic and abiotic linkages. The actual paper is:

Hallmann, C. A., Foppen, R. P., van Turnhout, C. A., de Kroon, H., and Jongejans, E. 2014. Declines in insectivorous birds are associated with high neonicotinoid concentrations. *Nature* 511: 341–344.

Sinclair, A. R. E. 1977b. The eruption of the ruminants. In *Serengeti: Dynamics of an Ecosystem*, ed. A. R. E. Sinclair and M. Norton-Griffiths. Chicago, IL: University of Chicago Press, pp. 82–103.

A very readable summary of Sinclair's early work exploring why some large mammal species increased in abundance while others did not.

Sinclair, A. R. E and 17 others. 2013. Asynchronous food-web pathways could buffer the response of Serengeti predators to El Niño Southern Oscillation. *Ecology* 94: 1123–1130.

A challenging but fascinating study of how El Niño may be influencing the dynamics of the Serengeti ecosystem, creating a 5-year periodicity to shifts in abundances of different species.

White, K. S., Barten, N. L., Crouse, S., and Crouse, J. 2014. Benefits of migration in relation to nutritional condition and predation risk in a partially migratory moose population. *Ecology* 95: 225–237.

Good introduction to hypothesis testing in this very accessible study that evaluates the costs and benefits of migration in a marked moose population. Nice discussion of the limitations of the findings in the context of a rapidly changing environment.

END-OF-CHAPTER QUESTIONS

Review questions

1. Outline the wildebeest migration pattern and tie that together with rainfall patterns, the availability of nutritious grass, and the timing of when wildebeest give birth to their offspring.
2. What were Sinclair's three hypotheses for increases in buffalo and wildebeest abundance in the 1960s and 1970s. How did he test the predictions of each hypothesis, and what did he conclude based on each test?
3. Give two examples of community-level biotic interactions discussed in this chapter. In what ways may abiotic factors be linked to each example?
4. What are the levels of the biological hierarchy most often considered by ecologists? Give an example of a question that an ecologist might ask that pertains to each level of the hierarchy that you cited.
5. What are three general questions that ecologist ask?

Synthesis and application questions

1. In Sinclair's (1975) exclosure experiments (Figure 1.3), grasshoppers and rodents were able to access the exclosures, and eat some of the grass. This might decrease grass growth within the exclosures. Is this a problem for Sinclair's use of rainfall as a measure of food availability? Why or why not?
2. Dennis Normile (2008) wrote an article entitled "Driven to extinction," in which he argues that rinderpest may be the second disease that has been driven to extinction by an aggressive

vaccination campaign (smallpox being the first). What types of evidence would you need before you felt confident that an infectious virus had indeed been driven to extinction? How would you collect those data?

3. What do you think would happen to lion cub survival following an unusually wet and cool dry season in the Serengeti? Explain your reasoning.
4. Think of a model that influences your everyday life. Why is this model useful? In what way is this model a simplification of reality? Is the model primarily descriptive, or predictive, or both?
5. If you were given 3 years to do research in the Serengeti, what question might you ask? How would you go about answering it?

Chapter 2

The physical environment

INTRODUCTION

Sunlight filtering down through the forest is intercepted by branches, so that by the time it reaches the surface of the ground, its intensity is literally only a shadow of its former self. The branches are arranged in multiple layers, with the top layers accessing the most sunlight, and lower layers receiving greatly diminished intensity. The branches host many types of plants and animals, including photosynthetic organisms that harvest the sunlight to power their cellular activities. Brilliant butterflies flit through the specks of light, foraging, mating, and creating new generations, as they have done in similar environments for millions of years. Interacting with some species, but unaffected by others, these animals and plants – and a host of organisms less conspicuous to our eyes – are part of a biome found in tropical latitudes.

A **biome** is a large geographical area with characteristic groups of organisms adapted to that particular environment. Terrestrial biomes are most influenced by temperature, moisture, and soils, while aquatic biomes are most influenced by temperature, chemical composition of the water, and water current. The boundaries and species composition of biomes change constantly, through both natural causes and human impact. Our opening case study looks at similarities and differences in how some terrestrial and aquatic biomes are structured and in how they are threatened by human activities. We will then consider the role climate plays in structuring biomes. We will explore the diversity of terrestrial and aquatic biomes, and discover that even though biomes are large geographical areas, researchers continue to find new biomes in unexpected places. In a world that has been so extensively changed by human actions, some ecologists question whether the traditional biome concept is still useful, or should be replaced by an approach that accounts for the effects of human actions.

KEY QUESTIONS

CASE STUDY: Biomes compared

Biomes that appear very different may have striking similarities in form and function. Reading this introduction, you may have surmised that the first paragraph described a tropical rainforest. You are correct! But this same paragraph also describes a coral reef, where the branches are coral and the photosynthetic organisms are zooxanthellae, algae that have a **symbiotic** – living together – relationship with the coral reef (Figure 2.1A). Ecologists describe this relationship as a **mutualism**, because both species benefit (see Chapter 15). Corals provide zooxanthellae with a secure place to live and a steady supply of nitrogenous waste to fuel their metabolism. In return, zooxanthellae share with the corals some of the organic compounds they construct from photosynthesis. Similar to coral reefs, tropical rainforests also harbor photosynthetic organisms on their branches. These **epiphytes** use tree branches for support, allowing them to access the Sun's rays for photosynthesis. Some epiphytes don't have any impact on the success of their tree hosts, while others actually provide the trees with nutrients, in a mutualism resembling the coral/zooxanthellae relationship. To complete the comparison of biomes, the brilliant butterflies in the opening paragraph are butterflyfish in the ocean – highly conspicuous animals in many coral reef ecosystems (Figure 2.1B).

Tropical forests and coral reefs share many other similarities. Both biomes have an extraordinarily high number of species, or high species richness. Both biomes also have a very high level of **primary production** – a term ecologists use to describe the chemical energy generated by the **autotrophs** within an ecosystem. Both trees and zooxanthellae are autotrophs, because they convert energy from sunlight to chemical bond energy.

Marine and aquatic biomes also face similar challenges from human activity. As one example, since the beginning of the Industrial Revolution, human activity has caused atmospheric CO_2 levels to increase about 100 times faster than they have in the past 650 000 years. About 30% of these emissions have been absorbed by the oceans, and transported by ocean currents, shifting to the right the equilibrium favoring the following reaction:

$$CO_2 + H_2O \rightleftharpoons H_2CO_3(\text{carbonic acid})$$

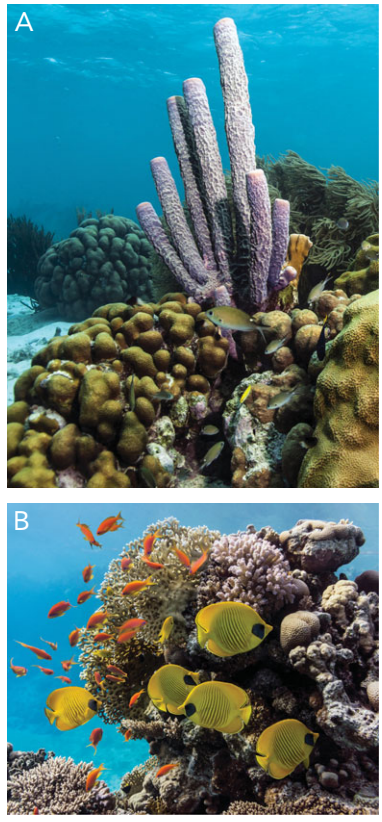


Figure 2.1 A. Coral with zooxanthellae. B. Butterflyfish in coral reefs.

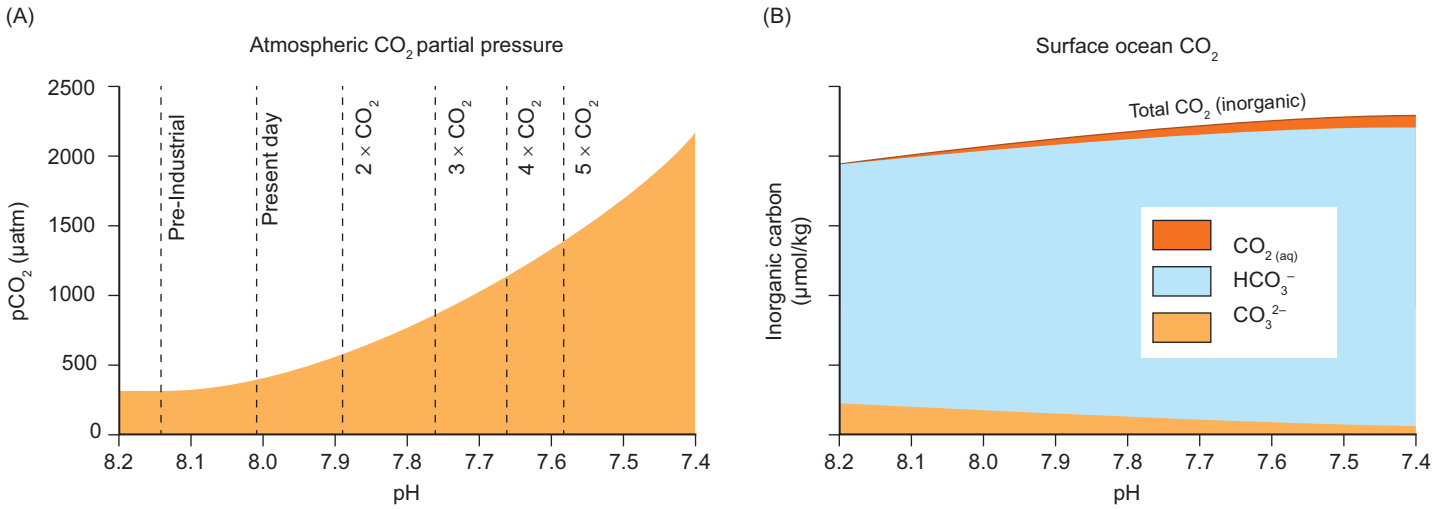


Figure 2.2 A. Increasing atmospheric CO_2 causes an increase in the partial pressure of CO_2 (pCO_2) dissolved in the ocean's surface, which increases the concentration of carbonic acid and reduces ocean pH. B. Reduced ocean pH increases the total amount of dissolved inorganic carbon, by increasing the concentration of dissolved carbon dioxide and bicarbonate. Note, however, that even though total dissolved inorganic carbon increases, the concentration of carbonate declines sharply with acidification.

This carbonic acid increases hydrogen ion concentration through the following reaction:

$$H_2CO_3 \rightleftharpoons HCO_3^-(\text{bicarbonate}) + H^+$$

This increases the acidity, or more properly, decreases the alkalinity of the ocean. Since the onset of industrialization, the mean ocean pH has declined about 22%, from 8.16 to 8.05.

Coral and many other marine organisms use calcium carbonate to build their skeletons with the following reaction:

$$Ca^{2+} + CO_3^{2-}(\text{carbonate}) \rightleftharpoons CaCO_3(\text{calcium carbonate})$$

But as the ocean becomes more acidic, the higher concentration of dissolved hydrogen ions shifts the equilibrium of the following reaction to the right:

$$CO_3^{2-} + H^+ \rightleftharpoons HCO_3^-$$

This robs coral of the carbonate needed for making skeletons. Figure 2.2 shows the relationship between pH and levels of CO_2, HCO_3^-, and CO_3^{2-} in the ocean.

How bad is this trend for the future of the ocean's most productive biome? Joan Kleypas and her colleagues (2006) summarized the results of 12 laboratory studies conducted on 11 species of scleractinian corals, the most important components of coral reefs. Each study found that a doubling of CO_2 levels from preindustrial times, which is projected to occur within the next 50 years, led to a reduction in calcification rates; the average reduction was about 30%. As they also experience coral bleaching brought on by rising ocean temperatures, and damage from fishing trawlers, coral reefs are one of the most endangered biomes.

Terrestrial ecosystems are also suffering from human-induced acidification. In many industrial temperate zones, coal-fueled power plants emit large quantities of sulfur dioxide and nitrogen oxides. In the atmosphere, these substances react to form sulfuric acid (H_2SO_4) and nitric acid (HNO_3), strong acids that descend in rain, fog, or dust over large areas downwind from these sources. Acid deposition reduces soil pH, and can kill soil microorganisms that have mutualistic interactions with plants. Acid deposition can also release toxic metals that are bound to rocks, and can leach away vital soil nutrients. In many areas, numerous trees are dead and overall species richness has declined dramatically from acid deposition.

Acid deposition is a global problem (Figure 2.3). Though primarily affecting temperate biomes, the problem is now spreading as countries in tropical regions become more industrialized and dependent on fossil fuel. One recent study indicates that in the near future, tropical regions will lose biological diversity at a much higher rate from acid deposition than will any other terrestrial biome (Azevedo *et al*. 2013).

As we have just seen, prevailing currents and the chemical environment have a major influence on species richness and overall ecosystem functioning. Other physical conditions, such as air and water temperature, also influence which organisms live where. Let's explore some of the basic principles underlying global variation in these defining factors.

2.1 HOW DO PHYSICAL PRINCIPLES INFLUENCE CLIMATIC VARIATION ACROSS THE GLOBE?

In almost every respect, the Sun is the primary driver of life on Earth. *Photons* – particles or waves of solar radiation – stream into space in all directions. Though only a miniscule fraction of these photons are intercepted by Earth's atmosphere, enough radiation penetrates to Earth's surface to support most

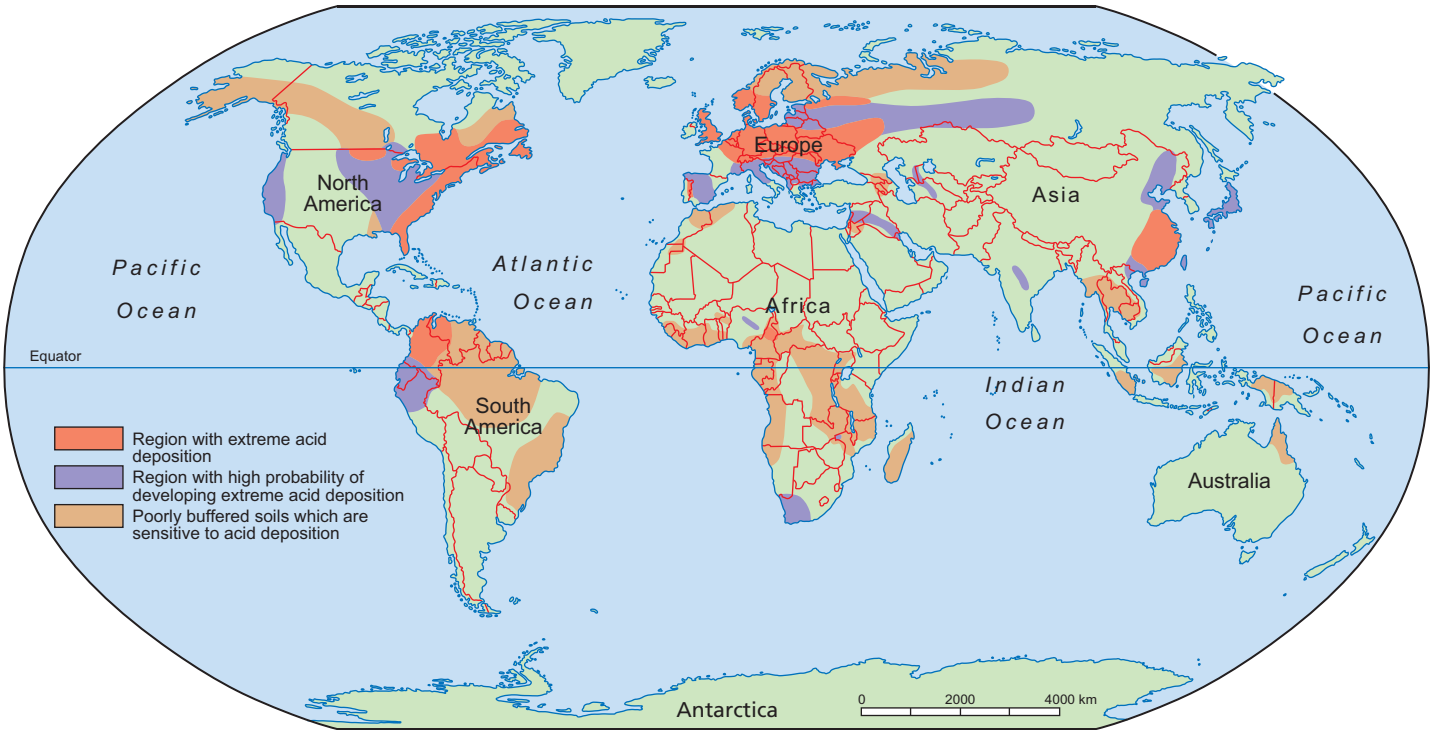


Figure 2.3 Terrestrial regions of the world with problematic levels of acid deposition.

ecosystems. Though the Sun is an unbiased emitter, showing no favor in the direction it sends its photons, Earth's curvature makes the planet a very biased receiver, favoring some latitudes over others.

Influence of latitude and season on surface temperature

It should come as no surprise that it is hotter near the equator than at the poles and that, outside of the tropics, it is hotter in the summer than the winter. Figure 2.4 demonstrates two reasons for this relationship. The arrows represent photons as they strike Earth's atmosphere. On average, photons will be an equal distance apart as they travel from the Sun. However, because of Earth's curvature, photons headed toward the equator will be more closely packed than those destined for polar regions. Thus, on average, more photons strike a unit of area of the equatorial atmosphere than the polar atmosphere. A second influence of Earth's curvature is that there is more atmosphere for a photon to travel through near the poles than near the equator (Figure 2.4). Overall, almost 50% of the photons never reach Earth's surface, either being absorbed or reflected back into space by molecules or atmospheric particles. Over the course of a year, about twice as many photons reach Earth's surface at the equator in comparison to the amount at 60° latitude (Buffo *et al.* 1972). This contrast is illustrated by global differences in direct radiation, a measure of the amount of energy striking a defined area over time (Table 2.1). Such data can be extrapolated to estimate direct radiation at other

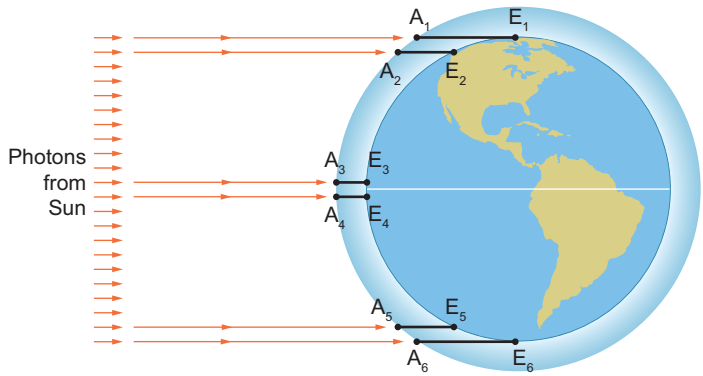


Figure 2.4 Photons traveling parallel and equidistant from each other are further apart when striking the atmosphere because of Earth's curvature. Compare the distance between A3 and A4 to A1 and A2 or A5 and A6. Then notice that photons passing through the atmosphere near the poles have much more atmosphere to go through (A1 to E1, or A6 to E6) before reaching the Earth's surface than do photons near the equator (e.g. A3 to E3).

locations (see Dealing with data 2.1 for a discussion of extrapolation).

