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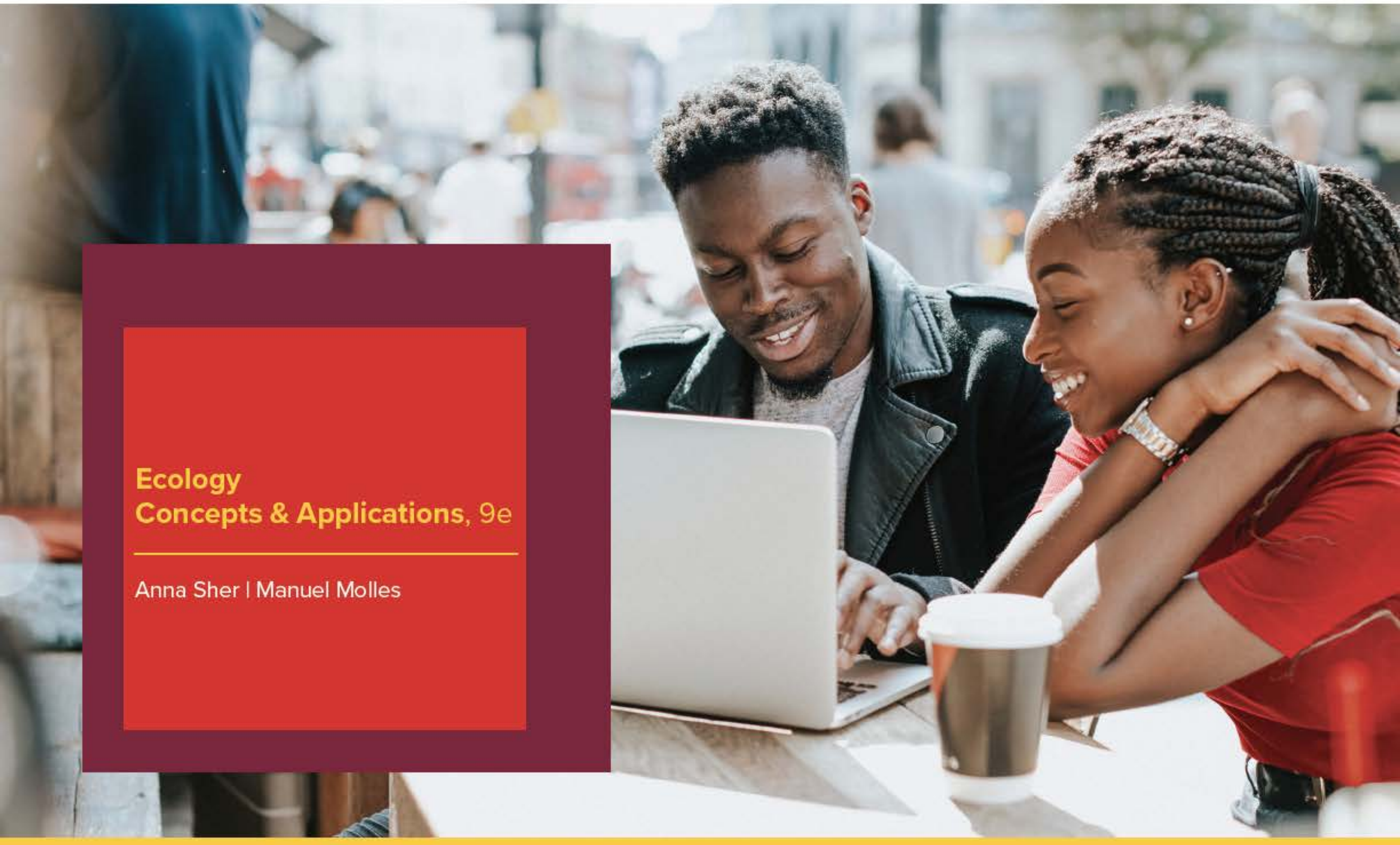


Ecology Concepts & Applications, 9e

Anna Sher | Manuel Molles

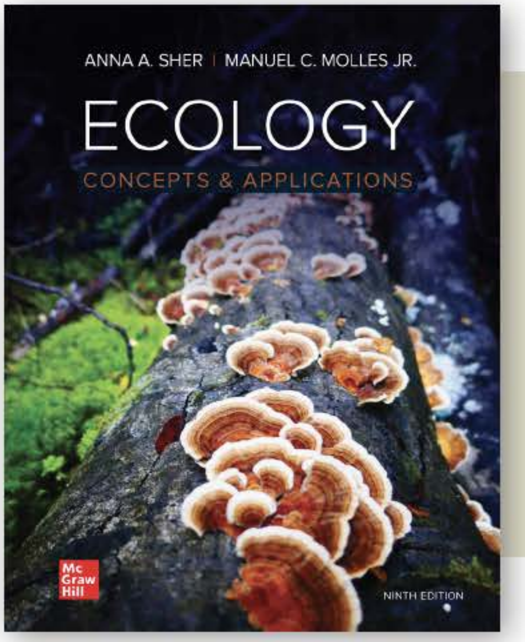
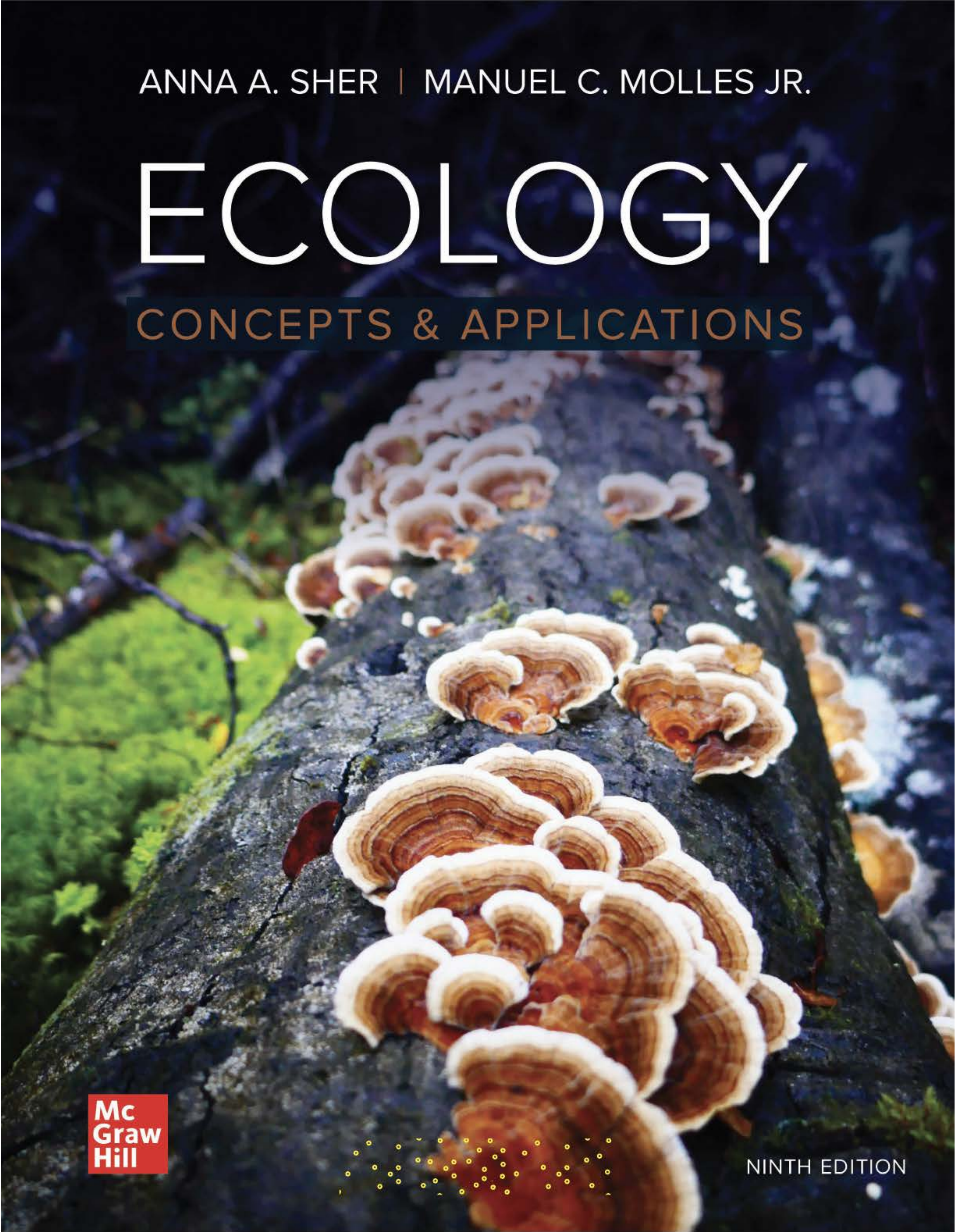


Table of Contents



ANNA A. SHER | MANUEL C. MOLLES JR.

ECOLOGY

CONCEPTS & APPLICATIONS

NINTH EDITION

ECOLOGY: CONCEPTS AND APPLICATIONS, NINTH EDITION

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About the Authors

Courtesy of Anna Sher

Anna A. Sher is a full professor in the Department of Biological Sciences at the University of Denver, where she has been faculty since 2003. Until 2010 she held this position jointly with the Denver Botanic Gardens as the Director of Research and Conservation. As a student, she was a double major in Biology and Art at Earlham College, where she has also taught ecology, and was the co-leader of the Earlham Study Abroad Kenya Program. She received her PhD from the University of New Mexico, where she also taught botany as a visiting lecturer. As a postdoctoral researcher, Dr. Sher was awarded a Fulbright postdoctoral research fellowship to conduct research on plant interactions in Israel at Ben Gurion University's Mitrani Department of Desert Ecology, and she also studied the ecology of an invasive grass at the University of California, Davis. She has also been a visiting professor at the University of Otago, Dunedin, New Zealand.

Dr. Sher's primary research focus has been on the ecological dynamics associated with the removal of invasive riparian plants. She is known as a leading expert in the ecology of *Tamarix,* a dominant exotic tree, and she was the lead editor of the first book exclusively on the topic. Her research interests and publications have spanned several areas within ecology, including not only restoration ecology, competition, and invasive species ecology, but also interactions between plants and soil chemistry, mycorrhizae, insect diversity and trophic cascades, ethnobotany, phenology, climate change, and rare species conservation. She is also lead author of the textbook series *An Introduction to Conservation Biology* (Oxford University Press). Dr. Sher has a particular interest in quantitative ecological methods, with her lab specializing in multivariate methods and spatial models at both individual organism and regional scales. She is currently principal investigator of a National Science Foundation award to investigate the human dimension of the restoration of damaged ecosystems, and she has been a TEDx speaker on the way ecosystems can teach us how to solve human problems.

Above all, Dr. Sher loves to teach and mentor students doing research at both undergraduate and graduate levels.

Courtesy of Manuel Molles

Manuel C. Molles Jr. is an emeritus Professor of Biology at the University of New Mexico, where he has been a member of the faculty and curator in the Museum of Southwestern Biology since 1975. He received his BS from Humboldt State University and his PhD from the Department of Ecology and Evolutionary Biology at the University of Arizona. Seeking to broaden his geographic perspective, he has taught and conducted ecological research in Latin America, the Caribbean, and Europe. He was awarded a Fulbright Research Fellowship to conduct research on river ecology in Portugal and has held visiting professor appointments in the Department of Zoology at the University of Coimbra, Portugal, in the Laboratory of Hydrology at the Polytechnic University of Madrid, Spain, and at the University of Montana's Flathead Lake Biological Station.

Originally trained as a marine ecologist and fisheries biologist, the author worked mainly on river and riparian ecology at the University of New Mexico. His research has covered a wide range of ecological levels, including behavioral ecology, population biology, community ecology, ecosystem ecology, biogeography of stream insects, and the influence of a large-scale climate system (El Niño) on the dynamics of southwestern river and riparian ecosystems. His current research interests focus on the influence of climate change and climatic variability on the dynamics of populations and communities along steep gradients of temperature and moisture in the mountains of the Southwest. Throughout his career, Dr. Molles has attempted to combine research, teaching, and service, involving undergraduate as well as graduate students in his ongoing projects. At the University of New Mexico, he taught a broad range of lower division, upper division, and graduate courses, including Principles of Biology, Evolution and Ecology, Stream Ecology, Limnology and Oceanography, Marine Biology, and Community and Ecosystem Ecology. He has taught courses in Global Change and River Ecology at the University of Coimbra, Portugal, and General Ecology and Groundwater and Riparian Ecology at the Flathead Lake Biological Station. Dr. Manuel Molles was named Teacher of the Year by the University of New Mexico for 1995–1996 and Potter Chair in Plant Ecology in 2000. In 2014, he received the Eugene P. Odum Award from the Ecological Society of America based on his "ability to relate basic ecological principles to human affairs through teaching, outreach and mentoring activities."

Design elements: Anna A. Sher

Dedication

To the Sher Lab and the whole next generation
of ecologists, who inspire me to do this work.
Also, I dedicate this edition to my co-author
and mentor, Manuel.
–Anna A. Sher

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Brief Contents

Design elements: Anna A. Sher

Contents

Section I
NATURAL HISTORY AND EVOLUTION

Section II
ADAPTATIONS TO THE ENVIRONMENT

Section III
POPULATION ECOLOGY

Section IV
INTERACTIONS

Section V

SECTION VI

LARGE-SCALE ECOLOGY

Appendix A Investigating the Evidence

Design elements: Anna A. Sher

Preface

This book was written for students taking their first undergraduate course in ecology. We have assumed that students in this one-semester course have some knowledge of basic chemistry and mathematics and have had a course in general biology, which included introductions to evolution, physiology, and biological diversity.

Organization of the Book

An evolutionary perspective forms the foundation of the entire textbook, as it is needed to support understanding of major concepts. The textbook begins with a brief introduction to the nature and history of the discipline of ecology, followed by section I, which includes two chapters on earth's biomes—life on land and life in water—followed by a chapter on population genetics and natural selection. Sections II through VI build a hierarchical perspective through the traditional subdisciplines of ecology: section II concerns adaptations to the environment; section III focuses on population ecology; section IV presents the ecology of interactions; section V summarizes community and ecosystem ecology; and finally, section VI discusses large-scale ecology, including chapters on landscape, geographic, and global ecology. These topics were first introduced in section I within its discussion of the biomes. In summary, the book begins with an overview of the biosphere, considers portions of the whole in the middle chapters, and ends with another perspective of the entire planet in the concluding chapter. The features of this textbook were carefully planned to enhance the students' comprehension of the broad discipline of ecology.

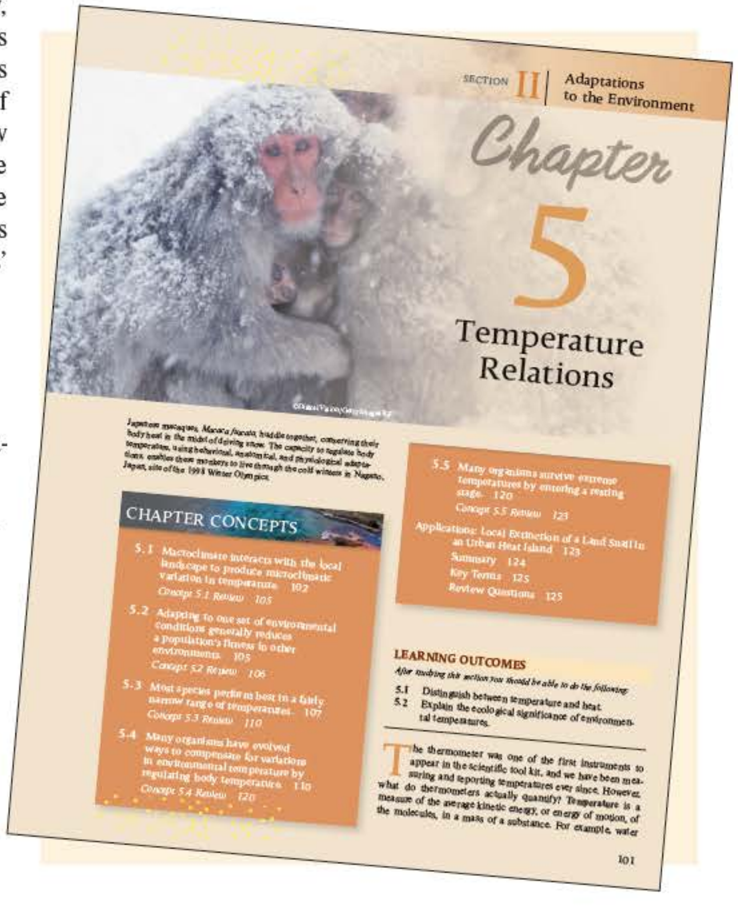
Features Designed with the Student in Mind

All chapters are based on a distinctive learning system, featuring the following key components:

Student Learning Outcomes: Educators are being asked increasingly to develop concrete student learning outcomes for courses across the curriculum. In response to this need and to help focus student progress through the content, all sections of each chapter in the ninth edition begin with a list of detailed student learning outcomes.

Introduction: The introduction to each chapter presents the student with the flavor of the subject and important background information. Some introductions include historical events related to the subject; others present an example of an ecological process. All attempt to engage students and draw them into the discussion that follows.

Concepts: The goal of this book is to build a foundation of ecological knowledge around key concepts, which are listed at the beginning of each chapter to alert the student to the major topics to follow and to provide a place where the student can find a list of the important points covered in each chapter. The sections in which concepts are discussed focus on published studies and, wherever possible, the scientists who did the research are introduced. This case-study approach supports the concepts with evidence, and introduces students to the methods and people that have created the discipline of ecology. Each concept discussion ends with a series of concept review questions to help students test their knowledge and to reinforce key points made in the discussion.



SECTION II | Adaptations to the Environment

Chapter 5

Temperature Relations

Japanese macaques, Macaca fuscata, huddle together, conserving their body heat in the midst of driving snow. The capacity to regulate body temperature, using behavioral, anatomical, and physiological adaptations, enables these monkeys to live through the cold winters in Nagano, Japan, site of the 1998 Winter Olympics.

CHAPTER CONCEPTS

5.1 Macroclimate interacts with the local landscape to produce microclimatic variation in temperature. 102
Concept 5.1 Review 105

5.2 Adapting to one set of environmental conditions generally reduces a population's fitness in other environments. 105
Concept 5.2 Review 106

5.3 Most species perform best in a fairly narrow range of temperatures. 107
Concept 5.3 Review 110

5.4 Many organisms have evolved ways to compensate for variations in environmental temperature by regulating body temperature. 110
Concept 5.4 Review 120

5.5 Many organisms survive extreme temperatures by entering a resting stage. 120
Concept 5.5 Review 123

Applications: Local Extinction of a Land Snail in an Urban Heat Island 123
Summary 124
Key Terms 125
Review Questions 125

LEARNING OUTCOMES

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

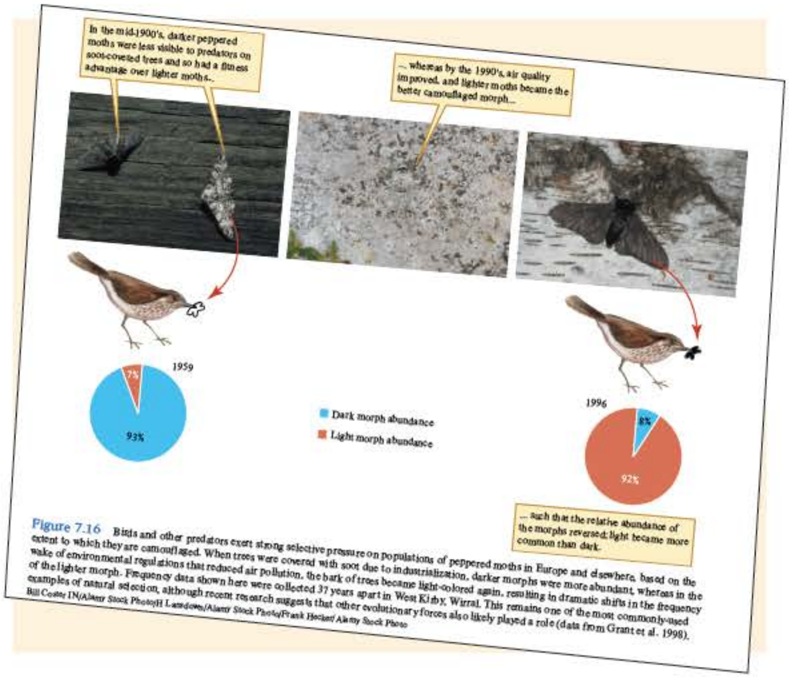
5.1 Distinguish between temperature and heat.
5.2 Explain the ecological significance of environmental temperatures.

The thermometer was one of the first instruments to appear in the scientific tool kit, and we have been measuring and reporting temperatures ever since. However, what do thermometers actually quantify? Temperature is a measure of the average kinetic energy, or energy of motion, of the molecules, in a mass of a substance. For example, water

101

Illustrations: A great deal of effort has been put into the development of illustrations, both photographs and line art. The goal has been to create more-effective pedagogical tools through skillful design and use of color, and to rearrange the traditional presentation of information in figures and captions. Much explanatory material is located within the illustrations, providing students with key information where they need it most. The approach also provides an ongoing tutorial on graph interpretation, a skill with which many introductory students need practice.

Detailed Explanations of Mathematics: The mathematical aspects of ecology commonly challenge many students taking their first ecology course. This text carefully explains all mathematical expressions that arise to help students overcome these challenges. In some cases, mathematical expressions are dissected in illustrations designed to complement their presentation in the associated narrative.