Because Earth's rotational axis is approximately 23.5°, the position of the greatest direct solar radiation varies seasonally. On December 21, the most direct rays strike at 23.5° S (the Tropic of Capricorn). As the year progresses, the position of the most direct solar radiation gradually moves northward, reaching the equator on March 21, and 23.5° N (the Tropic of Cancer) on June 21. After June 21, the position of the most direct solar radiation returns southward, revisiting the equator on September

Table 2.1 Annual direct radiation striking Earth at different latitudes.

Latitude (°)	0	10	20	30	40	50	60
Direct radiation (Cal./cm^2/day)	266 271	261 965	249 369	228 998	201 947	169 828	135 941

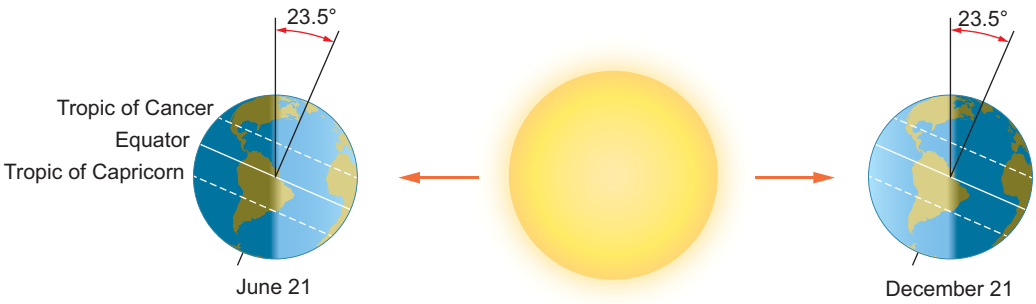


Figure 2.5 The position of Earth in relation to the Sun determines which latitude receives the most direct solar radiation over the course of one solar revolution. All dates in the figure and text above are ±2 days.

Dealing with data 2.1 Extrapolation

Extrapolation estimates new data points that lie outside the range of existing data points. For example, if you had a series of data points 2, 3, 4, 5, and 6, you might extrapolate, with a fair degree of confidence, that the next data point will have the value of 7. The confidence of your extrapolation depends on how well you understand the mechanism that is creating the data points. For example, if you had the data points 1, 2, and 4, you could extrapolate, but with much lower confidence, that the next value is 8, reasoning that each point was the previous point multiplied by two. However, it is equally likely that the next data point would be 7, with each point being the previous point plus the position the previous point occupies in the sequence.

In the case of Buffo's data, we can see quite clearly from Figure 2.4 that the number of photons striking the Earth should continue to decrease more sharply with increasing latitude, because the influence of the curvature of the Earth becomes more significant as we approach the North Pole. Without knowing all the mathematical computations, we could not come up with a precise extrapolation/projection, but we could probably come pretty close to the actual number. Buffo and his colleagues only computed to 60° north, because the computers they had available in 1972 were overwhelmed by the task of dealing with the absence of light during some winter days in the polar regions.

The confidence in your extrapolation also decreases as you move further outside the range of existing data points. If you were to estimate direct radiation values for 70° N and for the North Pole, you would expect your estimate for 70° N to be closer to the actual value.

Thinking ecologically 2.1

John Buffo and his colleagues (1972) wanted to know how much direct radiation struck the Earth at different latitudes. Can you extrapolate from Table 2.1 an estimate of the direct radiation striking the North Pole over a 1-year time period (See Dealing with data 2.1)?

21, and completing the cycle on December 21. Thus December 21 heralds the beginning of summer for the southern hemisphere and winter for the northern hemisphere, while the reverse is true for June 21 (Figure 2.5).

Only a small portion of direct solar radiation actually heats Earth's surface. Much of the solar radiation striking Earth is radiated back into the atmosphere in the form of longwave radiation. Much of this energy is absorbed by atmospheric molecules such as water vapor, carbon dioxide, and ozone, and reradiated back to the Earth, helping to warm Earth's surface even more. This greenhouse effect (Chapter 23) is responsible for the approximately linear decrease in temperature with increasing distance away from Earth and into the troposphere (Figure 2.6).

As we will discuss in later chapters, many other factors influence global temperature patterns as well. Now we'll investigate some of the primary factors that influence global precipitation patterns.

Influence of latitude and season on precipitation

The bases of global precipitation patterns have confounded scientists for many centuries. Some aspects are very well understood, while others continue to be mysterious, even to professional meteorologists.

The relationship between precipitation and atmospheric pressure

Earth's atmosphere is made up of molecules of gas, primarily nitrogen (78%) and oxygen (21%), with many other gases present in much smaller quantities. The atmospheric pressure per m^2 exerted by the weight of the air above Earth's surface averages 1013.25 millibars (mb) or 101.3 kilopascals at sea level. There are

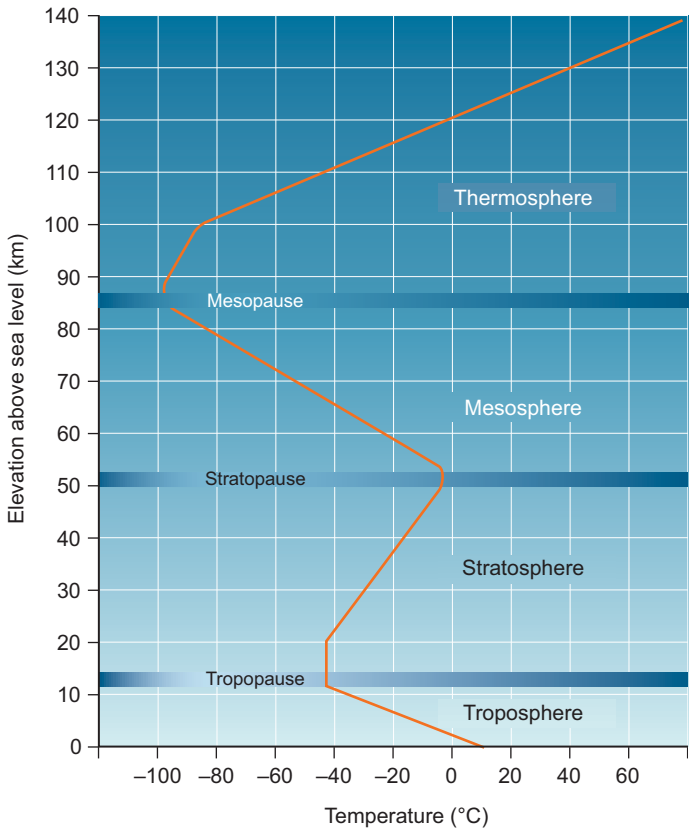


Figure 2.6 Atmospheric temperature profile in relation to elevation above sea level. Note the nearly linear temperature decrease in relation to elevation in the troposphere and the abrupt transition to different relationships in the other atmospheric layers.

many more gas molecules near the surface, in part because of Earth's gravitational attraction, so the atmospheric pressure decreases sharply with elevation above sea level (Table 2.2).

But air masses vary in pressure. Areas of low pressure form from warm air that rises, because warm molecules have higher kinetic energy, and are spaced farther apart than cooler molecules. As the air cools at higher altitudes in the troposphere, the water vapor condenses and forms clouds and rain. Some parts of Earth get a lot of rain, because these low-pressure systems consistently form over them.

Variation in precipitation from the equator to the poles

One important factor influencing precipitation patterns is differential heating of Earth's surface. For simplicity, let's consider Earth at one of the equinoxes, with direct solar radiation striking the equator. The resulting hot air mass is forced upward, cooling as it rises. Because cool air holds less water than hot air, the water vapor molecules condense, forming clouds and ultimately producing the heavy rains characteristic of equatorial regions. This zone of upwelling, warm moist air is the **Intertropical Convergence Zone (ITCZ)**. Because hot air is being generated below it, this initial air mass, now high in the troposphere, is forced away from the equator, both north and south.

At around 30° latitude, north and south, this air mass, now much cooler, begins its descent toward the surface from the upper troposphere. As it descends, it warms, and because it has already lost much of its moisture on its ascent near the equator, it tends to create a very dry environment at this latitude. Many of the world's

Table 2.2 Relationship between mean atmospheric pressure (kPa = kilo Pascals) and elevation above sea level for selected geographical landmarks (many are discussed in this chapter).

Geographic landmark	Elevation (m)	Atmospheric pressure (kPa)
Dead Sea	-423	107
Sea level	0	101
Lake Yoa	378	97
Ulaanbaatar	1350	86
Mount Marcy (Adirondack State Park)	1629	83
San Pedro de Atacama (Atacama desert)	2407	75
Mauna Loa	4169	60
Mount Kilimanjaro	5895	48
Mount Everest	8850	31

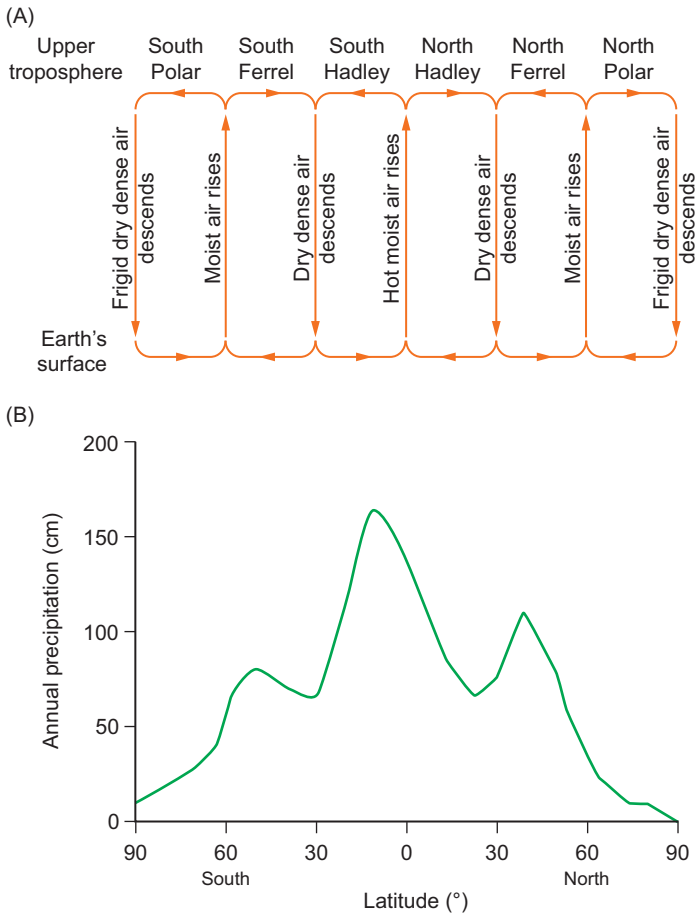


Figure 2.7 A. Formation of the Hadley, Ferrel, and polar cells. These cells are constantly shifting, so the latitudes are only approximate. B. Annual precipitation in relation to latitude. The peaks in the graph result from rising air masses cooling as they rise, causing condensation and precipitation. The low points in the graph result from descending air masses warming as they descend, and becoming even drier.

great deserts are found at about 30° latitude. Now at the surface, some of this dry air mass flows toward the equator, completing a cell of circulating air known as the **Hadley cell**, and the rest flows away from the equator, forming the surface component of a second circulatory cell, the **Ferrel cell** (Figure 2.7A). We will leave the Ferrel cell for a brief digression to the polar regions.

The key to understanding the formation of a **polar cell** is to recognize that the poles receive the least solar radiation, and have the coldest temperatures. As the cold air masses over the poles sink toward the surface, they absorb heat and become warmer, which increases their ability to hold moisture. Thus polar regions receive very little rain (or snow). As this cold air reaches the surface, it is forced away from the poles by the cold air descending from above. As it moves away from the poles, it tends to warm somewhat. At about 60° latitude, this polar air mass collides with the warmer air from the Ferrel cell. As we've already described for air at the equator, warm air tends to rise. As it rises to higher elevations it cools down, forming a second region of heavier precipitation at 60° latitude (Figure 2.7B).

As happened at the equator, some of the air mass, now high in the troposphere, where it has become much cooler and has lost much of its moisture, is forced toward 30° latitude, completing the circulation of the Ferrel cell. The remainder of the air mass is forced toward the poles, completing the circulation of the polar cell. Thus both the northern and southern hemispheres have three major circulatory cells, which result in a pattern of high precipitation near the equator and 60° latitude, and lower precipitation at 30° latitude, and especially at each pole (Figure 2.7B).

Seasonal shifts in precipitation peaks

Our previous discussion of air cells neglects the periodicity of direct solar radiation. As you might expect, the ITCZ migrates north of the equator during the northern spring and summer, and migrates south of the equator during the southern spring and summer. This migration is in part responsible for the great monsoons in India and the Sahel region of Africa that usually begin in July, and in northern Australia that usually begin in December.

Because water has a very high specific heat (4.1855 J/g or 1 cal/cm^3), it takes much more solar radiation to heat water than land. In addition, water absorbs about 2260 J/g as it vaporizes, which slows down its rate of heating during the summer. As a result, landmasses that receive the Sun's direct rays tend to heat up much more rapidly than nearby oceans. These large masses of warm air develop into strong low-pressure systems, which when coupled with moisture-laden prevailing winds can cause tremendous amounts of rain to fall within relatively short time periods. As the ITCZ moves away from these regions, the disproportionate heating subsides, and monsoon rains abate for another year.

Meteorology would be a very simple science if the air cells and precipitation shifts described thus far made up the entire picture. However, many other factors influence the movement of air masses, which in turn also influences the movement of water in the oceans. One important factor is the **Coriolis effect**, which tends to deflect air masses away from a linear path.

Deflection of air masses by the Coriolis effect

If we were to view the Earth from a stationary reference point in space, an object on the equator would speed from west to east at a velocity of 1674 km/h. It is moving so quickly, because it will do one complete rotation along the equator (*c.* 40 176 km) every 24 h. But this same object at 45° latitude has only 28 290 km to cover in the same time period, so it will travel a somewhat more mundane 1179 km/h. Meanwhile, an object at the poles will appear to not travel at all, merely making one complete rotation every 24 h while fixed in space.

This has important implications for understanding wind currents, and the formation and movement of storms. For example, if we consider the north Hadley cell, the air mass from 30° N is moving near the surface toward the equator, and encountering

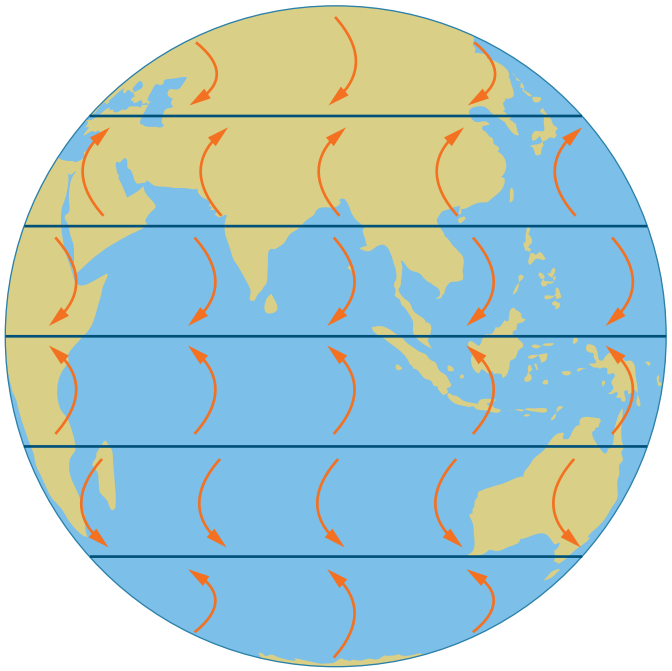


Figure 2.8 Coriolis effect deflects air currents to the right in the northern hemisphere and to the left in the southern hemisphere.

an Earth that is spinning from west to east faster than it is. So it tends to lag behind, or curve to the right as it moves south. Conversely, if we consider the south Hadley cell, the air mass from 30° S will also lag behind as it moves toward the equator, curving to the left as it moves north. Wind currents are named by the direction from which they come. Thus the northeast trade winds in the northern Hadley cell originate in the northeast and flow to the southwest (Figure 2.8).

Overall, air masses in the northern hemisphere tend to deflect toward the right, while air masses in the southern hemisphere tend to deflect toward the left. If you are having trouble visualizing this, you should do the following experiment. Grab a ball and a marker pen. Circumscribe the ball at the approximate locations of the equator, 30° N, and 30° S, to mark the outlines of the two Hadley cells. Rotate the ball from west to east along the equatorial plane. If you view it from above, you will notice it is rotating counterclockwise, but if you view it from below, you will note it is rotating in a clockwise direction. Thus the direction of rotation is a matter of perspective. While rotating your ball, draw a line due south from 30° N to the equator. You will note that your "line" is actually a curve that is deflected to the right, analogous to the northeast trade winds in the north Hadley cell. Then repeat this experiment to simulate the southeast trade winds of the south Hadley cell.

The Coriolis effect also influences the ocean's currents. The ocean's **gyres**, or large-scale surface circulations, tend to be deflected to the right in the northern hemisphere, and toward the left in the southern hemisphere.

We've only scratched the surface in describing the relation between solar radiation, precipitation, and currents. We have focused our discussion on temperature and moisture, because these two factors are viewed by most ecologists as responsible for the formation of the world's terrestrial biomes.

2.2 WHAT ARE TERRESTRIAL BIOMES?

A terrestrial biome is a large land area with characteristic groups of organisms adapted to its environment. In his classic book, *Communities and Ecosystems*, Robert Whittaker (1975) recognizes 26 types of terrestrial biomes. You will learn the major characteristics of only eight types of terrestrial biomes, but should appreciate that condensing this list necessitates that there will be substantial variation within biomes regarding climate and types of organisms (Figure 2.9).

Defining and distinguishing biomes: an exercise in ambiguity

Few ecologists agree on how many terrestrial biomes there actually are, for several reasons. First, subjectivity enters into deciding whether two geographical areas have sufficiently different characteristic organisms to be classified as defining two distinct biomes. For example, Whittaker (1975) described one biome as a tropical seasonal forest, and a second with somewhat less precipitation as a woodland. Is this distinction biologically meaningful? Second, the boundaries between biomes are not distinct, and one biome will usually grade into another. This again makes it difficult to evaluate whether there is one highly variable biome in a region, or two adjacent biomes that differ from each other only marginally.

Finally, new biomes are still being discovered. For example, Li-Hung Lin and his colleagues (2006) described a subterranean biome dominated by one group of Firmicutes bacteria living at a depth of 3–4 km below the surface. These organisms reduce SO_4^{2-} (sulfate) to H_2S (hydrogen sulfide) in a many-step process that produces enough ATP for their metabolic needs. The sulfate is leached from volcanic rocks. The researchers estimate that this particular site has been functioning for at least 3 million years. There is no reliance on photosynthesis as an energy source, in contrast to the plant-dominated biomes, so some ecologists argue that this ecosystem should be classified as a distinct biome.

How climate influences Earth's terrestrial biomes

Rainfall and temperature are the two most important factors influencing the development of terrestrial biomes. Whittaker (1975) summarized how these two variables interact to create the eight biomes that we discuss below (Figure 2.10). But several other factors, such as soil characteristics and the frequency and type of disturbances, such as fires or monsoon floods, can also influence the type of biome characteristic of a region.

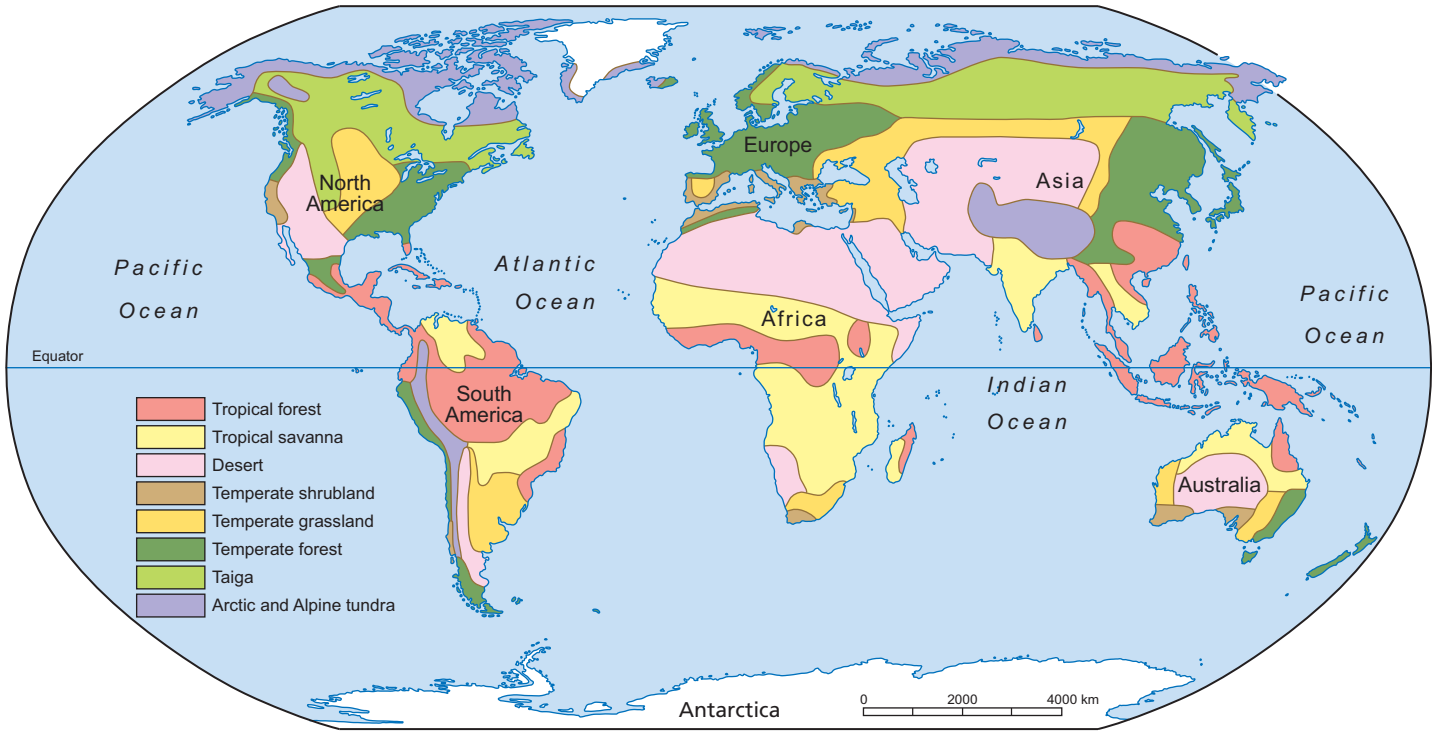


Figure 2.9 Terrestrial biomes of the world.

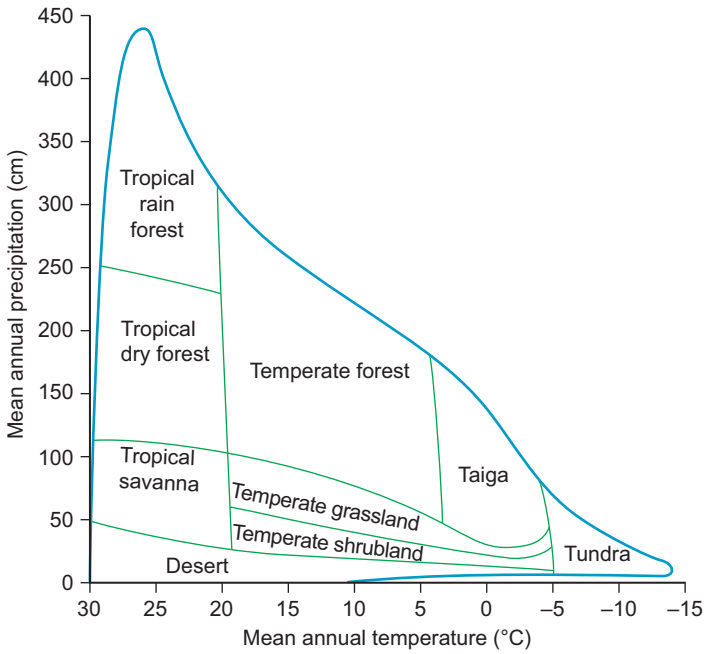


Figure 2.10 Pattern of terrestrial biomes in relation to mean annual temperature and precipitation.

Whittaker's summaries were a breakthrough in understanding the relationship between climate and biomes. However, you will note that his axes are mean annual temperature and mean annual precipitation. As Whittaker acknowledges, it is not only the annual data that are important, but also how the temperature and precipitation are distributed over the course of a year that influence the establishment of a particular biome in a given region. For each biome, we will provide a representative graph that illustrates this variation over the course of a year by providing mean values for each month (see Dealing with data 2.2).

Tundra: frigid and dry

If you like extremes, you'll love **tundra**. This is the dominant biome of the northern rims of Asia, North America, and, increasingly, sections of Antarctica. Most tundra is quite flat and very dry, with extremely cold winter temperatures and cool summers. Most tundra has a permanently frozen soil layer called *permafrost*, and a thin, nutrient-poor upper soil layer that freezes each fall and thaws each spring.

Species diversity is low, but abundances of species adapted to the tundra may be extraordinarily high. Because of the permafrost, plant root systems are shallow, and cold temperatures and low levels of solar radiation create a short growing season. Thus plants tend to be small, with dwarf willows, birches, and alder the commonest trees. Ground cover is provided by lichens, *Sphagnum*, grasses, and **forbs** – nonwoody plants other than grasses. Most insects go through periods of *diapause* – metabolic and developmental dormancy – during the winter, and then metamorphose into huge swarms in the spring. Some bird species undergo vast migrations to reap the benefits of this entomological bounty, in some cases producing several clutches of babies over the brief breeding season. Small mammals are often abundant but may go through regular

Dealing with data 2.2 Means, sampling, and why we do statistics

The sample mean is probably the most commonly used statistic in all of science, in part because it is so easy to calculate, and in part because it is intuitively meaningful. We use the sample mean to estimate the population mean, which is often unmeasurable (usually because you can't find or measure the entire population). For example, if we want to estimate how much it rains in July in the tundra, we might find rainfall data from four different tundra locations in a database, add those values up and divide by four (our sample size), and that result would be our mean. These four different sites on the tundra are our samples, and we use these samples to make inferences about our population, which is theoretically made up of all the different locations on the tundra.

More formally:

$$\overline{X} = \frac{\sum X}{N}$$

where $\overline{X}$ = the sample mean,
ΣX = the sum of all the samples, and
N = the number of values in the sample.

In this case my research found the following July rainfall values (in mm) from our four locations: 118, 67, 44, 41.

Then the mean ($\overline{X}$) = (118 + 67 + 44 + 31)/4 = 65

There are three major problems with the preceding procedure.

1. I am actually interested in a representative number for the tundra biome as a whole. The tundra is a population of many (theoretically infinitely) different sites, each of which has its own characteristic rainfall totals for July. I should definitely use a much larger sample size.
2. To estimate the population mean, I must choose my samples randomly. This means that every location on the tundra should have an equal probability of being chosen for my calculation. From a practical standpoint, this is impossible. But I could have been more random by using a very large database of tundra locations, and then randomly selecting within that database the values for my calculation. This procedure is still not completely random, because sites that were easy to measure were more likely to be in my database than were less accessible sites.
3. There is a great deal of variation among samples. The mean gives no indication of this variation. See Dealing with data 2.3 page 36 for a discussion of variation around a mean.

population cycles, while large mammals such as caribou (*Rangifer tarandus*) and musk ox (*Ovibos moschatus*) form herds that eat lichens, grasses, and new woody growth (Figure 2.11). Major mammalian predators are the wolf (*Canis lupus*) and Arctic fox (*Alopex lagopus*).

Alpine tundra occurs in high mountain ranges, just above the treeline. Climatic conditions for alpine tundra are also very cold, but moisture levels range from dry to quite wet. Alpine tundra generally lacks permafrost.

Taiga: cold, moist, and covered with forest

The **taiga**, or boreal forest, is a forester's dream. Spruce, fir, and pine trees dominate the landscape that occupies a wide swath just south of the tundra throughout most of North America, Europe, and Asia. The climate can be as extreme as the tundra directly to its north, with long frigid winters, and short but often warm summers. Precipitation levels are moderate, and moisture is generally abundant, because low temperatures and thick forest cover reduce evaporation rates. Soils are generally nutrient poor because of low decomposition rates in the cold climate. Though taiga plant diversity is very low, the animal communities there are somewhat more diverse than in the tundra, with many spectacular additions to the faunal landscape, including moose (*Alces alces*) and lynx (*Lynx canadensis*) (Figure 2.12).

Temperate forest: moderate climate, fertile soils, and diverse forests

The name of this biome implies moderation, and indeed **temperate forests** grow under relatively moderate conditions: warm summers, cool winters, and significant rainfall – generally 600 to 2000 mm per year. Soils are usually fertile, and the growing season is much longer than that of the taiga. Deciduous trees dominate most temperate forests, with the exception of southeast Australia, where evergreen eucalyptus are abundant,

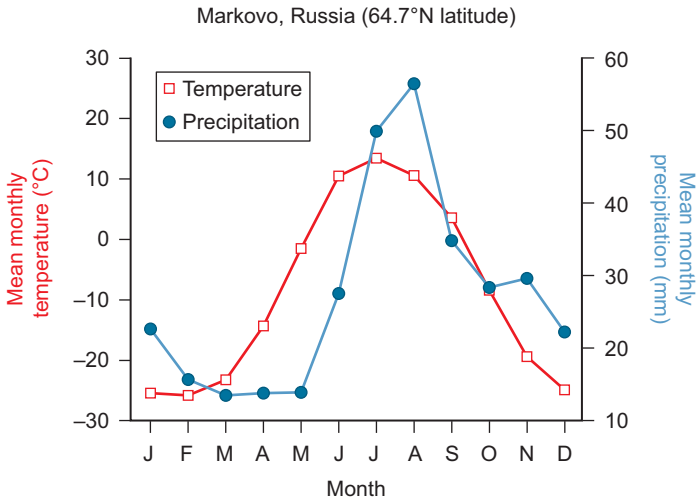


Figure 2.11 Reindeer grazing on Siberian tundra (top). Climate diagram of Markovo, Russia (bottom).

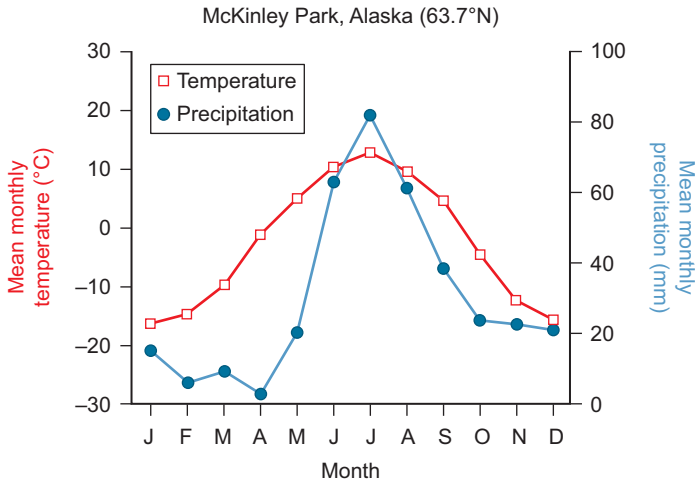


Figure 2.12 Bull moose bugling his mating call in an opening in the Alaskan taiga (top). Climate diagram of McKinley Park, Alaska (bottom).

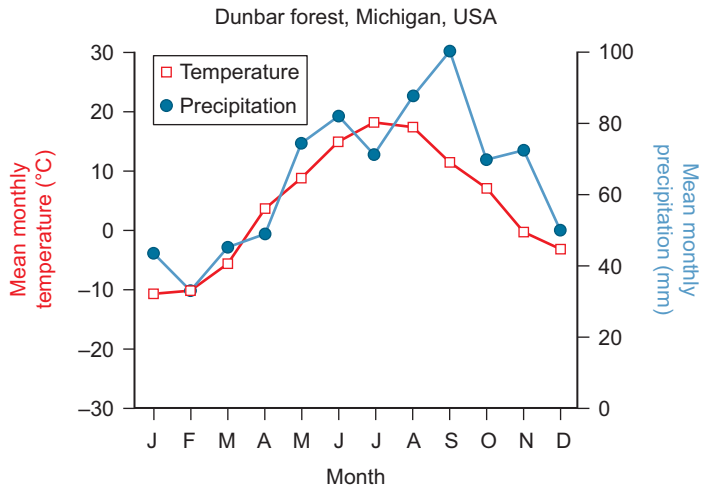


Figure 2.13 Temperate forest in Michigan, USA, highlighted by maple trees showing off their fall foliage (top). Climate diagram of Dunbar forest (bottom).

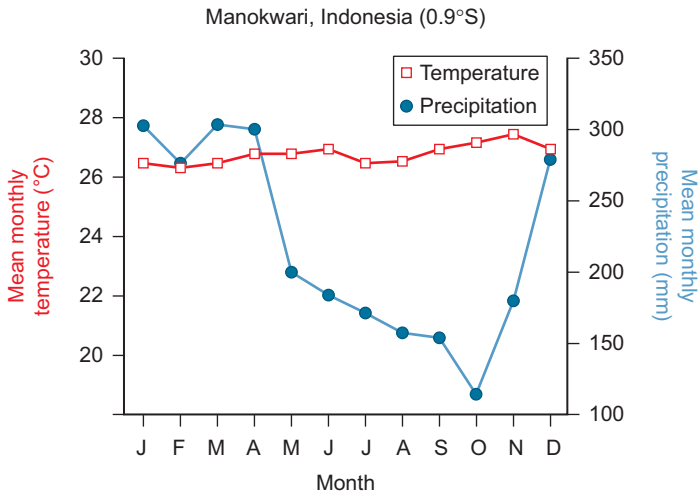
and the northwest United States, which is primarily dominated by conifers. Most temperate forests are stratified, with a canopy layer above one or several layers of understory trees, and a layer of shrubs and herbaceous plants just above the surface. With warmer temperatures and high moisture levels, there is substantial decomposition and generally fertile soils. All of this structure and relatively benign climate support a moderately diverse animal community (Figure 2.13).

Tropical forest: hot, humid, and species rich

The area between the two tropics is dominated by forests of two types: **tropical rainforest** (Figure 2.14A) and **tropical dry forest** (Figure 2.14B). Due to constant proximity to the ITCZ, the region within 10° of the equator is constantly warm and wet, supporting primarily rainforest, and stratified with luxurious deciduous evergreen trees looming over several layers of subcanopy trees, and shrubs, herbaceous plants, and ferns on the forest floor. Competition for light is intense within the rainforest; common growth forms adapted to this biome include **lianas**, vines that use the trees for support as they climb toward the canopy, and epiphytes. Tree species richness is extraordinarily high – a single hectare may support over 500 species. Stratification and high plant diversity create tremendous habitat diversity for other organisms. For example, 90% of primate species are native to tropical rainforests, and estimates of insect diversity range into the tens of millions of species.