In the mid-1900's, darker peppered moths were less visible to predators on soot-covered trees and so had a fitness advantage over lighter moths...

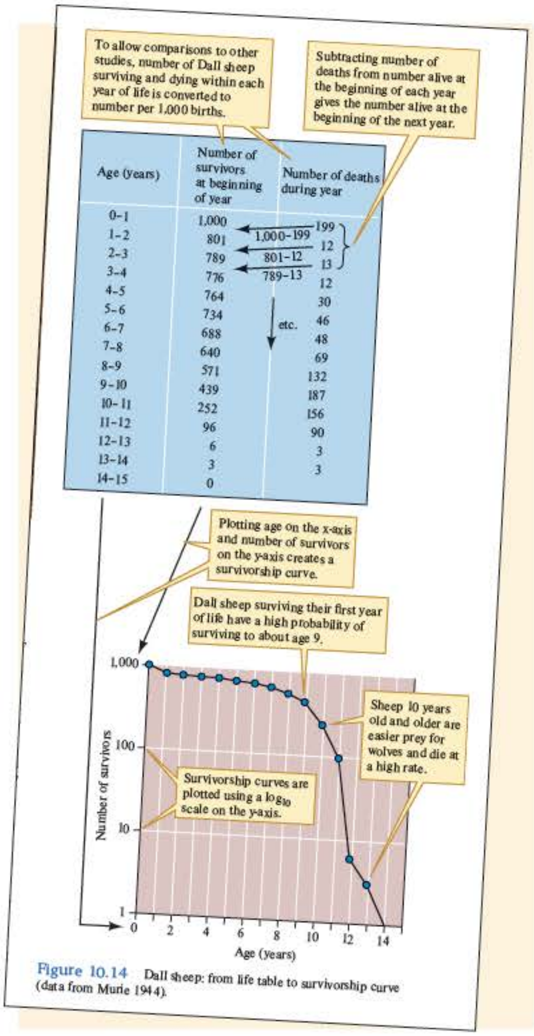
... whereas by the 1990's, air quality improved, and lighter moths became the better camouflaged morph...

... such that the relative abundance of the morphs reversed; light became more common than dark.

Figure 7.16 Birds and other predators exert strong selective pressure on populations of peppered moths in Europe and elsewhere, based on the extent to which they are camouflaged. When trees were covered with soot due to industrialization, darker morphs were more abundant, whereas in the wake of environmental regulations that reduced air pollution, the bark of trees became light-colored again, resulting in dramatic shifts in the frequency of the lighter morph. Frequency data shown here were collected 37 years apart in West Kirby, Wirral. This remains one of the most commonly-used examples of natural selection, although recent research suggests that other evolutionary forces also likely played a role (data from Grant et al. 1998).

Bill Coster IN/Alamy Stock Photo/H Lansdown/Alamy Stock Photo/Frank Hecker/Alamy Stock Photo

A visualization of a population bottle neck, using data from published research.



To allow comparisons to other studies, number of Dall sheep surviving and dying within each year of life is converted to number per 1,000 births.

Subtracting number of deaths from number alive at the beginning of each year gives the number alive at the beginning of the next year.

Age (years)	Number of survivors at beginning of year	Number of deaths during year
0–1	1,000	199
1–2	801	12
2–3	789	13
3–4	776	12
4–5	764	30
5–6	734	46
6–7	688	48
7–8	640	69
8–9	571	132
9–10	439	187
10–11	252	156
11–12	96	90
12–13	6	3
13–14	3	3
14–15	0	

Plotting age on the x-axis and number of survivors on the y-axis creates a survivorship curve.

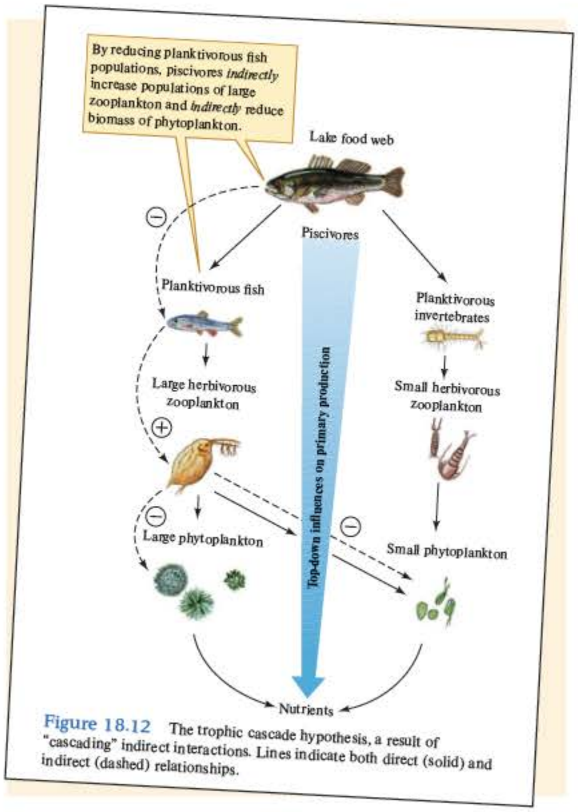
Dall sheep surviving their first year of life have a high probability of surviving to about age 9.

Sheep 10 years old and older are easier prey for wolves and die at a high rate.

Survivorship curves are plotted using a $\log_{10}$ scale on the y-axis.

Figure 10.14 Dall sheep: from life table to survivorship curve (data from Murie 1944).

Helps students work with and interpret quantitative information, involving converting numerical information into a graph.



By reducing planktivorous fish populations, piscivores *indirectly* increase populations of large zooplankton and *indirectly* reduce biomass of phytoplankton.

Figure 18.12 The trophic cascade hypothesis, a result of "cascading" indirect interactions. Lines indicate both direct (solid) and indirect (dashed) relationships.

Provides a visual representation of a hypothesis involving a set of complex ecological interactions.

Applications: Many students are concerned with the practical side of ecology and want to know more about how the tools of science can be applied to the environmental problems we face in the contemporary world. Including a discussion of applications at the end of each chapter can motivate students to learn more of the underlying principles of ecology. In addition, it seems that environmental problems are now so numerous and so pressing that they have erased a once easy distinction between general and applied ecology.

End-of-Chapter Material:

- ***Summary*** The chapter summary reviews the main points of the content. The concepts around which each chapter is organized are boldfaced and redefined in the summary to reemphasize the main points of the chapter.
- ***Key Terms***
- ***Review Questions*** The review questions are designed to help students think more deeply about each concept and to reflect on alternative views. They also provide a place to fill in any remaining gaps in the information presented and take students beyond the foundation established in the main body of the chapter.

  Note: Suggested Readings are located online.

End-of-Book Material:

- ***Appendixes*** Appendix A, "Investigating the Evidence," offers "mini-lessons" on the scientific method, emphasizing statistics and study design. They are intended to present a broad outline of the process of science, while also providing step-by-step explanations. The series of features begins with an overview of the scientific method, which establishes a conceptual context for more specific material in the next 21 features. The last reading wraps up the series with a discussion of electronic literature searches. Each Investigating the Evidence ends with one or more questions, under the heading "Critiquing the Evidence." This feature is intended to stimulate critical thinking about the content. Appendix B, "Statistical Tables," is available to the student as a reference in support of the Investigating the Evidence features. Appendix C, "Abbreviations" is a handy guide to the scientific and other abbreviations used throughout the text, including units of measurement. Appendix D is a global map of the biomes.
- ***Glossary*** List of all key terms and their definitions.
- ***References*** References are an important part of any scientific work. However, many undergraduates are distracted by a large number of references within the text. One of the goals of a general ecology course should be to introduce these students to the primary literature without burying them in citations. The number of citations has been reduced to those necessary to support detailed discussions of particular research projects.
- ***Index***

Appendix A Investigating the Evidence 531

✓ Information
Hypothesis
Predictions
Testing

Investigating the Evidence 16

Estimating the Number of Species in Communities

LEARNING OUTCOMES

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

16.1 Explain the difficulties involved in trying to estimate the total number of species in a community.
16.2 Discuss ways to reduce the effort necessary for making a comparison of the relative species richness of communities.

How many species are there? This is one of the most fundamental questions that an ecologist can ask about a community. With increasing threats to biological diversity, species richness is also one of the most important community attributes we might measure. For instance, estimates of species richness are critical for determining areas suitable for conservation, for diagnosing the impact of environmental change on a community, and for identifying critical habitat for rare or threatened species. However, determining the number of species in a community is not a simple undertaking. Sound estimates of species richness for most taxa require a carefully designed, standardized sampling program. Here we will review some of the basic factors that an ecologist needs to consider when designing such a sampling program to gather information about species richness within and among communities.

Sampling Effort

The number of species recorded in a sample of a community increases with higher sampling effort. We reviewed a highly simplified example of this in Investigating the Evidence 6, where we considered how numbers of quadrats influenced estimates of species richness in the benthic community of a small Rocky Mountain stream. In that example, a relatively small sample size was required. However, often far more effort is required. For example, Petri Martikainen and Jari Kouki (2003) estimated that to verify the presence or absence of threatened beetle species in the boreal forests of Finland required a sample of over 400 beetle species. They also suggested that a sample of over 100,000 individual beetles may be required to assess just 10 forest areas in Finland for their suitability to serve as conservation areas for threatened beetle species. To reduce the sampling effort required to estimate species richness, community ecologists and conservationists often focus on groups of organisms that are reliable indicators of species richness.