Terry Erwin (1982) made an early attempt to estimate species richness in a tropical forest. Working in Panama, he fumigated the canopy of 19 individual linden trees, *Luehea seemanni*, and collected all the dead insects that drifted down onto sheets he laid next to the trees (Figure 2.15). He found over 1200 species of beetles, and estimated that 163 species were unique to that species of tree. His research indicated that approximately two-thirds of the species live in the canopy and one-third live in the bark and roots, so he extrapolated that the linden tree probably had about 245 unique beetle species. Zoologists estimate that approximately 40% of the forest's arthropods are beetles, so Erwin estimated that the linden tree probably had about 612 unique arthropods. Finally, he knew that tropical forests have perhaps 50 000 different tree species. If *L. seemanni*

(A)



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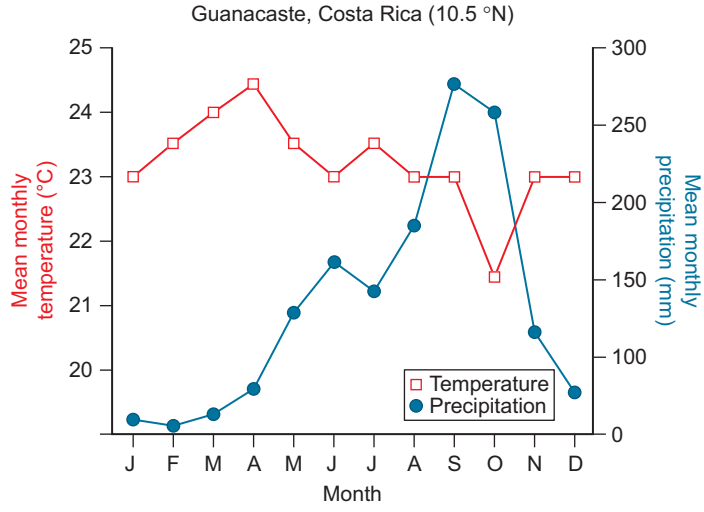

Figure 2.14 A. Understory of a tropical rainforest in Gunung Meja Nature Reserve, Irian Jaya, Indonesia (top, left). Climate diagram of Manokwari, Indonesia (bottom, left). B. Tropical dry forest during the dry season (top, right) and the rainy season (middle, right). Climate diagram of Guanacaste, Costa Rica (bottom, right).

Figure 2.15 Terry Erwin fumigates the forest canopy, and captures the dead insects on sheets placed below a linden tree.

supports average species richness, then the tropical forest should be home to over 30 million (612 × 50 000) arthropod species!

Panama, where Erwin did his research, is at about 9° N latitude. Because the ITCZ migrates seasonally, tropical regions somewhat distant from the equator tend to have substantial seasonal variation in rainfall, often with a pronounced dry season. Consequently, tropical rainforests tend to grade into tropical dry forests at about 10 to 15° latitude, north or south. Most tree species in tropical dry forests shed their leaves during the dry season as an adaptation to drought. Trees tend to be shorter, the forest is less stratified, and habitat diversity is lower. As a result, overall species richness is lower in dry forests than rainforests, but is still higher than in other terrestrial biomes. Surprisingly, soils in tropical rainforests and dry forests tend to be nutrient poor; ecologists have demonstrated that most of the available nutrients are quickly taken up by the abundant vegetation. Thus these forests are slow to recover from deforestation.

Thinking ecologically 2.2

What assumptions does Erwin's extrapolation make? How might you test whether these assumptions are valid?

Tropical savanna: prolonged dry season, abundant grasses, and occasional trees

Tropical dry forests grade into **tropical savannas** at about 15 to 20° latitude, north or south. Temperatures are warm all year, but there is a prolonged dry season, again partly in response to the movement of the ITCZ. Because tropical savanna is drier than most tropical dry forests, periodic fire has historically prevented the intrusion of woody growth there. However, savannas often have trees that are adapted to both fire and the relatively impermeable clay subsoil that prevents water from draining during the rainy season. This lack of drainage forms temporary lakes, which help irrigate the vast herds of herbivores and the surrounding vegetation. Grasses that escape a herbivore's attention create large numbers of seeds, most of which are harvested by an abundant and diverse assemblage of ants. There are many species of insectivorous birds that live in the grasses. The large mammals of the African savanna are legendary (and discussed in Chapter 1). It is puzzling that the savannas of South America and Australia have a much lower diversity and abundance of large mammals (Figure 2.16).

Desert: hot and dry with a wide range of species diversity

Many of Earth's great **deserts** , are found near 30° latitude, north and south, where moisture-starved air masses complete the Hadley cell. In the most extreme cases, some deserts, such as the Atacama Desert along the West Chilean coast, receive almost no rain. Under these conditions, the primary organisms are *hypolithic cyanobacteria*–photosynthetic microorganisms able to subsist on the moisture absorbed by stones (Warren-Rhodes *et al.* 2006), reflected sunlight, and tiny quantities of nutrients. But even these organisms are very limited by moisture availability (Figure 2.17).

However, most deserts are much rainier – some average up to 300 mm of rain annually. Desert soils are generally poor because the sparse vegetation does not contribute much organic matter to the soil when it decomposes. Sparse assemblages of salt-tolerant shrubs are common in the saline soils found in some deserts. Many plants imbibe and store water during the brief rainy season, while others lose their leaves during the dry season and are dormant during periods of water shortage. Many animals avoid temperature extremes by seeking out microhabitats that are protected from the Sun. But if you really want to experience the diversity of the desert fauna, you should spend a night there during the spring or early summer. As the Sun goes down, the

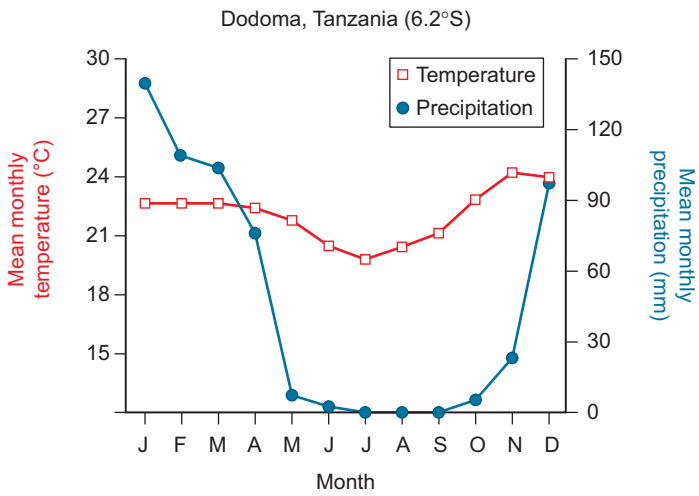

Figure 2.16 An impala joins a group of wildebeest under the shade of a tree in a savanna in Mikumi National Park, Tanzania (top). Climate diagram of Dodoma, Tanzania (bottom).

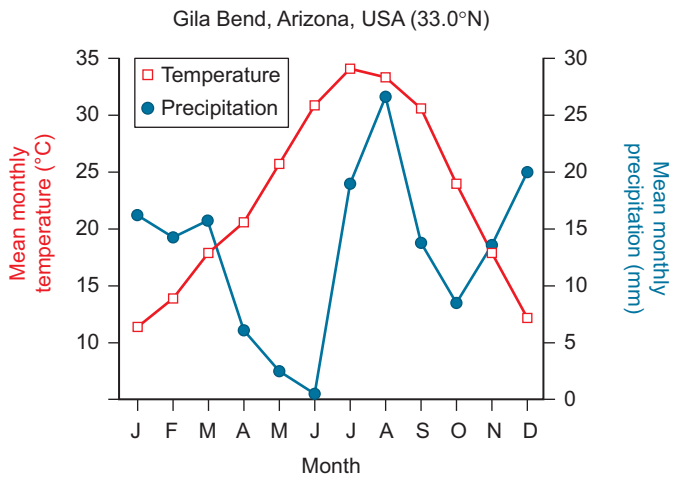

Figure 2.18 A coyote surrounded by desert vegetation in Joshua Tree National Park (top). Climate diagram of Gila Bend, Arizona (bottom).

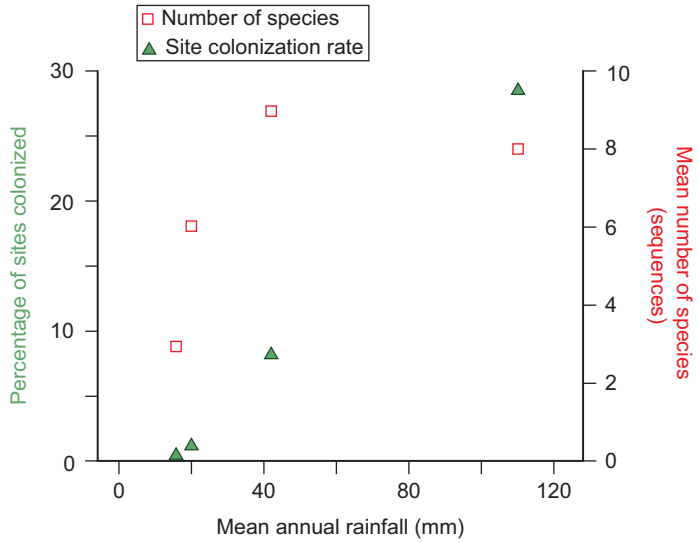

Figure 2.17 Relationship between mean annual rainfall and site colonization rate (triangles) and number of species (squares) of hypolithic cyanobacteria per site. Number of species is estimated based on the number of distinct DNA sequences (see Chapter 3).

desert transforms to a frenzied arena of animal activity. You may hear immense groups of insects singing, frogs calling out their mating choruses, or kangaroo rats thumping the ground with their huge hind feet. Reptiles and mammals that had been inactive during the day are now present in astonishingly large numbers (Figure 2.18).

Temperate grassland: cold winters, warm summers, and lots of grass

Temperate grasslands dominate the interior of Eurasia, North America, and to a lesser extent, South America. Far removed from the moderating effect of ocean proximity, this biome has cold winters and warm summers, but there is considerable variation when comparing the temperature profile of different grasslands (Dealing with data 2.3). Precipitation is moderate – generally 300 to 1000 mm annually. As the biome name implies, grasses and forbs are the dominant vegetation. Grasslands are similar to savannas in that fire helps to prevent woody vegetation from taking over. Temperate grassland is perhaps the most endangered terrestrial biome, because it has deep fertile soils, is easy to clear

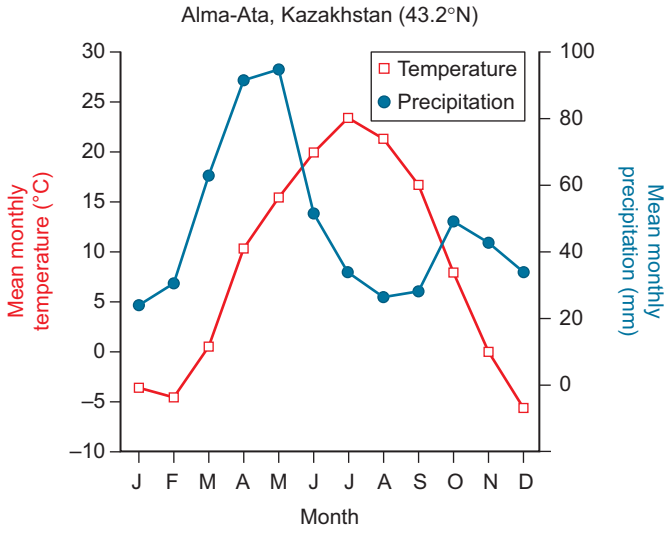

Figure 2.19 A Kazakh yurt stands in the Assy plateau grasslands in Almaty, Kazakhstan (top). Climate diagram of Alma-ata, Kazakhstan (bottom).

for agriculture, and has a relatively benign climate. Though the landscape is dotted with some grassland/prairie preserves, most people have never experienced the spring bouquet of flowers presented by an undamaged grassland. Also missing are the vast herds of large herbivores and the packs of wolves which either directly or indirectly derived their sustenance from the abundant vegetation (Figure 2.19).

Temperate shrubland: mild wet winters, hot dry summers, and occasional fires

In October, 2007, southwestern California, USA, and Baja California, Mexico, were ablaze, courtesy of very strong winds, a prolonged dry season, and various incendiary devices, including lightning, power lines knocked down by the winds, and matchsticks. All told, over 2000 km^2 of **temperate shrubland** burned over approximately 2 weeks. Over 1500 homes were destroyed, and many others were damaged. Though these fires were somewhat unusual in their coverage, fires are very common in temperate shrubland biomes.

Only nine people died in the fires, a relatively small number considering the devastation. People survived in part because they had been through this ordeal many times before (Figure 2.20), and many recently built residences were well adapted to fires, with well-insulated and fire-resistant windows and concrete roof tiles. The plants in this biome are fire adapted as well; they produce well-insulated seeds that germinate rapidly after fire, and shrubs that re-sprout after fire from a resilient root system.

Temperate shrublands are characteristic of the southwest sides of large landmasses at latitudes of 30 to 40°, north and

Dealing with data 2.3 Measures of variation

Each temperate grassland site will have a different climate, soil type, and chemical environment. But how different are the grassland sites from each other? Scientists use several related measures of variation to describe and analyse the amount of variation in their samples. Table D2.3.1 shows the mean monthly temperatures of five temperate grassland sites from around the world.

Whenever you see a new data set, your first step should be to look for trends. Obviously, June, July, and August are the warmest months, while December, January, and February are coldest. But which months are more variable from site to site? One approach is to consider the range – the difference between the largest and smallest value. It looks like May has the smallest range, 8.0°C, which is equal to Topeka (17.8°C) minus Ulaanbaatar (9.8°C). In this data set, the warmest months generally have a smaller range than the coldest months.

However, the range is not particularly useful, as it only considers the extreme values in a sample. Much more useful are the variance, standard deviation, and standard error. The formula for the sample variance is:

$$\text{Sample variance} = \frac{\sum(X - \overline{X})^2}{N - 1}$$

Σ indicates that we will sum up the values
X = the value of each observation,
$\overline{X}$ = the mean value for the sample,
and N = the sample size (5 in this case).

Table D2.3.1 Mean monthly temperatures (°C) from five different cities in temperate grassland biomes.

City	Country	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Volgograd	Russia	−11.0	−8.0	−2.5	8.5	15.0	20.0	23.0	20.0	15.0	6.5	0.5	−2.5
Ulaanbaatar	Mongolia	−21.1	−17.8	−8.9	1.4	9.8	15.0	16.9	15.6	8.9	0.3	−10.3	−18.9
Debrecen	Hungary	−2.5	0.6	5.6	11.1	15.8	18.9	20.1	20.0	16.4	11.1	4.7	0
Edmonton	Canada	−14.4	−10.8	−5.6	3.6	10.3	14.2	15.8	15.0	10.0	4.4	−5.8	−12.2
Topeka	USA	−2.8	0.8	6.7	12.5	17.8	23.3	25.8	24.7	20.0	14.2	5.8	−0.3
	Mean for each month	−10.4	−7.0	−0.9	7.4	13.7	18.3	20.3	19.1	14.1	7.3	−1.0	−6.8

Data from "Weather Underground" website (various dates).

Let's use this formula to calculate the variance for May.

1. We will calculate $(X - \overline{X})$ for each observation.
2. We will square each value of $(X - \overline{X})$.
3. We will add up (sum) the squares.

$$\begin{aligned} (X-\overline{X}) \qquad & \qquad (X-\overline{X})^2 \\ 15-13.7=(1.3) \qquad & \qquad (1.3)^2=1.69 \\ 9.8-13.7=(-3.9) \qquad & \qquad (-3.9)^2=15.21 \\ 15.8-13.7=(2.1) \qquad & \qquad (2.1)^2=4.41 \\ 10.3-13.7=(-3.4) \qquad & \qquad (-3.4)^2=11.56 \\ 17.8-13.7=(4.1) \qquad & \qquad (4.1)^2=16.81 \\ & \qquad \sum(X-\overline{X})^2=49.68 \end{aligned}$$

$$\text{The sample variance} = \frac{\sum(X-\overline{X})^2}{N-1} = \frac{49.68}{5-1} = 12.42$$

There are two other commonly used measures of variation.

$$\text{The standard deviation (SD)} = \sqrt{\text{Variance}} = \sqrt{12.42} = 3.52$$

$$\text{The standard error of the mean (SE)} = \frac{\text{SD}}{\sqrt{N}} = \frac{3.52}{\sqrt{5}} = 1.57$$

To make sure you understand how this works, try calculating the three measures of variation for January. Looking at the data before you do the analysis, you should expect January to show considerably more variation than May.

south. This same biome goes by many different names in different parts of the world, such as Mediterranean shrubland, chaparral, maquis, matorral, and fynbos (Figure 2.21). The winters are wet and mild, while the summers are hot and very dry, leading to a short growing season. Consequently, production is usually low and decomposition rates are moderate in the cool winter, and moisture limited in the summer drought. Low production and low decomposition rates tend to create soils that are nutrient poor. The plants in this biome have small, thick, and waxy leaves, which help conserve moisture during the regular summer droughts. Their **stomata**, organs that regulate water and CO_2 balance, tend to be sunken and covered with

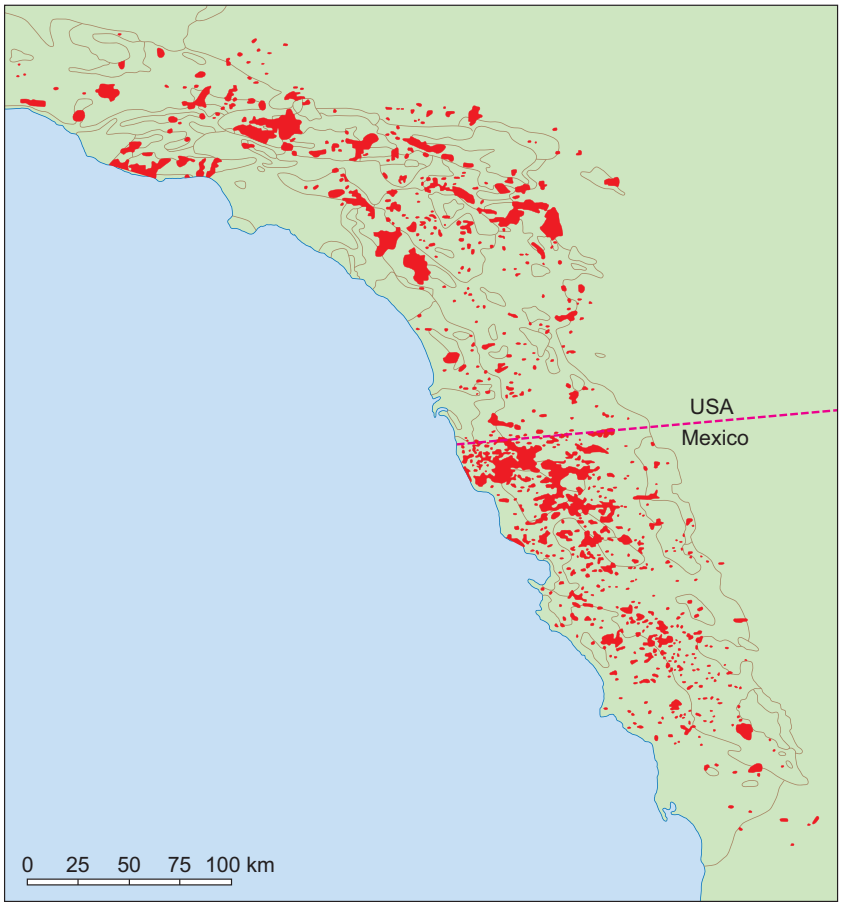

Figure 2.20 Fire boundaries (red) in 1972 to 1980 in southwestern California, USA, where fires had been suppressed historically, and Baja California, Mexico, where fires were allowed to burn historically.

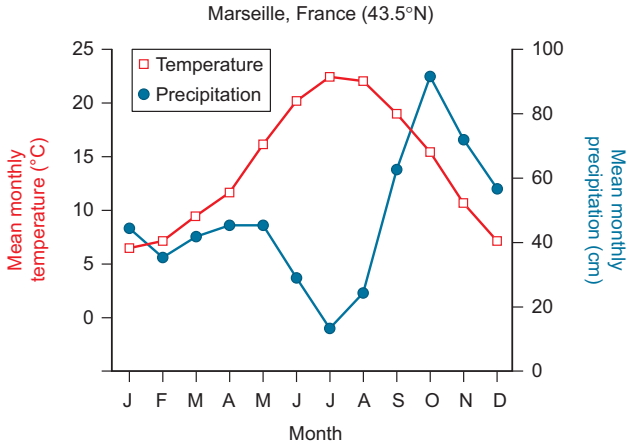

Figure 2.21 Temperate shrubland (maquis) near the southern coast of France (top). Climate diagram of Marseille, France (bottom).

trichomes or hairs that reduce water loss. Temperate shrublands host a high diversity and abundance of animals, including many mammals that browse leaves and branches from the shrubs and forbs.

Biomes, their borders, and their species composition are constantly changing. We will use an unlikely lake in the middle of the arid Sahara Desert as a portal to see how these changes occur.

2.3 HOW DO BIOMES CHANGE OVER TIME?

The Sahara is the world's largest desert, at about 9 million km^2. Recent evidence indicates that beginning about 15 000 years ago, the Sahara was primarily tropical savanna, laced with numerous lakes and wetlands, and even some tropical vegetation (Holmes 2008). What happened to convert the "Green Sahara" into the massive desert we know today? How can we be sure that the events I just described actually happened, and when did this conversion from savanna to desert actually take place? These are simple questions with complex answers, and we will explore a few of them here.

Figure 2.22 A. Researchers collecting core sample from the bottom of Lake Yoa. B. Part of 9 m long core sample, with 5 cm of sample in inset.

Inferring ecological history from sediment cores

Lakes have geological histories, which we can infer from several sources. Perhaps the most useful source of information is the layer of sediment that forms on the bottom of a lake, because it contains a record of conditions in the lake, and – equally important for our questions about the Sahara – of conditions in the surrounding terrestrial environment.

Paleoecologists reconstruct the history of the distribution and abundance of species. When working on lakes, researchers can

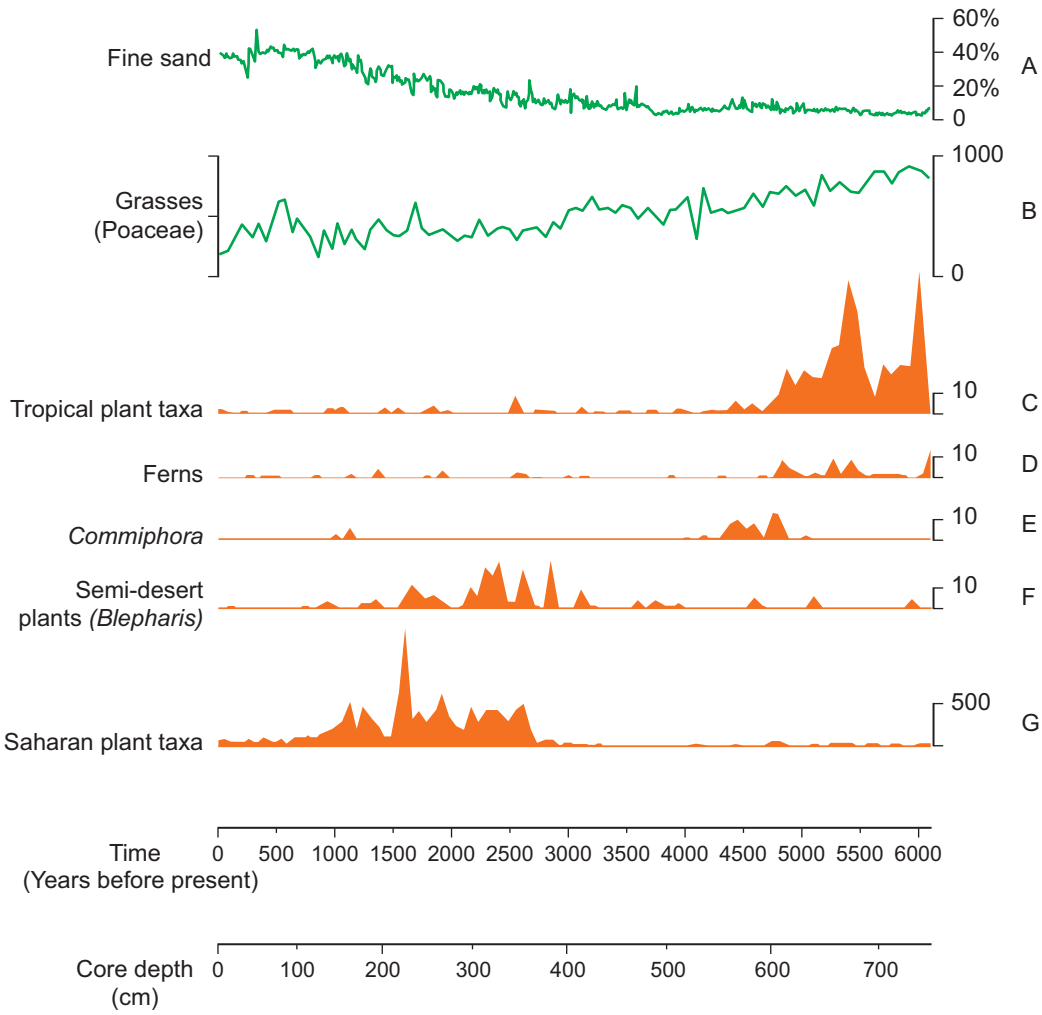

Figure 2.23 Changes to the terrestrial ecosystem surrounding Lake Yoa in the past 6000 years as inferred from sediment cores. All pollen measures are scaled as number of grains of pollen present per cm^2 of the core sample over a year time span. A. Steady increase in fine sand (measured as percent of the sample). B. Decrease in pollen from grasses (genus *Poa*). C. Decrease in tropical plant taxa. D. Decrease in ferns. E. Near extinction of flowering plants in genus *Commiphora* beginning 4200 years before the present (YBP). F. Increase in *Blepharis* beginning 2700 YBP. G. Increase in Sahara-type desert plants beginning 2500 YBP.

drive a core sampler into the sediment that has collected over thousands of years at the bottom of a lake, to extract a core sample that contains pollen grains and animal microfossils from different depths. The hollow tube of the core sampler is designed to collect sediment and its contents with a minimum of disturbance to the sample (Figure 2.22). From this core sample, researchers estimate the abundance of each species, and the type of soil prevalent in the surrounding terrestrial environment. They then use either relative or absolute dating techniques to estimate the age of material collected at varying levels of the core sample. Pollen grains and microfossils buried deep in the lake sediment represent more ancient species, while materials near the surface represent more recent species.

Lake Yoa in northeastern Chad has an area of about 3 km^2 and a maximum depth of about 25 m. Despite a tremendous evaporation rate of about 6 m per year, it has not dried up because it receives a continuous influx of water from an *aquifer* – an underground layer of water-bearing rock or soil – that was formed during the Green Sahara age. So long as the aquifer continues to supply Lake Yoa with water, it will continue to exist. But when the aquifer dries up, the lake will evaporate very quickly.

Inferring Sahara transitions from Lake Yoa sediment cores

Stephan Kröpelin and his colleagues (2008) used the information buried in the Lake Yoa sediment to infer both the history of the terrestrial environment and the history of the lake itself over the past 6000 years. Their cores showed a steady increase in fine sand particulate coupled with a fairly steady decrease in grass pollen, indicating a gradual transition from the Green Sahara to more arid conditions (Figure 2.23A and B). Tropical trees and ferns were well represented in their fossil record beginning at 6000 years ago, until dropping rather abruptly about 4500 years ago (Figure 2.23C and D). Shrubs (genus

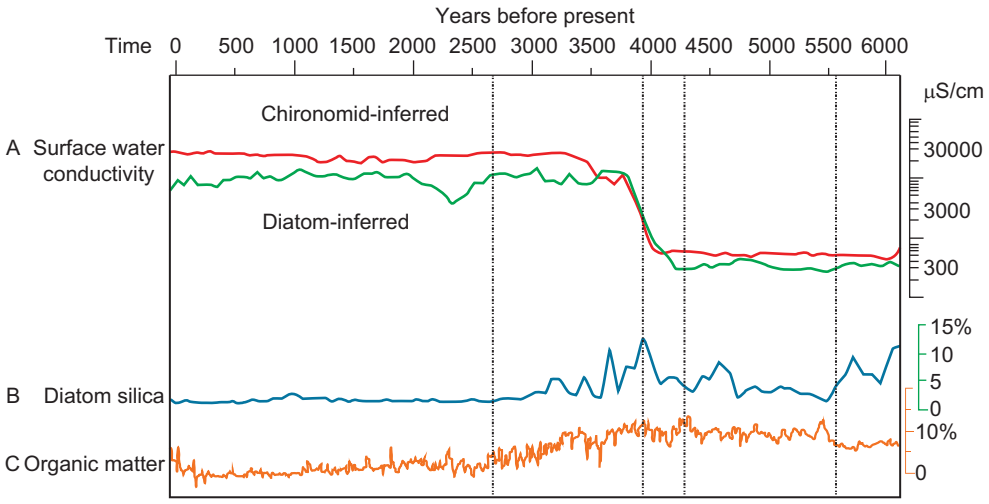

Figure 2.24 Chemical and biological changes to Lake Yoa in the past 6000 years inferred from sediment cores. A. Surface-water conductivity (µS/cm), a measure of salinity, as inferred from the record of diatoms and chironomids. B. Abundance of diatoms as measured by quantity of silica in the sample (diatom cell walls are made from silica). C. Decline in the amount of organic matter in the sample beginning about 4000 YBP.

Thinking ecologically 2.3

There were many different types of diatoms and chironomids at different depths of the Lake Yoa core. Modern African lakes vary in salinity and in the species composition of diatoms and chironomids, with lakes of similar salinity levels tending to have similar species composition. The researchers inferred salinity levels in the past 6000 years by comparing the species composition of the core with salinity levels and species composition of modern lakes. What assumptions does this inference make, and does it seem valid to you?

Commiphora) characteristic of the current Sahel region (a dry tropical savanna biome about 500 km south) increased about 4700 years ago but abruptly passed out of the record about 4200 years ago (Figure 2.23E). Lastly, semi-desert plants (genus *Blepharis*) became more common about 3000 years ago, while plants in the current desert biome became common about 2700 years ago (Figure 2.23F and G). So we see a gradual transition from tropical savanna, to shrubland, to semi-desert, and lastly to the arid desert of today.

Kröpelin and his colleagues used the same cores to reconstruct the chemical and biological history of the lake. The fossil evidence indicates that about 4000 years ago Lake Yoa transitioned from a stable freshwater lake to a salt lake over a period of about 200–300 years. Over that time span, salt-tolerant fly larvae (from the family Chironomidae) and salt-tolerant diatoms became abundant (Figure 2.24A). About 3300 years ago, as salinity levels continued to rise, even the most salt-tolerant freshwater organisms disappeared. Diatoms are scarce in the fossil record beginning 2700 years ago (Figure 2.24B). Because diatoms are highly productive phytoplankton of lake ecosystems, a decline in diatoms usually accompanies a decline in production. In addition, the decline in overall production is implied by the decrease in organic matter (Figure 2.24C). By 2700 years ago, diatoms completely disappeared and the salt-loving chironomids dominated the fossil record.

This study highlights that both terrestrial and aquatic biomes can undergo relatively rapid transitions. Let's turn our attention to the aquatic realm, and investigate the diversity of biomes we find there.

2.4 WHAT ARE AQUATIC BIOMES?

As was the case with terrestrial biomes, the number of aquatic biomes is highly subjective (Figure 2.25). Analogous to terrestrial biomes, temperature and sunlight are critical factors influencing the development of aquatic biomes. Nutrient levels are particularly important, because they are so variable even within the same body of water. However, new variables enter into the equation, most importantly salinity, water current, and water depth.

Water's unique properties

Oceans and lakes have a much narrower temperature range over the course of a year than does a landmass at the same latitude. Water has a very high specific heat – it takes about 4.2 J of energy to heat 1 cc (= 1 ml) of water 1°C, while an

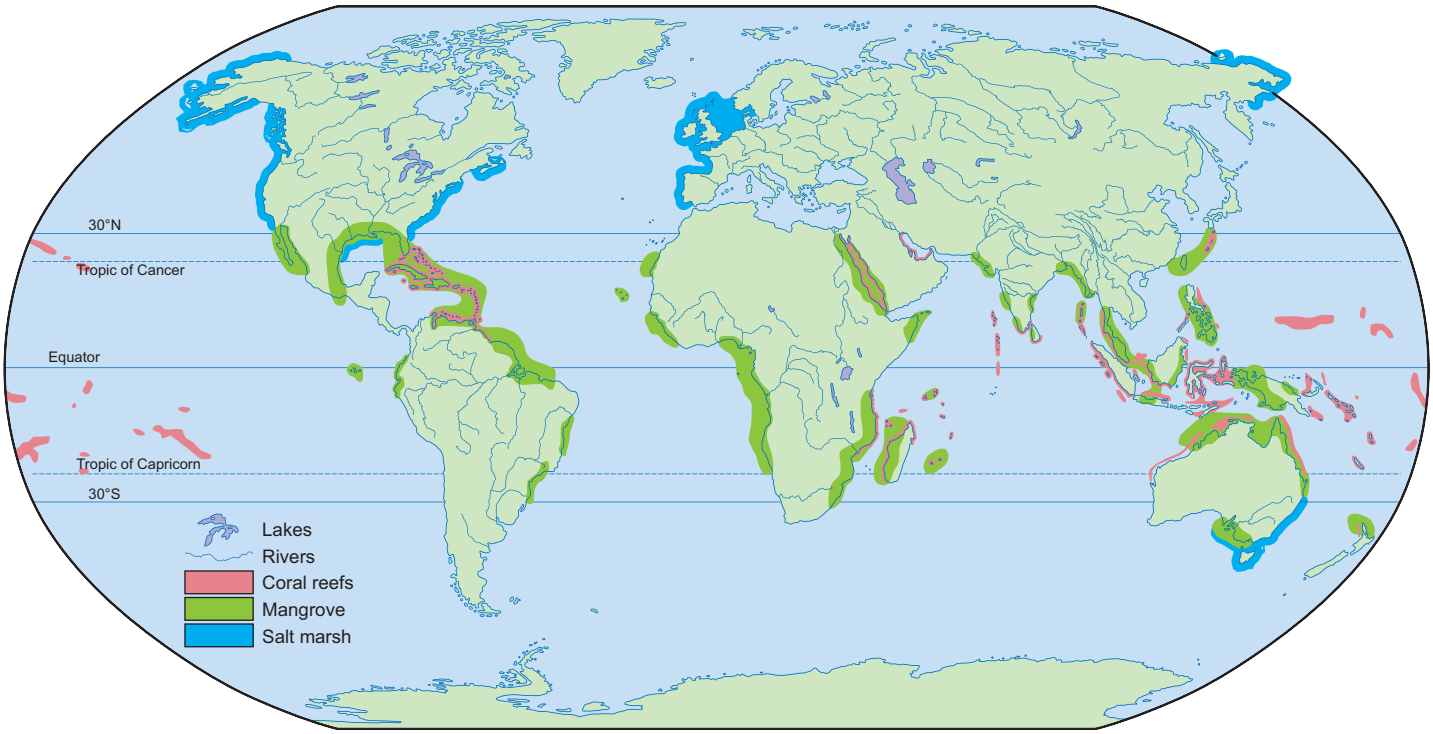

Figure 2.25 The world's aquatic biomes. The term "biome" was originally coined for terrestrial systems, but for consistency I am applying it to aquatic systems as well. Other authors use the following terms instead: realm, zone, ecosystem, and environment.

equivalent piece of land, depending on its composition, would generally require only 10–30% as much solar energy. Most large bodies of water do not heat up much above 30°C, nor cool below −2°C.

Water has another important property that influences life in some aquatic biomes. As water cools down to 4°C, its density increases. Other fluids show the same property. But below 4°C, water's density begins to decrease, and when it forms ice at 0°C, its density declines abruptly. Because of its low density, ice floats above the surface, helping to insulate organisms below from temperature extremes in polar climates. In more temperate or tropical climates, the water that is warmed by the Sun's rays remains at the surface, while cooler, denser water sinks, leading to **thermal stratification** – the formation of distinct layers along a temperature profile.

Lastly, light intensity and quality vary with depth. In oceans, less than 1% of the available light penetrates to 200 m under ideal conditions (with no interfering organisms or sediment). Thus almost all of the ocean's production occurs in this relatively narrow **photic or epipelagic zone**.

Variation in nutrient availability

Aquatic autotrophs have similar nutrient needs as terrestrial autotrophs. Nutrients are in short supply near the surface in much of the open ocean and in many deep lakes, because dead organisms tend to sink to the bottom – the **benthic zone** – where they decompose, and their nutrients are released. However, the problem is that the benthic zone is often very cold, while the photic zone, where production takes place, is much warmer. Cold water is denser than warm water, so there may be very little mixing between the nutrient-rich benthic zone and the potentially productive photic zone.