Indicator Taxa

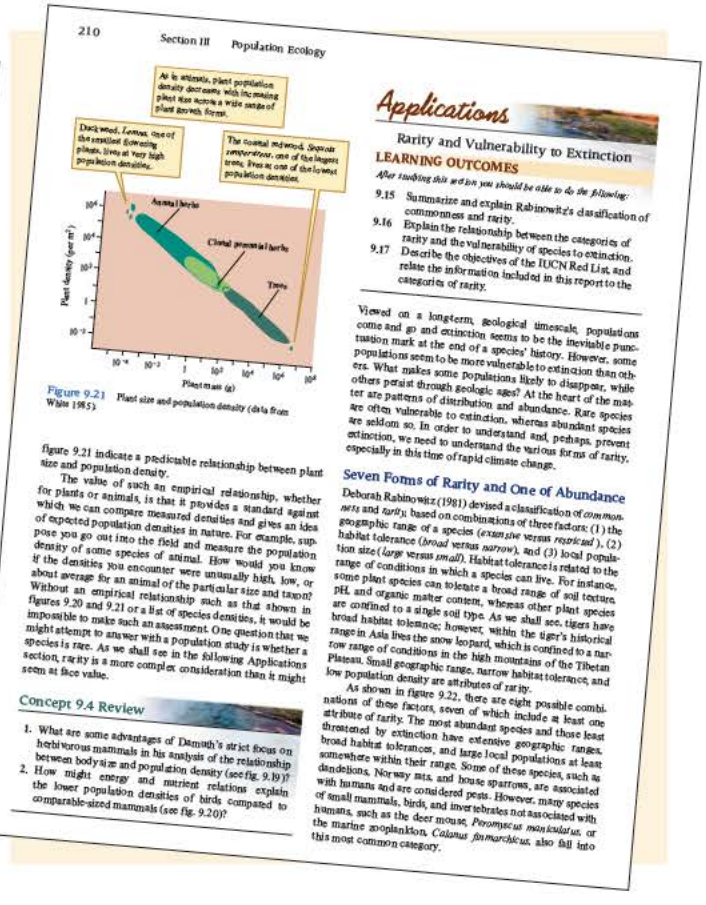
Because of the great cost and time of making thorough inventories of species diversity, ecologists have proposed a wide variety of taxa as indicators of overall biological diversity. Indicator taxa have generally been well-known and conspicuous groups of organisms such as birds and butterflies. However, it appears that indicator taxa need to be chosen with caution. For example, John Lawton of Imperial College in the United Kingdom and 12 colleagues (Lawton et al. 1998) attempted to characterize biological diversity along a disturbance gradient in the tropical forest of Cameroon, Africa, using indicator taxa. In addition to birds and butterflies, Lawton and his colleagues sampled flying beetles, beetles living in the forest canopy, canopy ants, leaf-litter ants, termites, and soil nematodes. They sampled these taxa from 1992 to 1994 and spent several more years sorting and cataloging the approximately 2,000 species collected. This work required approximately 10,000 scientist hours. Unfortunately, the conclusion at the end of this massive study was that no one group serves as a reliable indicator of species richness for other taxonomic groups. Lawton and his colleagues estimated that their survey included from one-tenth to one-hundredth the total number of species in their study site. Citing their own experience, they concluded that characterizing the full biological diversity of just 1 hectare of tropical forest would require from 100,000 to 1 million scientist hours. As a consequence of these time constraints, ecologists will likely continue to focus their studies of diversity on smaller groups of taxa. However, even with a restricted taxonomic focus, it is important to standardize sampling across study communities.

Standardized Sampling

Standardizing sampling effort and technique is generally necessary to provide a valid basis for comparing species richness across communities. For example, Frode Ødegaard of the Norwegian Institute for Nature Research took great care to standardize sampling as he compared species richness among plant-feeding beetles living in a tropical dry forest and in a tropical rain forest in Panama (Ødegaard 2006). Ødegaard sampled both forests from a canopy crane that provided access to similar areas of forest (~0.8 ha). He standardized the amount of time he spent sampling each tree or vine, and he used the same sampling techniques in both forests. Ødegaard also sampled the beetles on approximately the same number of plant species—50 species in the dry forest and 52 in the rain forest. His efforts resulted in the capture of very similar numbers of individual beetles in the two forests: 35,479 in dry forest versus 30,352 in rain forest. However, his collections in rain forest included 37% more beetle species than in dry forest: 1,603 species in rain forest versus 1,165 in dry forest. Because Ødegaard took care to standardize sampling, we can conclude that the species richness of plant-feeding beetles was probably higher at his rain forest study site. If his sampling efforts were uneven, we could not reach such a conclusion.

CRITIQUING THE EVIDENCE 16

1. A complete list of species has not been determined for any area of substantial habitat anywhere on earth. Why not?
2. Why do most surveys of species diversity focus on restricted groups of relatively well-known organisms such as plants, mammals, and butterflies?



210 Section III Population Ecology

As in animals, plant population density decreases with increasing plant size across a wide range of plant growth forms.

Duckweed, *Lemna*, one of the smallest flowering plants, lives at very high population densities.

The coastal redwood, *Sequoia sempervirens*, one of the largest trees, lives at one of the lowest population densities.

Figure 9.21 Plant size and population density (data from White 1985).

figure 9.21 indicate a predictable relationship between plant size and population density.

The value of such an empirical relationship, whether for plants or animals, is that it provides a standard against which we can compare measured densities and gives an idea of expected population densities in nature. For example, suppose you go out into the field and measure the population density of some species of animal. How would you know if the densities you encounter were unusually high, low, or about average for an animal of the particular size and taxon? Without an empirical relationship such as that shown in figures 9.20 and 9.21 or a list of species densities, it would be impossible to make such an assessment. One question that we might attempt to answer with a population study is whether a species is rare. As we shall see in the following Applications section, rarity is a more complex consideration than it might seem at face value.

Concept 9.4 Review

1. What are some advantages of Damuth's strict focus on herbivorous mammals in his analysis of the relationship between body size and population density (see fig. 9.19)?
2. How might energy and nutrient relations explain the lower population densities of birds compared to comparable-sized mammals (see fig. 9.20)?

Applications

Rarity and Vulnerability to Extinction

LEARNING OUTCOMES

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

9.15 Summarize and explain Rabinowitz's classification of commonness and rarity.
9.16 Explain the relationship between the categories of rarity and the vulnerability of species to extinction.
9.17 Describe the objectives of the IUCN Red List, and relate the information included in this report to the categories of rarity.

Viewed on a long-term, geological timescale, populations come and go and extinction seems to be the inevitable punctuation mark at the end of a species' history. However, some populations seem to be more vulnerable to extinction than others. What makes some populations likely to disappear, while others persist through geologic ages? At the heart of the matter are patterns of distribution and abundance. Rare species are often vulnerable to extinction, whereas abundant species are seldom so. In order to understand and, perhaps, prevent extinction, we need to understand the various forms of rarity, especially in this time of rapid climate change.

Seven Forms of Rarity and One of Abundance

Deborah Rabinowitz (1981) devised a classification of *commonness* and *rarity* based on combinations of three factors: (1) the geographic range of a species (*extensive* versus *restricted*), (2) habitat tolerance (*broad* versus *narrow*), and (3) local population size (*large* versus *small*). Habitat tolerance is related to the range of conditions in which a species can live. For instance, some plant species can tolerate a broad range of soil texture, pH, and organic matter content, whereas other plant species are confined to a single soil type. As we shall see, tigers have broad habitat tolerance; however, within the tiger's historical range in Asia lives the snow leopard, which is confined to a narrow range of conditions in the high mountains of the Tibetan Plateau. Small geographic range, narrow habitat tolerance, and low population density are attributes of rarity.

As shown in figure 9.22, there are eight possible combinations of these factors, seven of which include at least one attribute of rarity. The most abundant species and those least threatened by extinction have extensive geographic ranges, broad habitat tolerances, and large local populations at least somewhere within their range. Some of these species, such as dandelions, Norway rats, and house sparrows, are associated with humans and are considered pests. However, many species of small mammals, birds, and invertebrates not associated with humans, such as the deer mouse, *Peromyscus maniculatus*, or the marine zooplankton, *Calanus finmarchicus*, also fall into this most common category.

New to the Ninth Edition

Nearly every chapter has significant changes in this edition. To update content and respond to reviewers' comments, we have incorporated the research and ideas of over 140 new citations, the majority of which (73%) were authored by underrepresented scientists. A particular effort was made to cite cutting-edge ecological research by women of color. With each edition, we continue toward the goal of making this text reflect the true diversity of researchers in the field.

There are over 100 updated examples in this edition, with 42 new figures, plus improvements or updates to 20 existing figures. Dozens of new questions have been written to correspond to the new material and, in response to reviewers, many other questions have been re-written to focus more on concepts rather than specific examples. Several new terms have also been added in the text and glossary to increase student understanding and to reflect the evolving nature of the field. We have also continued to expand connections with evolution and global change in this edition.

Significant Chapter-by-Chapter Changes

Chapter 1 In response to reviewer's comments, we have created a new section that describes the different tools used by ecologists, introducing five new terms including *ex situ* and *in situ.* There are a total of nine new figures. We have revised figure 1 and added microbial ecology as an important frontier. We have added new examples from recent literature, including about evolution in alpine chipmunks. Questions were updated.

Chapter 2 Three new figures were added, including from research on habitat conversion in India. Data on tropical forest loss was updated. New examples from publications by women of color on soils and on logging of boreal forests were added. Wording in several places was clarified in response to reviewers' comments. An explanation of the distinction between weather and climate change was added. Improvements were made to 10 figures, including updating the drought data in figure 2.41 to 2020 and relating it to fires. Questions were updated.

Chapter 3 Six citations were updated. Sections added on United Nations Decade of Ocean Science, microplastics from research by Chatterjee and Sharma (2019), and updated several examples. One figure was updated with current global ice levels.

Chapter 4 The "applications" section was re-written with an updated example of herbicide resistance by Sushila Chaudhari and her colleagues, including a new figure. Questions were updated, and an existing figure improved.

Chapter 5 A total of 13 new citations, including examples with current citations were provided of how global warming is affecting ecosystems. New example and figure created to describe relationship between water temperature and canopy cover. Research on endothermic fish updated, with a new figure created and concept of RM endothermy added. Old example replaced with new section on comparisons between endothermic and ectothermic fish with research by a man of color, including another new figure. Questions were updated.

Chapter 6 Section on water-harvesting re-written with updated information and a new figure adapted from the review by Guera and Bhushan (2020). Added concept of cohesion, per reviewer request. Concepts hydrophilic and hydrophobic introduced. Water isotope section re-written to clarify per reviewer request, including a new figure to explain. Applications section was re-written with updated example from the meta-analysis by Evaristo and McDonnell (2017). Questions and one figure were updated.

Chapter 7 Information about chemosynthesis was expanded and updated with example from Naples, Italy. Peppered moth example re-written and figure replaced with one that shows actual photographs and data. Old predation examples were replaced with those using wolf spiders and coral reef fishes research from teams led by women, including new figures. Questions were updated.

Chapter 8 Opening photo replaced with a more appropriate one, six references updated. Section on nonrandom mating in plants significantly updated and clarified. Paragraph on phylogenies based on genetic analysis added. Updated number of cooperative breeding species. Updated section on lion cooperation with research by Natalia Borrego, a woman of color. Questions were updated.

Chapter 9 New example of gorillas replaces an old example, and new paragraph added based on the 2020 Living Planet Report. One new image. More information about the Breeding Bird Survey with updated references. Term endemic added, with paragraph replaced with new example of bird from Hawaii. Figure on rarity and vulnerability to extinction significantly improved in response to reviewer request. Questions were updated.

Chapter 10 Seven citations updated. Research on "killer" bees updated with genetics research led by a man of color, including updated figure. Added information and example of pumas in Patagonia to migration section. Questions updated.

Chapter 11 Introduction re-written with example from the COVID-19 pandemic, including new figures. Three figures updated, including one for current numbers of whooping cranes and another with human population growth. Questions were updated.

Chapter 12 Paragraph replaced with section on life history trade-offs, based on ideas by Anurag Agrawal. Updated number of species of fish with 2020 data from IUCN. One figure improved. Questions were updated.

Chapter 13 Self-thinning section updated with research from people of color, and new figure added to better explain zero growth isocline, per reviewer request. Existing Lotka-Volterra figure simplified. Competition meta-analysis research by Jessica Gurevitch and colleagues added. Extra example of competition deleted, per reviewer request. Questions updated.

Chapter 14 Section on research by Utida shortened and simplified per reviewer request, including an improvement to an existing figure. Questions were re-written to focus on concepts rather than specific research. Two citations updated.

Chapter 16 The concept of a species rarefaction curve is introduced. A new example of sampling benthic macroinvertebrates replaces an old example, work done by a man of color that also introduces the concept of DNA barcoding, including new figures. Questions were updated.

Chapter 17 Four examples were updated, all from research led by underrepresented scientists. This includes a new "Applications" example on hyperparasitoids with a new figure. Questions were updated.

Chapter 18 Section on primary productivity of oceans was re-written with updated environmental factors and relating this to global change. Map on marine primary productivity has been updated. Research on top-down vs. bottom-up updated with a new section and figure from meta-analysis research conducted by Mayra Vidal, a woman of color, and Shannon Murphy. Concept of tri-trophic interactions added. Eleven citations were updated, most of which from papers with underrepresented lead authors. Paragraph on role of microorganisms added, per reviewer request. Questions were updated.

Chapter 20 All sections on succession at Glacier Bay section completely re-written to reflect more current research led by Brian Buma that changes interpretation of those research, including new figures. This case study becomes a more interesting story about how understanding can evolve with new information. Questions were updated.

Chapter 21 Reference to the 2020 California wildfires was added, including a short paragraph about research from UC Berkeley. Questions were updated.

Chapter 23 A total of five new figures added, including one that refers to the Australian wildfires of 2020. Figure on atmospheric CO_2 updated with current values. Section on nitrogen pollution re-written with more explanation and more current research. The forest section was re-written with forest biodiversity data from the FAO 2020 report on the State of the World's Forests and other current research. Corrections made to use of Spanish words, per reviewer request. Deforestation in Brazil was updated. There were a total of 13 new citations, 9 from underrepresented scientists. Questions were updated.

Online Materials

Available online are suggested readings and answers to concept review, chapter review, and critiquing the evidence questions.

Related Title of Interest from McGraw-Hill Education

***Ecology Laboratory Manual,* by Vodopich**
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Darrell Vodopich, coauthor of *Biology Laboratory Manual,* has written a new lab manual for ecology. This lab manual offers straightforward procedures that are doable in a broad range of classroom, lab, and field situations. The procedures have specific instructions that can be taught by a teaching assistant with minimal experience as well as by a professor.

Acknowledgments

First and foremost, I must thank my academic partner Dr. Eduardo González, without whose help I could have never completed this edition. I am also deeply grateful for pedagogical expertise of Julie Morris, who also went above and beyond. Thanks also go to the other members of the Sher Lab who pitched in with research and/or offered feedback on new figures for the ninth edition, including Ali Alghamdi, Violet Butler, Rhys Daniels, Alex Goetz, Annie Henry, Alex Kim, Lily Malone, Mandy Malone, and Allen Williamson. During the development of this textbook, many colleagues freely shared their expertise, reviewed sections, or offered the encouragement a project like this needs to keep it going: Anurag Agrawal, Brian Buma, Candice Galen, Diane Marshall, Scott Nichols, Mayra Vidal, and Dhaval Vyas. I am grateful to Patrick M. Burchfield and Hector Chenge Alvarez for keeping me up to date in data and photos of turtles. Special thanks to Jake Grossman for sharing his list of Ecologists of Color and Indigenous Ecologists.

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We gratefully acknowledge the many reviewers who, over the course of the many revisions, have given of their time and expertise to help this textbook evolve to its present ninth edition. Note that some feedback that did not make it into this edition will be incorporated into the next one. These reviewers continue our education, for which we are grateful, and we honestly could not have continued the improvement of this textbook without them.

Finally, I would like to thank my co-author Manuel Molles for entrusting me with this wonderful series, as well as my wife Fran and our son Jeremy for their support throughout the production of the ninth edition.

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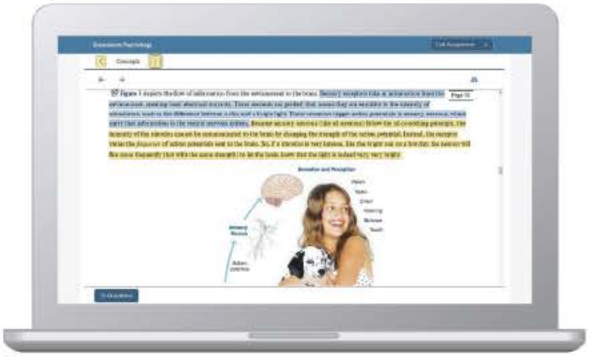

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SECTION I | Natural History and Evolution


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Chapter 2

Life on Land

Despite their often barren appearance, deserts are ecosystems with a diversity of life, uniquely adapted to the temperature and moisture of those environments.

CHAPTER CONCEPTS

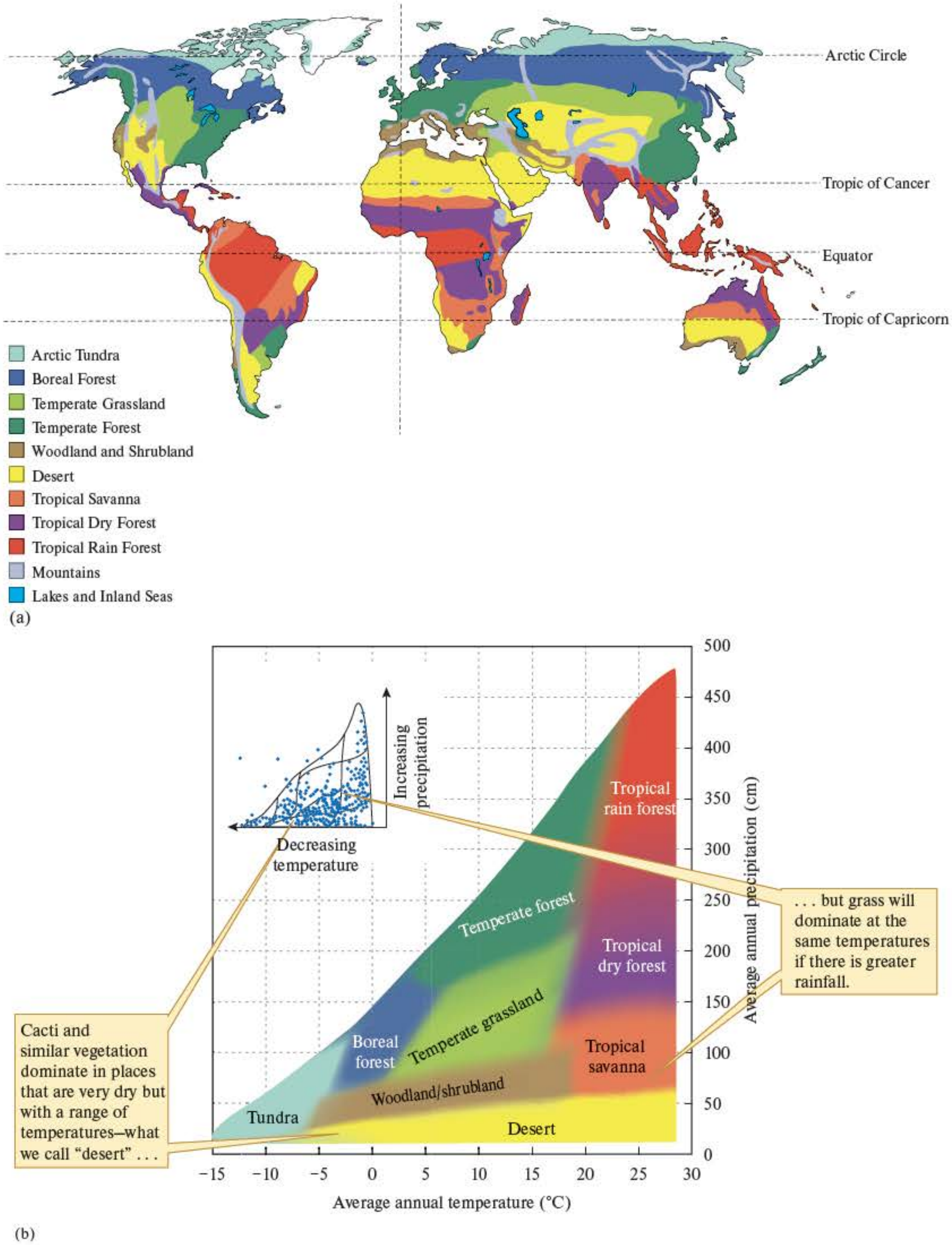
LEARNING OUTCOMES

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

2.1 Explain why plants are the basis of life on Earth and thus define terrestrial biomes.

2.2 List the main environmental features used to differentiate the various terrestrial biomes.

If you are standing on a ground of seemingly barren rock and sand, what little vegetation being thick-leaved and/or prickly, with a few vultures overhead and a lizard eating a scorpion at your feet, where are you? Although the details differ, this general description fits areas of the southwestern United States, western China, Libya, Australia, and elsewhere; we refer to this type of ecosystem as a desert. Desert is one of several types of **biomes,** major divisions of the terrestrial environment, distinguished primarily by their predominant plants (fig. 2.1*a*). In figure 2.1, the boundaries between biomes appear sharp, whereas in nature these transitions generally occur gradually over long distances along gradients of environmental variation. But why do we find the same biome in such disparate locations across the globe? And conversely, why don't we find desert at the top of a mountain or at the equator? The study of how organisms in a particular area are influenced by factors such as climate, soils, predators, competitors, and evolutionary history is called **natural history.** In this chapter, we explore the natural history of different types of terrestrial biomes, including the reasons why they are distributed the way that they are.



Cacti and similar vegetation dominate in places that are very dry but with a range of temperatures—what we call "desert" . . .

. . . but grass will dominate at the same temperatures if there is greater rainfall.

Figure 2.1 (*a*) Global distribution of biomes. (*b*) Biomes are generally defined by the average temperature (x-axis) and precipitation (rain, y-axis) of a given location. Robert Whittaker plotted the vegetation type of various locations against these two variables (inset) to determine the boundaries of the various biomes, but boundaries between these are not distinct, due to the many other influences of the environment (adapted from Whittaker 1975).

Terrestrial Biomes and the Importance of Plants

The most important factor for understanding the distribution of biomes has to do with climate. Whether an ecosystem is dominated by cacti, grass, deciduous trees, conifers, or other types of plants will primarily depend on temperature and water availability (fig. 2.1*b*). If we plot the combination of these two variables for locations across the globe by their dominant plant types, we can see clear patterns of how different natural histories can be defined by temperature and precipitation (fig. 2.1*b* inset).