There are two important cases when mixing does occur and nutrients become widespread in the photic zone. The first case, turnover, occurs during fall or early winter in temperate and polar regions, when water-surface temperatures become cooler than deep-water temperatures. At that temperature, surface waters, now denser than the deeper waters, will sink, forcing the nutrient-rich deeper waters to the surface. The second case, **upwelling**, occurs in oceans near the western shores of landmasses, where the prevailing winds tend to move surface waters away from the shore, causing deeper, nutrient-rich waters to move in, where they form a highly productive region. Many of the world's great fisheries depend on upwelling to provide nutrients for the phytoplankton, which are the foundation of the food web.

Variation in salinity

Lakes and rivers are primarily freshwater, but as we've already discussed, some lakes develop salinity levels that are even higher than are found in the ocean. Rivers too, where they enter the ocean, may develop high salinity levels, which vary with the

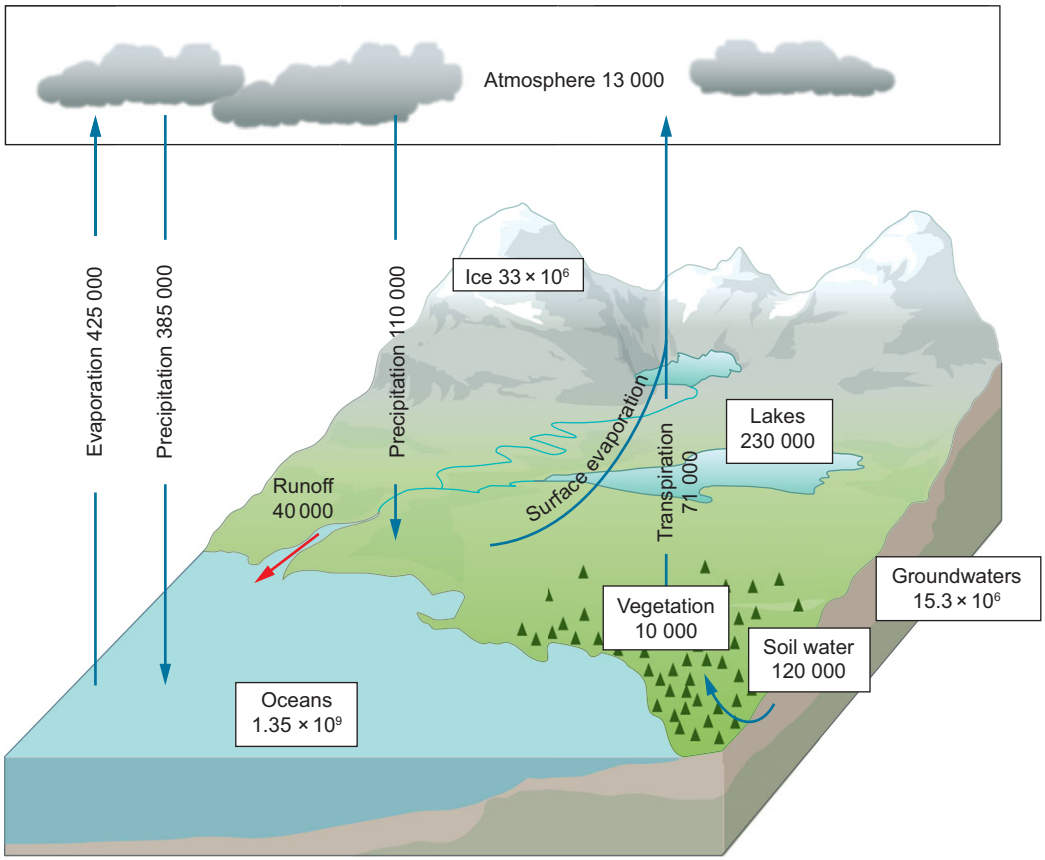

Figure 2.26 The hydrological cycle showing fluxes (km^3/year) and reservoirs (km^3). Atmospheric turnover time = atmospheric reservoir size divided by total flux (from precipitation) = 13 000 km^3/year divided by 496 000 km^3 (combined precipitation over the ocean and lands) = 0.0262 year or almost 10 days.

influence of the ocean tides. The ocean is saline because solutes are constantly washing in from streams and runoff, and of course the ocean has no outflow. In the open ocean, salinity averages about 35 g of salt per kg of water (parts per thousand or ‰). But there is some variation: areas with high precipitation (such as the tropics) have somewhat lower salinity, while areas with low precipitation and high evaporation rates (such as at 30° latitude) have somewhat higher salinity. Salinity in smaller seas covers a much wider range; the salinity level of the Dead Sea is about 330‰. Some of the nearshore aquatic biomes we will discuss are highly variable in their salinity levels, because they have considerable freshwater input.

Let's next consider how water moves through the world, and then we will turn our attention to the specific aquatic biomes.

The hydrological cycle

The vast majority of the world's water is stored in liquid form in the ocean, while the second greatest **reservoir** or storage is in frozen form, primarily on the island of Greenland and the continent of Antarctica. The hydrological cycle describes the basic patterns of water's journey through the atmosphere, between the atmosphere and the surface (in both directions), and between different surface reservoirs (Figure 2.26).

The primary **flux** or flow of water from the atmosphere to the Earth's surface is in the form of precipitation, while water returns to the atmosphere from the Earth's surface by evaporation and **transpiration**. We can measure **turnover time** – the average amount of time a water molecule remains in its reservoir – as the size of the reservoir (in km^3) divided by the flux (in km^3/year). Though the atmospheric reservoir seems pitifully small (13 000 km^3), it has a very quick average turnover time of about 10 days, which is why the atmosphere has such an important influence on global climate (Oki and Kanae 2006).

The short turnover time of atmospheric water helps charge the world's lakes and streams. We begin our description of aquatic biomes by following the fate of freshwater as it flows over land.

Freshwater biomes

Ecologists have identified up to 14 different freshwater biomes. For simplicity, we will discuss only two of them, which are distinguished from each other based on whether they contain relatively still or flowing water.

Rivers and streams

Streams and creeks are fed by many sources – headwaters may originate from melting glaciers, as springs or seeps from underlying rock or soil, or as outflows from lakes. The rest is simple: gravity rules. Most streams get larger as they follow the path dictated by gravity, as they are joined by other streams and water inputs. There is no rule about how large a stream or creek must be before it transitions into a river. On a small scale, many streams alternate between *riffles*, which are areas of high flow rate, and *pools*, where deep water moves at a very low flow rate. Riffles are highly oxygenated and very productive, while decomposition of sediment that settles in pools makes CO_2 available for photosynthesis.

A stream's character changes over its course, as the stream typically widens while its current slows near the end of its course. Mountain streams are usually rich in oxygen and contain large numbers of leaves that feed a diverse community of invertebrates. *Shredders*, such as caddisflies, stoneflies, and amphipods, consume leaves and large particulate matter, and *collectors*, such as mayflies and water beetles, feed on the smaller organic matter. Moving downstream, the waters become more productive from nutrient inflow and higher temperatures. A diverse group of *grazers*, including many species of snails and caddisflies, feed off the algae and other abundant aquatic vegetation. Of course, invertebrate and vertebrate predators are present throughout the stream – they too are adapted to differences in flow rate, oxygen availability, and prey species (Figure 2.27).

The stream or river ends its journey at a body of relatively still water, either a lake or an ocean, where it dumps all of its contents, including its load of sediment. We will first turn our attention to lakes.

Figure 2.27 Stream organisms. A. Stonefly (shredder) from the Duerna River that flows through León, Spain. B. A caddisfly collecting small prey items from its net.

Lakes

If a stream runs into an inland basin or depression, it (and any accompanying streams) will fill the depression up to the level of its outflow – either a stream or groundwater – and form a lake. Many lakes in temperate biomes and in the taiga formed when retreating glaciers left depressions; some are still fed by glacier melt. Lakes also can be formed by biotic processes; beavers damming up rivers form small ponds, while humans damming up rivers can form much larger lakes. Lakes formed from dams can have serious impacts on ecosystems; for example, four dams along the Snake River in Idaho, USA, have destroyed about one-third of the world's salmon runs, and led to the extinction of several salmon subspecies (Duncan 2001).

Some of the world's largest and deepest lakes were formed by impressive geological processes. Crater Lake, in Oregon, USA, formed from a massive eruption of Mt. Mazama about 7700 years ago. The resulting crater filled in with water, forming a lake with a maximum depth of almost 600 m. More impressive is Lake Baikal, which fills an ancient rift valley in southern Siberia, Russia. This rift valley formed when a tectonic plate began pulling apart; the rift is still pulling apart at the rate of 2 cm per year. At 1637 m, Baikal is the deepest freshwater lake in the world, and contains about 20% of the

Figure 2.28 A. The Holy Nose Peninsula juts into Lake Baikal. B. The Lake Baikal seal.

world's supply of liquid freshwater (Figure 2.28). Researchers estimate that over 80% of the species in Lake Baikal are **endemic** to the lake – found there and nowhere else. Over 90% of the zooplankton in the lake are one endemic species, *Epischura baikalensis*. On a larger scale, the endemic Baikal seal (*Phoca sibirica*) is one of only three freshwater species of seal in the world.

Lakes are classified according to their nutrient status and consequent level of production. An **oligotrophic** lake has low levels of nutrients and is relatively unproductive. A **eutrophic** lake has high levels of nutrients and is much more productive, courtesy of large populations of photosynthetic phytoplankton. Both climate and lake structure influence a lake's trophic status. Deep mountain lakes in unpolluted areas are often oligotrophic for several reasons. First, mountain environments tend to be cool, with short growing seasons, limiting production by phytoplankton. Second, mountain lakes are often situated in a relatively unpolluted environment, so fewer nutrients enter from the surrounding environment. In addition, mountain lakes are often relatively deep in relation to their surface area, which results in the dilution of nutrients that enter the lake in the relatively large volume of water. In contrast, shallow lakes in warm environments tend to be more eutrophic, as they have longer growing seasons and a greater nutrient concentration to support a highly productive phytoplankton community.

David Schindler and Everett Fee (1974) wanted to identify which nutrient components of the sediment were most important in the process of eutrophication. In one experiment, the researchers added 0.48 g/m^2 of phosphorus, and 6.29 g/m^2 of nitrogen over a period of 5 years to an Experimental Lake 227, located in a research area in the Canadian Shield region of Ontario. Figure 2.29A shows the dramatic increase in production in response to the treatment, in comparison to untreated lakes. To separate out the effects of nitrogen and phosphorus, the researchers used a curtain to divide a second lake, Experimental Lake 226, into two sections. One part of the lake was fertilized with carbon, nitrogen, and phosphorus, while the second part was fertilized with only carbon and nitrogen. Production increased dramatically in the part that had all three nutrients added (Figure 2.29B). Based on these experiments, Schindler and Fee concluded that phosphorus is the limiting nutrient for production in these Canadian lakes and may play an important role in eutrophication of freshwater lakes. Furthermore, carbon and nitrogen do not appear to limit production in these freshwater lakes.

Some lakes, both natural and artificial, tend to become shallower as nutrient-rich sediments drain into the lake and accumulate on the lake bottom. Over time, these lakes may transition from oligotrophic to eutrophic, particularly if the sediments have high levels of phosphorus. Desert lakes, as we saw earlier, can transition from freshwater to saline (Figure 2.22). All water has at least some dissolved salts, so continuing evaporation of freshwater should increase salinity. Most lakes in other biomes have both inflows and outflows (usually streams or rivers), so the salts are carried away before they can build up to high levels. But many desert lakes lack significant outflows, so salinity increases to very high levels. Kröpelin and his colleagues (2008) suggest that Lake Yoa's outflows dried up about 4300 years ago, resulting in the freshwater to saltwater transition.

Not all lakes have obvious inflows and outflows. There is a group of about 400 identified freshwater lakes beneath the Antarctic ice sheet, that are fed by ice sheet meltwater created by ambient heat deep within Earth. Recently, Brent Christner and his colleagues (2014) were able to bore through the West Antarctic Ice Sheet to collect 30 l of water samples from Lake Whillans, which lies about 800 m below the surface. The researchers discovered a community of almost 4000 species of bacteria and archaeans, which form a closed ecosystem that operates in total darkness. Energy is produced by **chemosynthesis** – the conversion of energy from chemical compounds in the environment into chemical bond energy stored in carbohydrates. In Lake Whillans, microorganisms

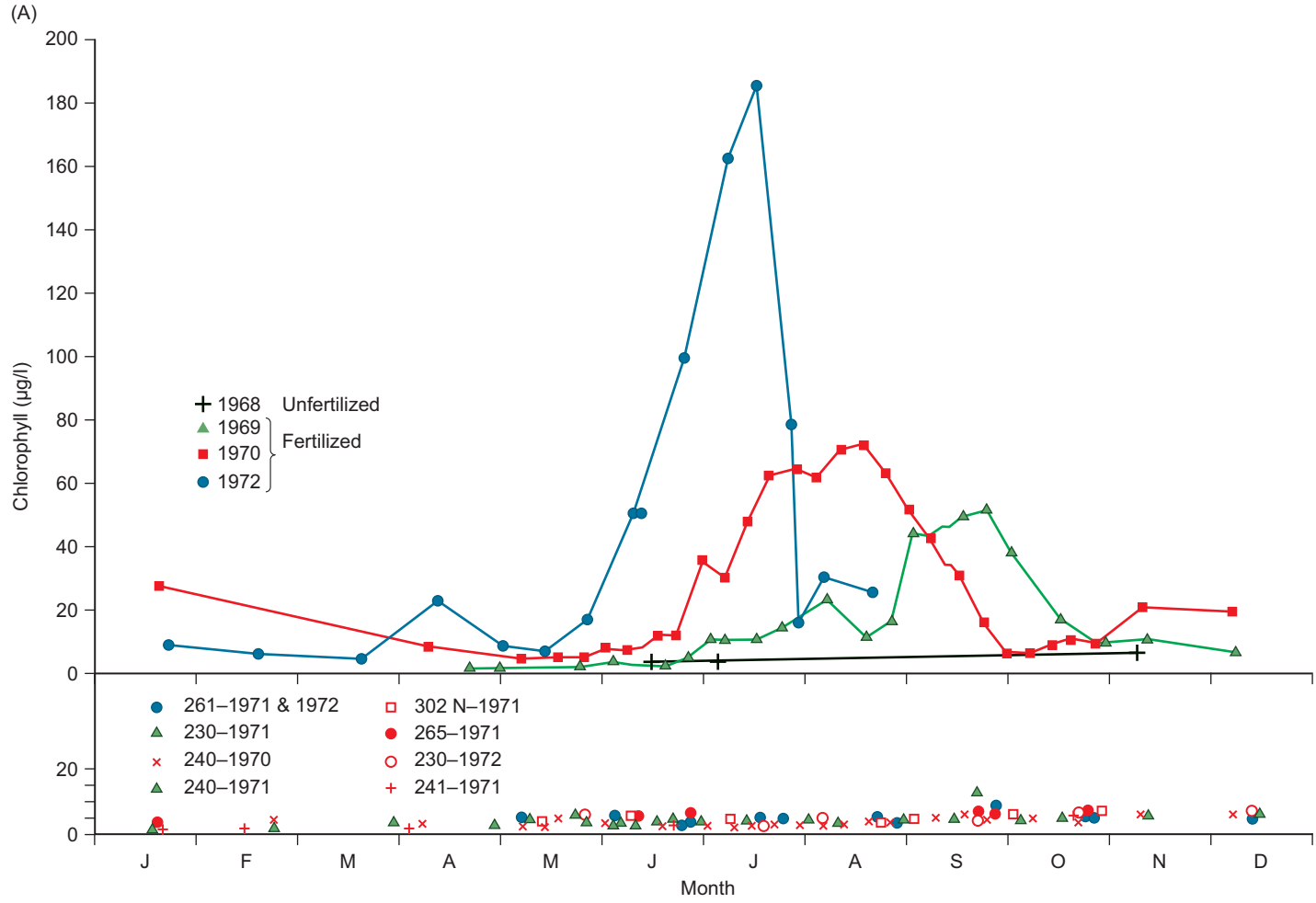

Figure 2.29 A. Production as measured by the chlorophyll level in Experimental Lake 227 (top graph) in comparison to numerous readings in 1970–2 from seven nearby control lakes (bottom graph). Only 3 years are included in the graph to reduce clutter, but chlorophyll levels rose sharply in all 5 years of the study. Note that chlorophyll levels never increased above 15 µg/l in any of the control lakes, nor in Experimental Lake 227 during the year before fertilization. B. Experimental Lake 226 is divided by a curtain to separate unfertilized section (foreground) from fertilized section (background).