But how does a particular environment result in similar plants? Returning to our desert scene described above, the dry environment will mean that regardless of which continent we are on, plants in a desert will have certain **functional traits:** particular characteristics that allow them to survive, such as waxy coatings on leaves that prevent water loss. These functional traits of plants arise through evolution via **selective pressure** by the environment, a subject explored in more detail in chapter 4. The section on deserts in this chapter contains a particularly compelling example of how selective pressure results in similar functional traits in unrelated plants on different continents.

But what about all of the animals, fungi, and other organisms in an ecosystem; why are biomes defined by plants? One reason for this is that plants form the foundation of life on this planet. On land, plants make the energy of the sun available to all other life-forms, including us, via photosynthesis (explained in more detail in chapter 7). For this reason, plants and other photosynthesizing organisms are called **primary producers** (fig. 2.2). The biomass produced by primary producers per unit time is *primary production*, which is discussed in detail in chapter 18. Animals and fungi cannot get their energy directly from the sun and so depend on this conversion by plants. For example, in the desert we visited above, the lizard is eating a scorpion that may have eaten a grasshopper that survived by eating a succulent plant, such as a cactus. When all of these organisms die, there will be fungi and insects and bacteria that eat them. Thus, all of these **consumer** organisms can be considered **secondary producers** of energy for the organisms that eat them. We will learn more about food webs and energy flow in ecosystems in chapters 17 and 18. Selective pressure by the climate will be felt *directly* by consumers in an ecosystem, but also *indirectly,* as each experiences the selective pressure of its food source. Each consumer will have traits that make it able to capture, eat, and digest the food available in that environment. Thus, the type and diversity of plants in a given region, determined primarily by climate, will have far-reaching implications for the rest of the ecosystem.

We devote chapters 2 and 3 to an overview of general types of ecosystems and where they occur, that is, the natural history of the biosphere. In chapter 2, we examine the natural history of life on land. We will explore why natural history is primarily based on latitude–that is, why we don't find desert at the

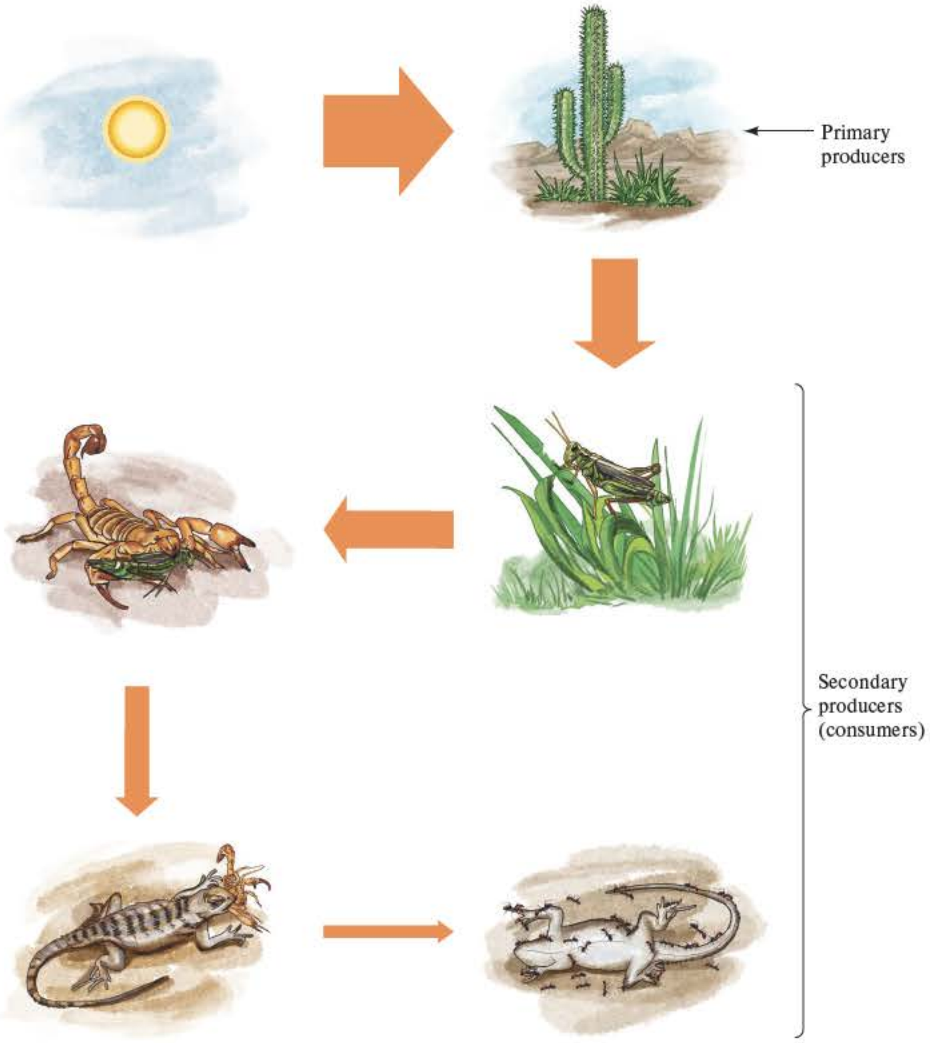


Figure 2.2 How energy moves through an ecosystem; size and direction of arrows indicate the movement and loss of energy through trophic groups. Plants such as cacti capture sun energy via photosynthesis; animals depend on that energy whether by eating the plants or other animals that have eaten plants, and so on. In this way, all organisms ultimately get their energy from the sun, forming the basis of all terrestrial biomes.

equator—but also how soil type and elevation can have strong influences as well, that is, why we also don't find desert on mountaintops. The main goal of chapters 2 and 3 is to take a large-scale perspective of nature before delving, in later chapters, into finer details of structure and process.

2.1 Large-Scale Patterns of Climatic Variation

LEARNING OUTCOMES

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

2.3 Diagram the position of the sun relative to the equator and tropics of Capricorn and Cancer, during the equinoxes and solstices.
2.4 Describe how solar driven air circulation produces regional differences in precipitation.
2.5 Interpret a climate diagram.
2.6 Explain the influence of the Coriolis effect on wind direction.

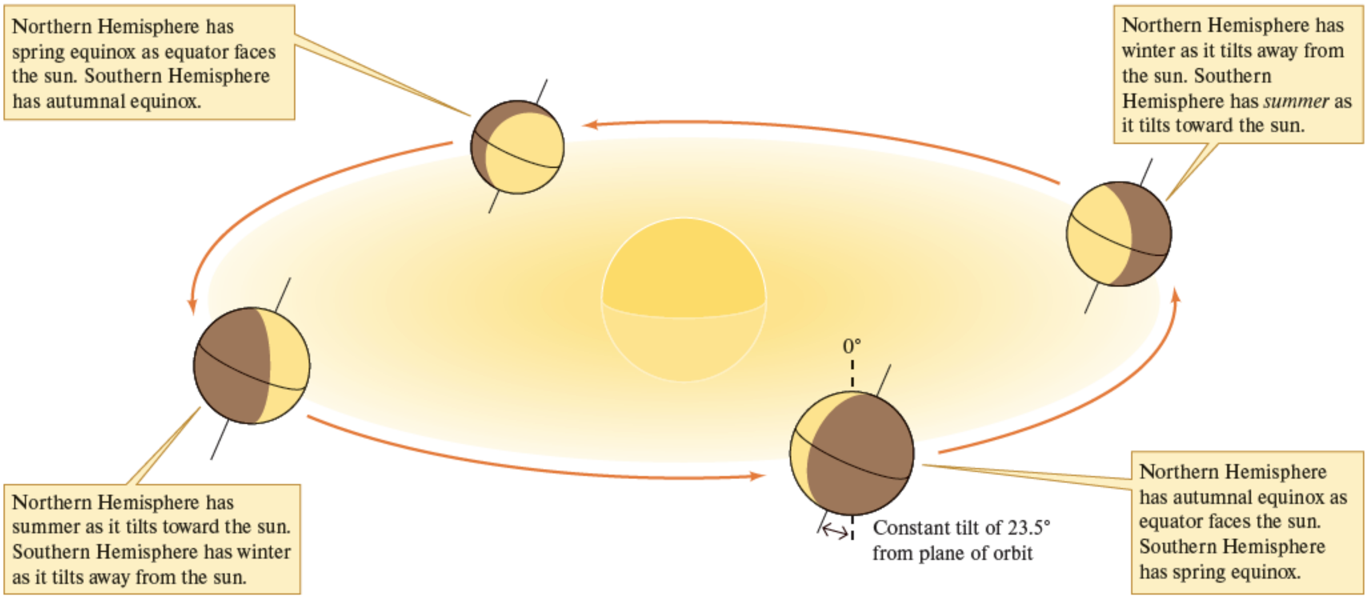
Uneven heating of the earth's surface by the sun and the tilt of the earth combine to produce predictable latitudinal and seasonal variation in climate. While the global distribution of biomes is determined primarily by climate, what determines the distributions of climate? Several attributes of climate vary predictably over the earth. For instance, average temperatures are lower and more seasonal at middle and high latitudes. Temperature generally shows little seasonality near the equator, while rainfall may be markedly seasonal. Deserts, which are concentrated in a narrow band of latitudes around the globe, receive little precipitation, which generally falls unpredictably in time and space. What mechanisms produce these and other patterns of climatic variation?

Temperature, Atmospheric Circulation, and Precipitation

The uneven heating of the earth's surface results from the spherical shape of the earth and the angle at which the earth rotates on its axis as it orbits the sun. Because the earth is a sphere, the sun's rays are most concentrated where the sun is directly overhead. However, the latitude at which the sun is directly overhead changes with the seasons. This seasonal change occurs because the earth's axis of rotation is not perpendicular to its plane of orbit about the sun but is tilted approximately 23.5° away from the perpendicular (fig. 2.3).

Because this tilted angle of rotation is maintained throughout earth's orbit about the sun, the amount of solar energy received by the Northern and Southern Hemispheres changes seasonally. During the northern summer, the Northern Hemisphere is tilted toward the sun and receives more solar energy than the Southern Hemisphere. During the northern summer solstice on approximately June 21, the sun is directly overhead at the tropic of Cancer, at 23.5° N latitude. During the northern winter solstice, on approximately December 21, the sun is directly overhead at the tropic of Capricorn, at 23.5° S latitude. During the northern winter, the Northern Hemisphere is tilted away from the sun and the Southern Hemisphere receives more solar energy. The sun is directly overhead at the equator during the spring and autumnal equinoxes, on approximately March 21 and September 22 or 23. On those dates, the Northern and Southern Hemispheres receive approximately equal amounts of solar radiation.

This seasonal shift in the latitude at which the sun is directly overhead drives the march of the seasons. At high latitudes, in both the Northern and Southern Hemispheres, seasonal shifts in input of solar energy produce winters with low average temperatures and shorter day lengths and summers with high average temperatures and longer day lengths. In many areas at middle to high latitudes, there are also significant seasonal



Northern Hemisphere has spring equinox as equator faces the sun. Southern Hemisphere has autumnal equinox.

Northern Hemisphere has winter as it tilts away from the sun. Southern Hemisphere has *summer* as it tilts toward the sun.

Northern Hemisphere has summer as it tilts toward the sun. Southern Hemisphere has winter as it tilts away from the sun.

Constant tilt of 23.5° from plane of orbit

Northern Hemisphere has autumnal equinox as equator faces the sun. Southern Hemisphere has spring equinox.

Figure 2.3 The seasons in the Northern and Southern Hemispheres.

changes in precipitation. Meanwhile, between the tropics of Cancer and Capricorn, seasonal variations in temperature and day length are slight, while precipitation may vary a great deal. What produces spatial and temporal variation in precipitation?

Heating of the earth's surface and atmosphere drives circulation of the atmosphere and influences patterns of precipitation. As shown in figure 2.4*a,* the sun heats air at the equator, causing it to expand and rise. This warm, moist air cools as it rises. Since cool air holds less water vapor than warm air, the water vapor carried by this rising air mass condenses and forms clouds, which produce the heavy rainfall associated with tropical environments.

Eventually, this equatorial air mass ceases to rise and spreads north and south. This high-altitude air is dry, since the moisture it once held fell as tropical rains. As this air mass flows north and south, it cools, which increases its density. Eventually, it sinks back to the earth's surface at about 30° latitude and spreads north and south. This dry air draws moisture from the lands over which it flows and creates deserts in the process.

Air moving from 30° latitude toward the equator completes an atmospheric circulation cell at low latitudes. As figure 2.4*b* shows, there are three such cells on either side of the equator. Air moving from 30° latitude toward the poles is part of the atmospheric circulation cell at middle latitudes. This warm air flowing from the south rises as it meets cold polar air flowing from the north. As this air mass rises, moisture picked up at lower latitudes condenses to form the clouds that produce the abundant precipitation of temperate regions. The air rising over temperate regions spreads northward and southward at a high altitude, completing the middle- and high-latitude cells of general atmospheric circulation.

The patterns of atmospheric circulation shown in figure 2.4*b* suggest that air movement is directly north and south. However, this does not reflect what we observe from the earth's surface as the earth rotates from west to east. We can see how air movement changes by this simple demonstration: with your finger, trace a line from the equator to the north pole on a globe while it is slowly turning. Do it again for the south pole. Your finger will draw diagonal lines in the same direction as winds will be dragged on the surface of the earth. That is, an observer at tropical latitudes observes winds that blow from the northeast in the Northern Hemisphere and from the southeast in the Southern Hemisphere (fig. 2.5). These are the *northeast* and *southeast trades.* Someone studying winds within the temperate belt between 30° and 60° latitude would observe that winds blow mainly from the west. These are the *westerlies* of temperate latitudes. At high latitudes, our observer would find that the predominant wind direction is from the east. These are the *polar easterlies.*

Why don't winds move directly north to south? The prevailing winds do not move in a straight north–south direction because of the **Coriolis effect.** In the Northern Hemisphere, the Coriolis effect causes an apparent deflection of winds to the right of their direction of travel and to the left in the Southern Hemisphere. We say "apparent" deflection because we see this deflection only if we make our observations from the surface of the earth. To an observer in space, it would appear that winds move in approximately a straight line, while the earth rotates beneath them. However, we need to keep in mind that the perspective from the earth's surface is the ecologically relevant perspective. The biomes that we discuss in chapter 2 are as earthbound as our hypothetical observer. Their distributions across the globe are substantially influenced by global climate, particularly geographic variations in temperature and precipitation.

Geographic variation in temperature and precipitation is very complex. How can we study and represent geographic variation in these climatic variables without being overwhelmed by a mass of numbers? This practical problem is addressed by a visual device called a climate diagram.

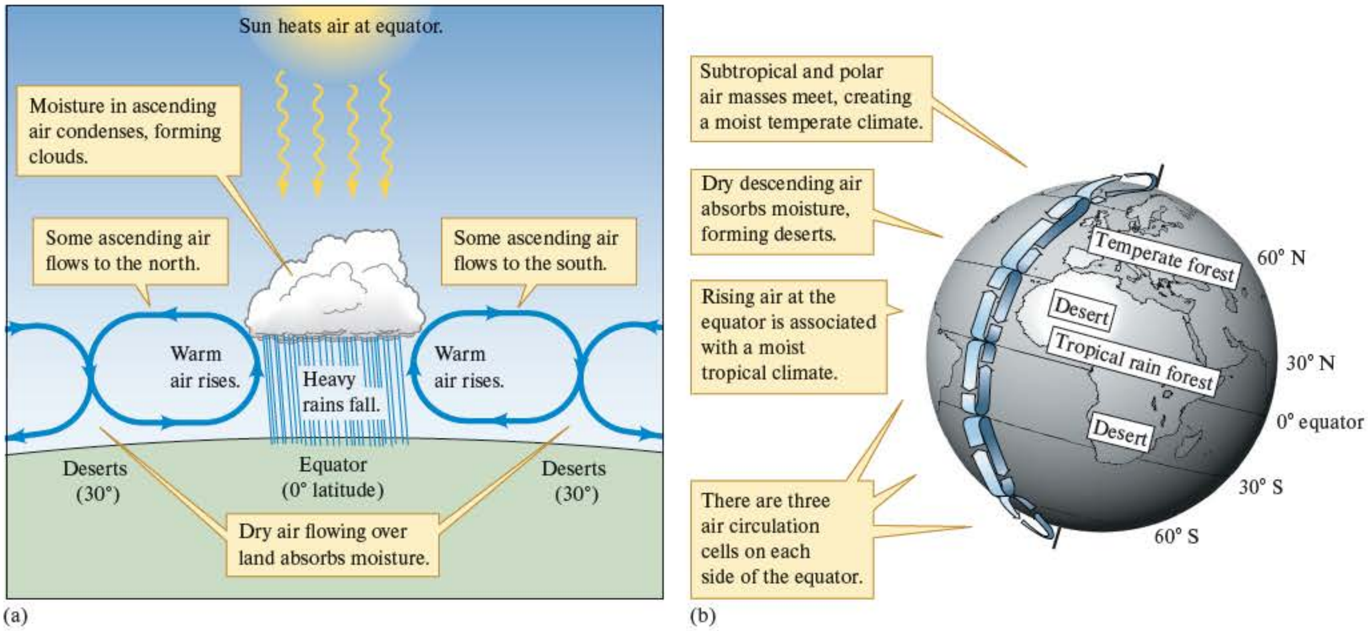


Figure 2.4 (*a*) Solar-driven air circulation. (*b*) Latitude and atmospheric circulation.

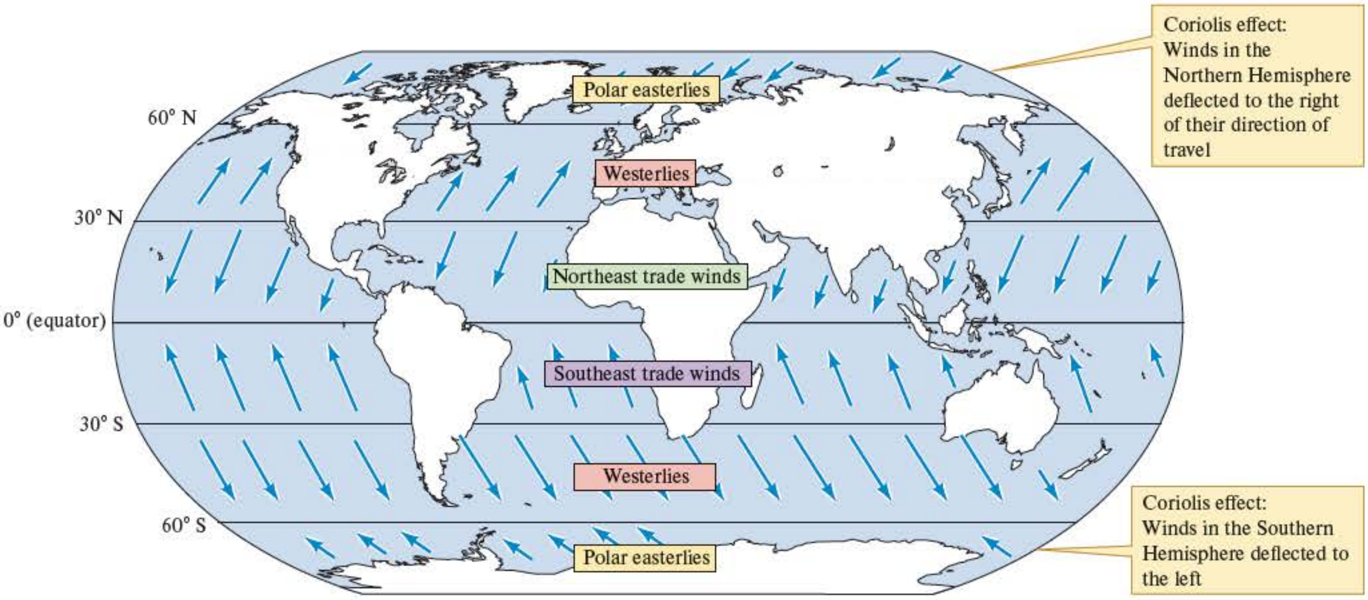


Figure 2.5 The Coriolis effect and wind direction.

Climate Diagrams

Climate diagrams were developed by Heinrich Walter (1985) as a tool to explore the relationship between the distribution of terrestrial vegetation and climate. Climate diagrams summarize a great deal of useful climatic information, including seasonal variation in temperature and precipitation, and the length and intensity of wet and dry seasons.

As shown in figure 2.6, climate diagrams summarize climatic information using a standardized structure. The months of the year are plotted on the horizontal axis, beginning with January and ending with December for locations in the Northern Hemisphere and beginning with July and ending with June in the Southern Hemisphere. Temperature is plotted on the left vertical axis and precipitation on the right vertical axis. Temperature and precipitation are plotted on different scales so that 10°C is equivalent to 20 mm of precipitation. Climate diagrams for wet areas such as tropical rain forest compress the precipitation scale for precipitation above 100 mm so that 10°C is equivalent to 200 mm of precipitation. With this change in scale, rainfall data from very wet climates can be fit on a graph of convenient size.

Because the temperature and precipitation scales are constructed so that 10°C equals 20 mm of precipitation, the relative positions of the temperature and precipitation lines reflect water availability. Theoretically, adequate moisture for plant growth exists when the precipitation line lies above the temperature line. When the temperature line lies above the precipitation line, potential evaporation rate exceeds precipitation.

As you can see, climate diagrams efficiently summarize important environmental variables. In Concept 2.3, we use climate diagrams to represent the climates associated with major terrestrial biomes.