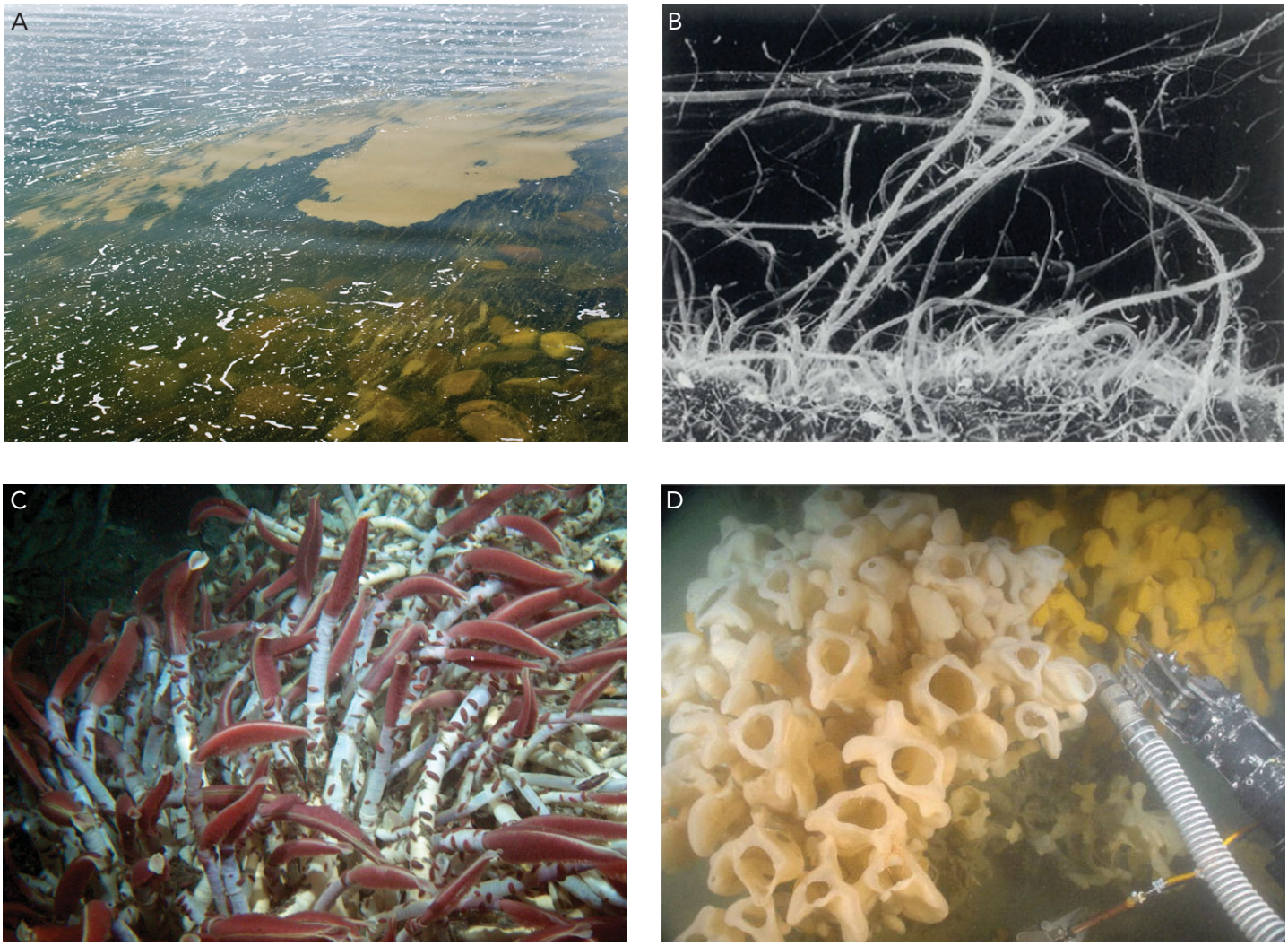

Figure 2.30 Organisms from open ocean ecosystems. A. Bloom of *Trichodesmium* cyanobacteria. B. Chemosynthetic bacteria form mats of tangled filaments on seafloor lava. C. Ocean vent communities feature giant tubeworms (*Riftia pachyptila*) that may be up to 1 m long. D. Glass sponge (*Heterochone calyx*) from Fraser Ridge.

oxidize ammonium to generate the energy to create carbohydrates. The researchers speculate that most of the ammonium originated from old marine sediments that accumulated in much warmer time when Antarctica was covered by a shallow sea. Given how large Antarctica is, and that 55% of its surface is estimated to harbor lakes or rivers beneath the ice shield, there is vast potential for discovering new and important ecosystems operating in this unexplored environment.

Let's turn our attention now to marine systems, which can be divided into several different biomes.

Marine biomes

The ocean contains over 97% of the world's water. We will divide the ocean into several different biomes, each of which has different physical and chemical processes and tends to have a different assemblage of characteristic organisms.

The open ocean

The open ocean is by far the world's vastest biome – vast in that it covers about 70% of the Earth's surface, and vast in its three-dimensionality. The average ocean depth is about 4000 m, while the deepest trench is over 11 000 m deep. Conventionally, the open ocean, or oceanic zone, begins at the end of the continental shelf, a shallow, highly productive region of the ocean that surrounds the continents and reaches a maximum depth of about 200 m before giving way to the open ocean.

Most of the open ocean is relatively unproductive because most of the nutrients are near the ocean floor, the primary site of decomposition. However, there are sufficient nutrients near the surface to support phytoplankton of various types. The most prevalent phytoplankton are cyanobacteria, but many other forms are also present in huge numbers (Figure 2.30A). Many different species of herbivorous zooplankton eat the phytoplankton, and many different species of carnivorous zooplankton eat

both carnivorous and herbivorous zooplankton. An accurate description of who eats whom gets very messy very quickly, as zooplankton are eaten by tiny larval fish and massive whales. The picture is even more complex than it first appears, because bacteria are actually the most abundant organisms in the ocean, and they are eaten by a diverse array of predators of different shapes and sizes. Most ecologists have abandoned the linear concept of a food chain, replacing it with the more descriptive concept of a **food web** – a summary of the feeding relationships within an ecological community. (See Chapter 16 for a more thorough exploration of food webs.)

Until recently, ecologists believed that the open ocean's benthic zone was relatively unproductive, with a low abundance of deep-sea organisms being nourished by the organic matter raining down from above. All this changed when Peter Lonsdale (1977) discovered a benthic ecosystem in some of the ocean's deepest trenches, where tectonic plates are separating and molten rock heats the water to over 400°C. Hot water passing through the underlying rocks releases many nutrients, including vast quantities of hydrogen sulfide. Chemosynthetic sulfur-oxidizing bacteria are adapted to the high pressures in the ocean depths and to the glut of a dependable sulfur source, oxidizing the hydrogen sulfide and using the energy released from this process to synthesize carbohydrates. A diverse array of organisms either feed on these bacteria or have symbiotic relationships with them (Figure 2.30B and C).

The deep-sea trench, however, was not the final ocean benthic zone ecosystem to be discovered. In 1984, a seafloor mapping expedition using sonar imaging revealed large mounds on the seafloor off the coast of British Columbia, Canada, at depths ranging from 150 to 250 m. In 1987, Kim Conway and Vaughan Barrie captured these mounds on film, which revealed the mounds to be massive reefs of glass sponges . Some of these reefs are at least 6000 years old, 18 m high, and 700 km^2 in surface area (Figure 2.30D). Sponges use silica to construct their glass skeletons, so these reefs are only found in water with high levels of dissolved silica. We know very little about their ecology, as they have not been studied extensively. But like coral reefs, these sponges provide a foundation that attracts many other species of animals. More recently, in 2007, Paul Johnson discovered a glass sponge reef about 50 km off the Washington coast (Dybas 2008). This reef is immediately adjacent to a huge methane gas seep, and Johnson proposed that these sponges get their energy from bacteria that use methane gas as their energy source. These sponges grow very slowly, only about 1–2 cm per year. One concern is that four of seven reefs surveyed in the Georgia Basin off the British Columbia coast had been damaged by fishing trawlers (Cook *et al*. 2008).

Ecologists eagerly anticipate discovering other benthic oases of species diversity. Yet much of the ocean's species diversity occurs in shallow waters, where high production can support a complex food web. Coral reefs are the most species-rich aquatic biome.

Figure 2.31 Numerous fish live in a rich coral reef community near Sulawesi, Indonesia.

Coral reefs

As we discussed in the opening case study, most coral reefs occupy warm shallow waters, usually growing within 50 m of the surface, where temperatures range between 20° and 30°C. In addition to corals themselves, coral reefs are home to a dazzling assemblage of invertebrate and vertebrate animals, including some of the world's great fisheries. Because coral reefs are declining worldwide, many of them have been closed to commercial fishing (Figure 2.31).

Many corals reproduce sexually by broadcasting immense quantities of eggs and sperm into the ocean. Successfully fertilized eggs develop into larvae, which if they are amazingly fortunate, will settle into the sediment and develop into adult polyps. Only a tiny fraction of eggs are fertilized, and a much smaller fraction of larvae make it to the polyp stage. Polyps can reproduce asexually, then develop into the characteristic adult colony.

Like their terrestrial high-diversity counterparts – tropical rainforests – coral reefs are associated with low nutrient levels. One hypothesis for the characteristic low nutrient level is that the high production in shallow and warm waters ties up most available nutrients in living organisms. Christian Wild and his colleagues (2008) tested this hypothesis by studying a dramatic event on Australia's Great Barrier Reef by Heron Island – the annual coral mass spawning that occurs a few days after November's full moon. Most of the gametes released into the ocean never achieve fertilization, but they do fertilize the ocean by adding nutrients, including organic carbon and nitrogen compounds, into the water column, ultimately getting incorporated into other organisms or into the sediment as they pass through a complex food web. The researchers predicted that nitrogen levels would increase immediately after the mass spawning, but that high production would return nutrient levels to their low-nutrient pre-spawning conditions very quickly.

In general, the data support these predictions. Immediately after spawning, nitrogen levels in the water column shot up

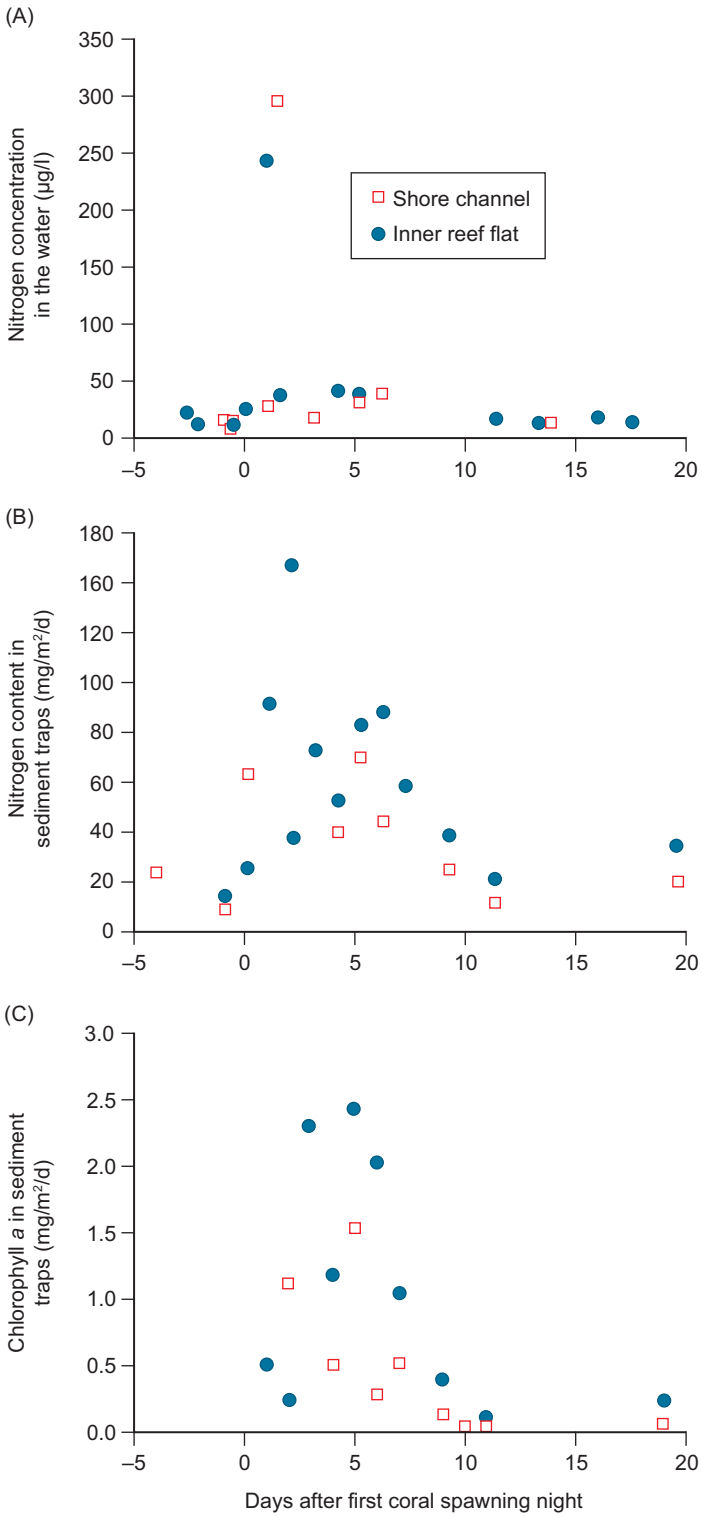

Figure 2.32 Effects of coral mass spawnings on nutrient levels in and near a coral reef. A. Nitrogen levels in water in relation to time since spawning. B. Nitrogen levels in sediments in relation to time since spawning. C. Chlorophyll *a* levels in sediment in relation to time since spawning.

dramatically, but returned to baseline levels after only 2 days (Figure 2.32A). Nitrogen levels in the sediment increased more slowly and took about 10 days to return to pre-spawning levels (Figure 2.32B). The rapid decrease of nitrogen compounds in the water column to pre-spawning levels could result from three factors. First, the tide might have washed the nitrogen away. Second, the nitrogen may have sunk down into the sediment. Third, the nitrogen may have been consumed by highly productive reef organisms, particularly phytoplankton, which have the capacity to reproduce very rapidly. It is very likely that all three factors are important. The slow return of nitrogen levels to pre-spawning values in the sediment indicates that nitrogen compounds did settle in the sediment. Moreover, the increase in chlorophyll *a* levels beginning about 2 days post spawning indicates a much higher phytoplankton abundance, mostly of the dinoflagellate *Prorocentrum* (Figure 2.32C).

Despite this nitrogen limitation, coral reefs have very high species richness. However, global warming is causing some ocean temperatures to rise rather rapidly. High ocean temperatures are associated with corals ejecting their symbiotic zooxanthellae, which leads to the death of the coral and the appearance of bleaching. We will investigate this phenomenon more closely in Chapter 15.

Because most reef-forming corals do poorly in temperatures below 20°C, their distribution is primarily restricted to the tropics. As we move into cooler regions, corals are replaced by kelp forests.

Figure 2.33 Kelp forest in Monterey Bay, California, USA.

Kelp forests

Kelp are large brown algae that live in shallow nutrient-rich waters in temperate latitudes, in water temperatures generally between 5° and 20°C. Kelp are anchored to the seafloor with holdfasts – structures that superficially resemble roots. Leaf-like blades extend from the stem or stipes, and, in some species, gas-filled pneumatocysts at the base of the blades provide buoyancy. Some kelp can reach heights of greater than 50 m, with growth rates of up to 0.5 m per day, forming dense forests (Figure 2.33).

Analogous to coral reefs, kelp forests have very high levels of production, and kelp are a foundation for complex communities. Many herbivores, including sea urchins and many species of

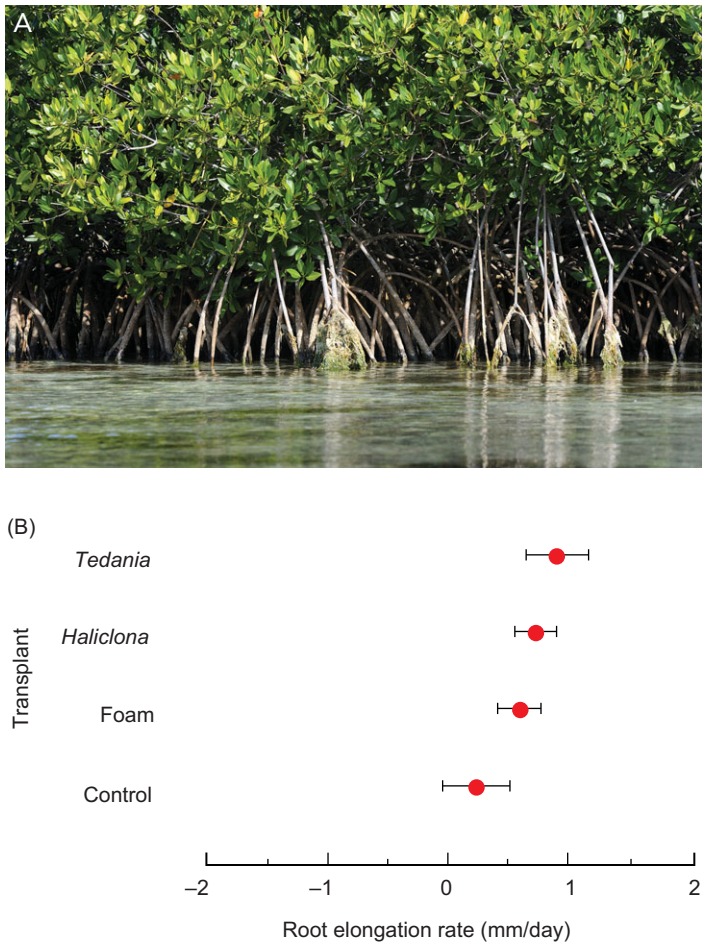

Figure 2.34 A. Red mangrove forest in south Florida, USA. B. Mean root elongation rate (mm/day) in relation to type of transplant.

herbivorous fish, graze on the kelp. Of course carnivorous fish graze on the herbivores, so depletion of carnivorous fish by fishermen can lead to overgrazing by herbivores. Because kelp grow so quickly, they can usually recover from overgrazing, and are considered less threatened than coral reefs.

Both kelp forests and coral reefs occur in shallow waters near the edge of continents or islands. Our final three aquatic biomes – mangrove forests, salt marshes, and estuaries – occupy the dynamic zone where land and sea meet.

Mangrove forests

If you're wandering along a tropical shoreline, particularly one with soft sediment and calm wave action, you may be surprised to discover yourself not on a sandy beach, but struggling through what appears to be a tropical forest. The trees in this mangrove forest are very specialized for life in challenging environmental conditions, which include low oxygen levels and limited nutrient availability. Mangroves produce aerial roots that exchange gas above the waterlogged environment (Figure 2.34A). Though relatively few plant species live in mangrove forests, they do harbor a very rich community of animals.

Aaron Ellison and his colleagues (1996) were particularly interested in the interaction between red mangrove (*Rhizophora mangle*) and two species of giant sponge (*Tedania ignis* and *Haliclona implexiformis*). The sponges attach themselves to the mangrove roots, covering an average of 30% of the root surface. For food, they filter small particles of organic matter from the ocean. Mangroves benefit from this symbiosis. In a previous study, when Ellison and Farnsworth (1990) removed sponges from mangrove roots, there was a 55% decrease in root growth as a result of the bare roots being attacked by isopods.

To more directly assess how this symbiosis actually works, Ellison and his colleagues subjected newly formed mangrove roots to one of four treatments: (1) *Tedania* transplant, (2) *Haliclona* transplant, (3) artificial sponge transplant made from polyurethane foam insulation, and (4) unmanipulated control. Roots with sponge or foam insulation all showed significantly higher elongation rates than did the unmanipulated controls (Figure 2.34B). This was not surprising, because the sponges were protecting the roots against isopod attack. But the researchers wanted to know whether there were additional benefits to the mangroves from this association.

One piece of evidence supporting the additional benefits hypothesis was that the majority of the mangroves with live sponges produced *adventitious rootlets* – fine rootlets projecting laterally from the main cable root – that permeated the body of the sponge. The researchers suspected that these adventitious rootlets functioned in nutrient exchange. To test this hypothesis, they conducted stable isotope analysis on the carbon and nitrogen present in cable roots. Stable isotope analysis (described in detail in Chapter 3) allows researchers to determine the source of elements such as carbon or nitrogen that are present in the body of an organism. This analysis revealed that sponges are transferring substantial quantities of nitrogen to the adventitious mangrove rootlets, while the rootlets are leaking substantial quantities of carbon compounds that are absorbed by the sponges.

Overall, sponges benefit from this association through increased carbon uptake, and by having a solid substrate to which they can adhere. Mangroves benefit directly from increased nitrogen uptake, and indirectly by being protected against predacious isopods. Ellison and his colleagues predict that many more mutualisms remain to be discovered in mangrove forests. We will now continue our journey along the coastline to temperate climates, where salt marshes replace mangrove forests as the dominant biome.

Salt marshes

In the introduction to their classic book, *Life and Death of the Salt Marsh*, John and Mildred Teal (1969) describe a seductive and elusive biome.

> The ribbon of green marshes, part solid land, part mobile water, has a definite but elusive border, now hidden, now

Figure 2.35 Numerous shorebirds live in this salt marsh along the Texas, USA coast.

> exposed, as the tides of the Atlantic fluctuate . . . At low tide, the wind blowing across *Spartina* grass sounds like wind on the prairie. When the tide is in, the gentle music of moving water is added to the prairie rustle. There are sounds of birds living in the marshes . . .You can hear the tiny, high pitched rustling thunder of the herds of crabs moving through the grass.

This evocative description of the salt marsh and its thundering crabs captures the ever-changing spirit of this biome. Salt marsh plants must deal with the dual challenges of fluctuating salinity and water levels. While the highly productive marsh plants trap sediment and lay down a layer of decaying organic matter, the tides and wave action erode away this developing soil layer. Plant species richness is very low, dominated by only a few very abundant plants that tend to grow in somewhat distinct zones parallel to the shoreline. These highly productive marsh plants – primarily grass species – form the foundation of the salt marsh ecosystem. Grazers, such as snails and amphipods, ingest the leaves while fungi and bacteria begin the decomposition process. Much of the production is decomposed by bacteria and fungi, rather than eaten by herbivores, but there is nonetheless a significant army of herbivores that feed on the leaves, seeds, and fruits, including mammals, birds, arthropods, and crustacea (Figure 2.35).

It's important to understand that not all of the shoreline biomes occur where land meets water. Our last biome exists where water meets water.

Estuaries

Estuaries are hydrologically and chemically very dynamic. The amount of freshwater entering the ocean from a river may vary tremendously over the course of the year, and also from year to year. For example, the flow rate of the Ganges River as it enters the Bay of Bengal is usually about 10 000 times higher in August

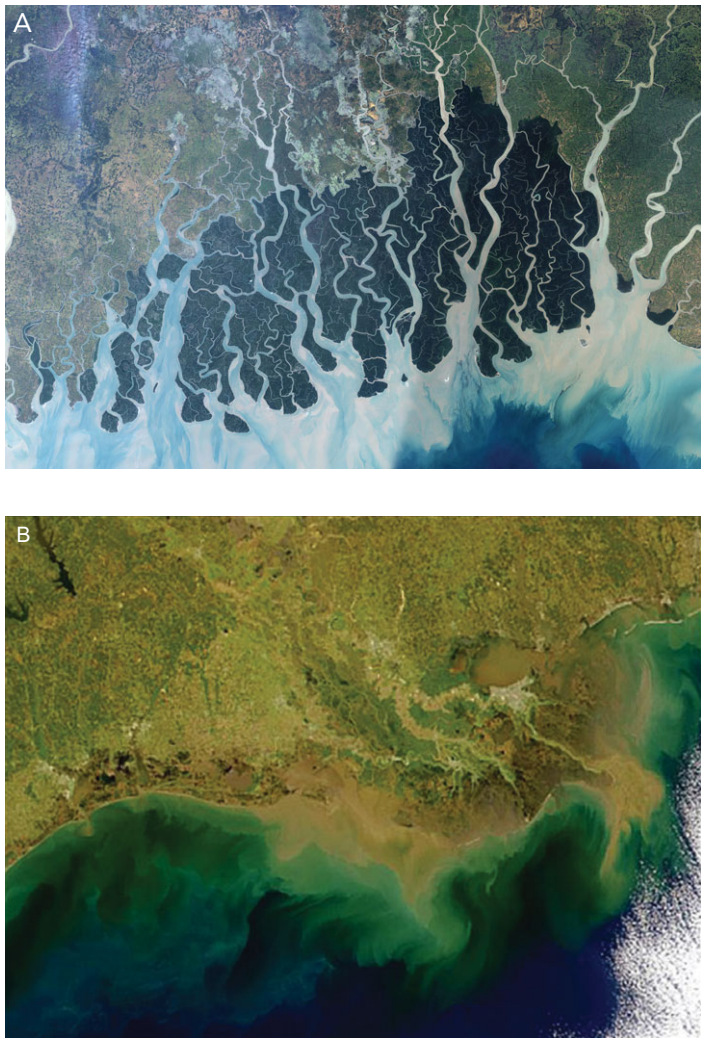

Figure 2.36 A. A portion of the Ganges river estuary and delta, as viewed from the space shuttle. B. Satellite image of northern Gulf of Mexico showing the dead zone (brown, green, and light blue water) formed from runoff, primarily from the Mississippi River delta.

than it is in April (Mondal and Wasimi 2006). The amount of salt in an estuary can fluctuate dramatically in relation to the tides. High tide may bring an influx of salty ocean water well upstream, which then recedes with low tide. Saline ocean water is denser than riverine freshwater, so the two flows may stratify, with ocean water moving upriver along the bottom of a river's course, and freshwater moving downstream over the top of the ocean water (Figure 2.36A).

Concurrently, rivers may carry with them very high levels of materials that they have accumulated from runoff, including sediment, nutrients, and toxic pollutants such as heavy metals. High nutrient levels lead to high phytoplankton productivity, supporting abundant populations of invertebrates and fish. However, species richness is usually very low, because most species are not adapted to the highly variable chemical environment. Primary production in estuaries is often limited by nitrogen

availability, so periodic increases in nutrients can significantly increase primary production in the form of algal growth. Massive algal death leads to rapid decomposition by microorganisms, which may consume most of the available oxygen for their own cellular respiration. This process has created vast **dead zones** in some of the world's largest estuaries (Figure 2.36B). In dead zones, the dissolved oxygen levels drop below 2.0 ml/l for an extended period of time, causing the death of most aerobic benthic organisms.

Humans use fertilizers for agriculture, which run off into rivers, and ultimately into estuaries. As a result, the number of reported dead zones on Earth has approximately doubled every decade since the 1960s (Diaz and Rosenberg 2008). Of course, estuaries are not the only biome that has been degraded by human activities. But biomes that are both readily accessible to people and are in relatively benign climates are most threatened by human disturbance. Some biomes have become so disrupted that many of the species adapted to them have gone extinct or are severely threatened.

REVISIT: Biomes reconsidered

Some ecologists propose modifying our portrait of the world's biomes by acknowledging the profound human impact on ecosystems operating within these biomes. They ask, is it meaningful to talk about the primary productivity of grassland biomes, when almost all native grasslands have been converted to croplands, many of which are supplemented with irrigation and artificial fertilizers? Erle Ellis and Navin Ramankutty (2008) recommend incorporating this huge human impact into a new taxonomy of biomes.

In their model, Ellis and Ramankutty considered three factors as most important in defining their biomes: human population (urban and non-urban), land use (percent in pasture, crops, irrigation, rice, and urban) and land cover (percent vegetated). They then used a statistical analysis to identify the distinct groupings that emerged based on these factors. Their analysis identified six major groupings of biomes: dense settlements, villages, croplands, rangelands (for livestock), inhabited (by humans) forests, and uninhabited wildlands. The five inhabited groupings yielded 18 **anthropogenic biomes** – biomes whose nature and character were determined by human impact. The uninhabited wildlands were classified into three biomes: wild forests, sparse trees, and barren biomes (Figure 2.37).

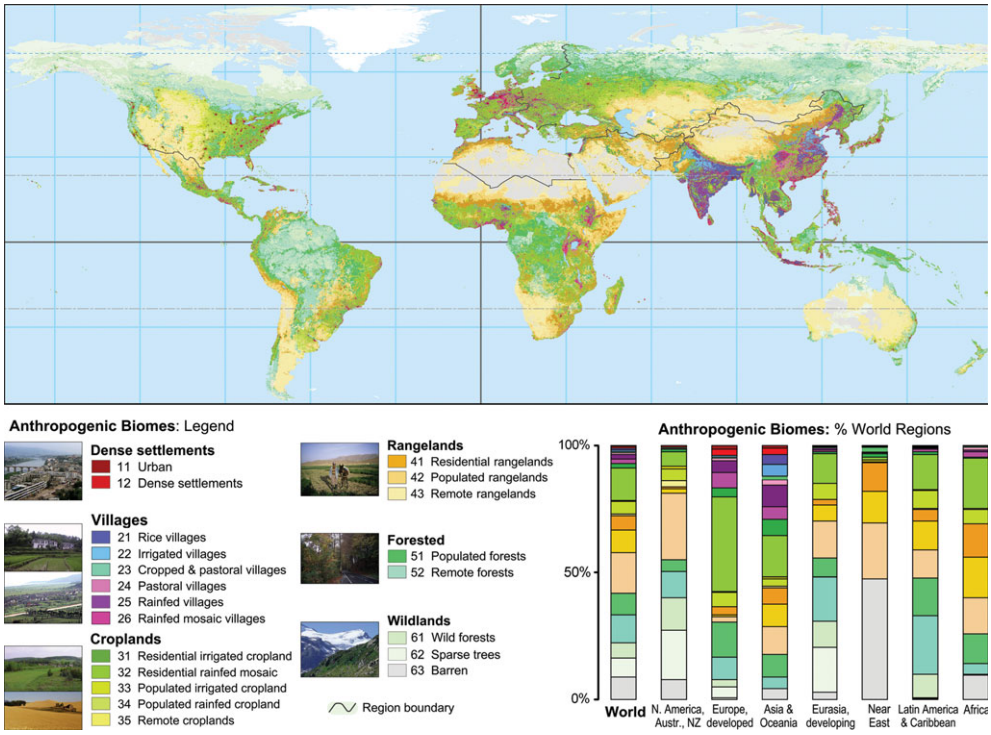

Figure 2.37 Anthropogenic biomes of the world.

Table 2.3 Mean population density, land use, land cover, and net primary production (NPP[a]) for each village biome.

Village-biome	Description of major components of biome	Population density (per km^2)	Pasture	Crops	Cover (%)				NPP[a] (g/m^2)
					Irrigated	Rice	Trees	Bare ground	
Rice	Paddy rice	774	1.9	71.9	40.4	62.3	6.8	2.1	550
Irrigated	Irrigated crops	500	7.0	67.6	60.1	9.1	4.4	7.6	380
Crop and pastoral	Mix of crops and pasture	300	29.8	42.3	15.9	1.0	1.2	43.0	180
Pastoral	Rangeland	256	68.8	26.4	8.3	2.1	11.7	7.7	500
Rainfed	Rainfed agriculture	243	8.1	62.7	8.4	10.3	8.4	6.6	440
Rainfed mosaic	Mix of trees and crops	230	8.3	18.9	3.6	4.3	27.8	1.1	750

[a]NPP measures the amount of new biomass produced by autotrophs (primarily plants) per year.

Each biome grouping comprises two to six biomes. As one example, villages, which are defined as densely populated agricultural populations, are broken down into six biomes. Together the village biomes have about 50% of the world's non-urban population. They are most common in Asia, where they cover more than 25% of the land mass. Table 2.3 summarizes the data used to break the village grouping down into six distinct biomes.

Are Ellis and Ramankutty intentionally making life more difficult for ecologists by imposing a new taxonomy of biomes? The two researchers argue that their taxonomy allows ecologists to make more realistic models of what occurs at the level of the ecosystem, region, and biosphere, by acknowledging the huge impact humans have on ecosystem-level processes. For example, if we want to predict an ecosystem's productivity over an extended period of time, we need to consider not only the patterns of precipitation, temperature, and natural nutrient levels, but also human influences operating over short and long timescales. Humans may increase nutrient levels by adding fertilizers, or decrease nutrient levels with land-use practices that lead to soil erosion. Similarly, humans may increase available moisture by irrigating, or decrease available moisture by cutting down vegetation that would otherwise reduce rates of evaporation and runoff. The researchers argue that, given the growing human population, anthropogenic biomes will become even more relevant in the future. For example, increasing populations may use more fossil fuels, leading to higher atmospheric CO_2 levels, and contributing to global warming. As we discussed in the opening case study, burning fossil fuels and higher atmospheric CO_2 levels also cause acidification of terrestrial and aquatic biomes, threatening their continued existence. As we discuss in Chapter 23, global climate change has already led to significant shifts in the geographical distributions of many different species.

SUMMARY

A biome is a large geographical region with characteristic groups of organisms adapted to its environment. Terrestrial biomes are influenced primarily by precipitation and temperature, but also by fire, soils, and nutrients. Aquatic biomes are also influenced by temperature and nutrients, but additionally by salinity, water depth, and current. Consequently, in order to understand why a certain biome exists in a particular region, it is essential to understand factors that influence that region's climate, and the processes that are responsible for the distribution of nutrients.

Though tropical rainforests are terrestrial and coral reefs are aquatic, both biomes share many important features. They are hubs of species richness, they have numerous similarities in their structure and functioning, and both are threatened by a variety of human activities, including acidification. All biomes are dynamic, with shifting borders and changing species composition. Several new biomes have been discovered in recent years, bringing home the message of how much we still don't know about how our planet functions. Humans have changed Earth's properties in so many ways that some researchers argue that ecologists should shift their focus to exploring how human activities influence the distribution of species.

FURTHER READING

Bednaršek, N., Feely, R. A., Reum, J. C. P., *et al*. 2014. *Limacina helicina* shell dissolution as an indicator of declining habitat suitability due to ocean acidification in the California Current Ecosystem. *Proceedings of the Royal Society B* 251 (1785) 20140123.

Challenging and informative paper on changes that are occurring to pteropods (sea snails) as a result of ocean acidification. Also provides predictions of future changes based on assumed reduction of ocean pH by 2050.

Fox, D. 2014. Antarctica's secret garden. *Nature* 512: 244–246.

This feature news summary gives a clear and fascinating behind-the-scenes account of the challenges facing the group of researchers that ultimately collected water samples from Lake Whillans beneath the Antarctic ice sheet. This could be read in conjunction with the actual research article:

Christner, B. C., and 37 others. 2014. A microbial ecosystem beneath the West Antarctic ice sheet. *Nature* 512: 310–313.

Kröpelin, S. and 14 others. 2008. Climate-driven ecosystem succession in the Sahara: the past 6000 years. *Science* 320: 765–768.

This is a great study for highlighting how ecologists can make inferences about the historical development of biomes in a particular region.

Lawler, A. 2014. In search of green Arabia. *Science* 345: 994–997.

In analogy to the Lake Yao study, Lawler describes how a large research team headed by Michael Petraglia is compiling evidence that the Arabian Peninsula has historically harbored a much more hospitable habitat, and may have served as an early migration route for humans leaving Africa, and that early humans, attracted to the benign conditions in the Arabian Peninsula, may have settled there for extended periods of time.

END-OF-CHAPTER QUESTIONS

Review questions

1. Which terrestrial and aquatic biomes have greatest species richness? How are these two biomes similar to each other, and how do they differ?
2. How does climate influence the distribution and structure of Earth's terrestrial biomes?
3. What factors are most important in determining the distribution and structure of each of Earth's aquatic biomes?

4. Describe five different ways in which nutrients influence the structure and functioning of terrestrial or aquatic biomes.
5. What factors do Ellis and Ramankutty identify as defining anthropogenic biomes? Do you believe their definition of biomes is useful? Why or why not?

Synthesis and application questions

1. The angle of the Earth's axis fluctuates between 22.5° and 24° over a regular 41 000-year cycle. How do you think this periodic fluctuation would affect global temperature patterns?
2. There is a dispute among conservation biologists regarding whether fire suppression leads to larger fires. As it turns out, fire suppression has been practiced extensively in the USA, but only to a very small extent in Baja California, Mexico. Based on Figure 2.20, can you conclude that fire suppression has led to larger fires? Why or why not?
3. Use Figure 2.26 to calculate the turnover time for ocean water. Why is this value so much larger than the value for atmospheric water?
4. Reconsider Schindler and Fee's (1974) experimental design for Experimental Lakes 226 and 227. Would the results be more convincing if the researchers had tried adding only carbon (C) to one lake, phosphorus (P) to a second lake, nitrogen (N) to a third lake, C and P to a fourth, C and N to a fifth, P and N to a sixth, and C, P, and N to a seventh lake? What would be the advantages to such a design, and in what way(s) would it be inferior to Schindler and Fee's experiments?
5. Do you think that mass spawning of coral will lead to an increase or a decrease in oxygen levels in the reef? Explain your rationale.
6. The mangrove/sponge interaction (Ellison *et al*. 1996) is an example of a mutualism. Do you think that mutualisms should be more common in stressed biomes like mangroves, or in less-stressed biomes, like coral reefs? Explain your reasoning and suggest how you might go about answering this question.
7. Based on Table 2.3, which of the village biomes seems most distinct from the other five? Which two village biomes seem most similar? Explain your answers.

Analyse the data 1

Reconsider the data in Table 2.1. This time do a linear regression analysis of the data. If you entered the numbers properly, you will get a regression equation that looks something like this: direct solar radiation = 283 048 − 2224 (latitude). If you plug in the value for the North Pole, your regression equation will estimate the direct solar radiation there. How does this estimate compare to your extrapolation estimate? Why is your extrapolation estimate likely to be more accurate than the value predicted by the linear regression equation?

Analyse the data 2

Refer back to Table D2.3.1. Graph the relationship between elevation and atmospheric pressure. What atmospheric pressure would you predict at 15 km? Did you use extrapolation or linear regression? Explain your choice.

PART II

Evolutionary and organismal ecology