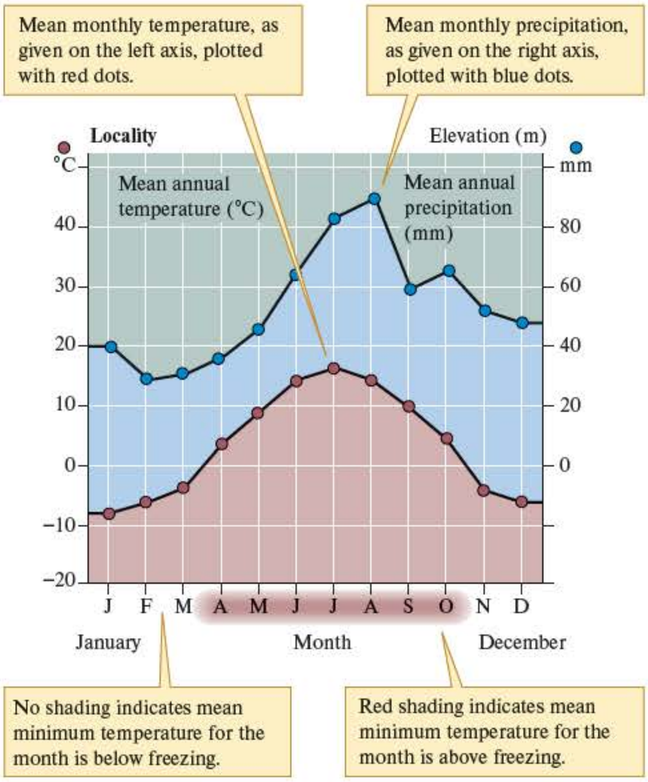


Figure 2.6 Structure of climate diagrams.

Concept 2.1 Review

1. How would seasonality in temperature and precipitation be affected if earth's rotation on its axis were perpendicular to its plane of orbit about the sun?
2. Why does the annual rainy season in regions near 23° N latitude begin in June?

2.2 Other Factors That Shape Terrestrial Biomes

LEARNING OUTCOMES

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

2.7 Explain the concept of rain shadow.
2.8 Describe the characteristics of each of the typical soil horizons.
2.9 Discuss how climate, organisms, topography, parent material, and time can influence the structure and development of soils and which organisms can survive there.

While terrestrial biome distribution is strongly associated with latitude, biomes are also influenced by microclimate and soil type. From the previous section, we know why deserts are not found at the equator: the angle of the sun's rays on the surface of the earth results in this being a wet area of the globe. However, latitude is not the only determinant of where we find biomes; we also do not find desert on mountaintops, regardless of latitude. Also consider the fact that at 35°N we can find temperate forest in North Carolina, grassland in Oklahoma, desert in Arizona, and Mediterranean scrubland in California.

The distribution of mountains partly explains why biomes do not form perfect horizontal stripes on the earth. It is colder at higher elevations, of course, but whether it will be wetter or drier depends on which side of the mountain you are on. To understand this, we can apply what we learned in the previous section about rising air losing its moisture in the form of rain or snow. Warm, moist air from the ocean that blows toward a mountain range will have lost much of its moisture when that air reaches the leeward side (fig. 2.7). The dry climate that results is called the **rain shadow effect.** When the temperature and moisture differ from the prevailing climate, we call these local environments **microclimates,** to be discussed in greater detail in chapter 5.

Microclimates can have dramatic influences on biome distribution; the western United States is one such example (fig. 2.8). Not only do we observe particular plant communities on high-altitude mountaintops, but because of the rain shadow effect, we observe a wide range of biomes on the sides and base of a mountain, even at the same elevation and latitude. Desert, for example, is found on the eastern side of the Sierra Nevada mountains.

Biomes are not only determined by temperature and moisture, however; in addition to and interacting with climate is the effect of soils. As you will see in the biome descriptions later in this chapter, soil type can determine if a region is savanna or desert, even at the same amount of precipitation. It is partly for this reason that there are blurry, rather than crisp, boundaries between biomes in figure 2.1*b*.

Soil is a complex mixture of living and nonliving material upon which most terrestrial life depends. The nonliving component of soil comes from its underlying geology; weathering slowly breaks down parent material, often bedrock, into smaller and smaller fragments to produce sand, silt, and clay-sized particles. The size of particles and the minerals associated with them can have profound impacts on what types of plants, microorganisms, and even animals can live in the associated soils. Here we summarize the general features of soil structure and development. The biome discussions that follow include specific information about the soils associated with each. Nonetheless, it should be kept in mind that variation within a biome is often due to different types of soils occurring there.

Though soil structure usually changes gradually with depth, soil scientists generally divide soils into several discrete horizons. In the classification system used here, the soil profile is divided into O, A, B, and C horizons (fig. 2.9). The **O, or organic, horizon** lies at the top of the profile. The most superficial layer of the O horizon is made up of freshly fallen organic matter, including whole leaves, twigs, and other plant parts, which become more fragmented and decomposed

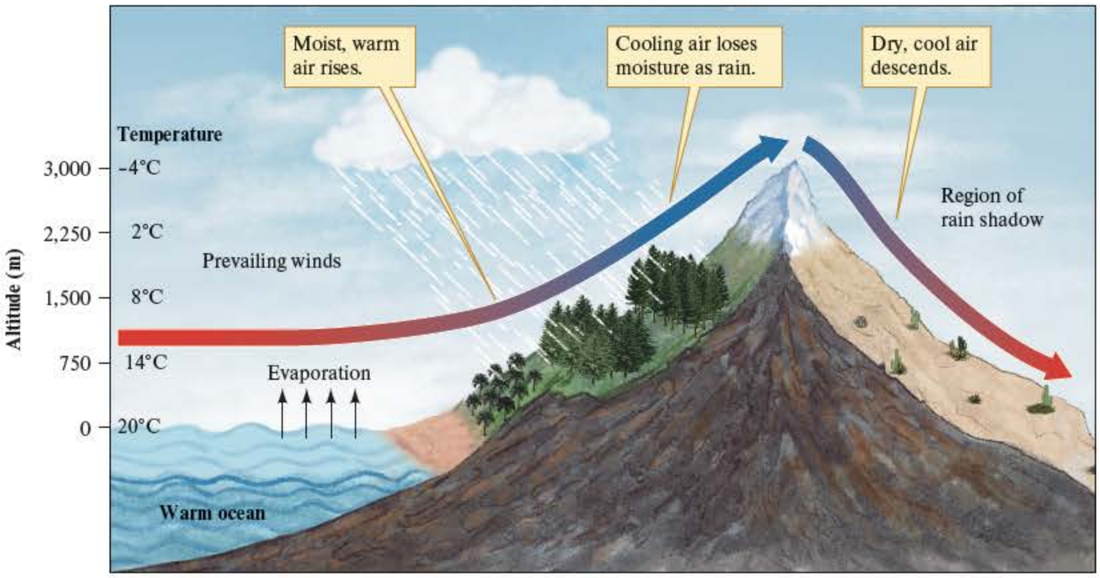
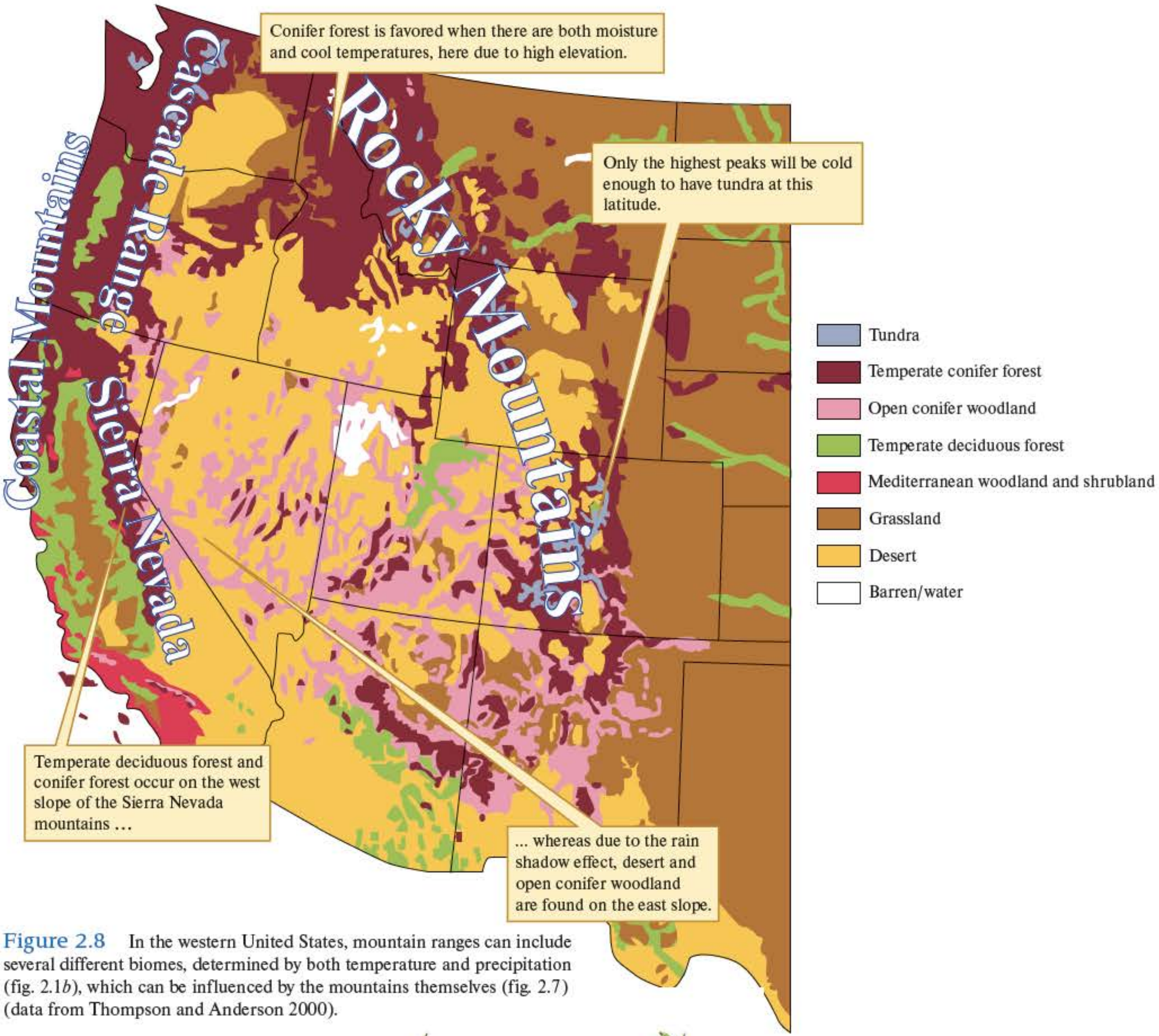


Figure 2.7 The rain shadow effect accounts for dramatic differences in climate and therefore biome on opposite sites of many mountain ranges.



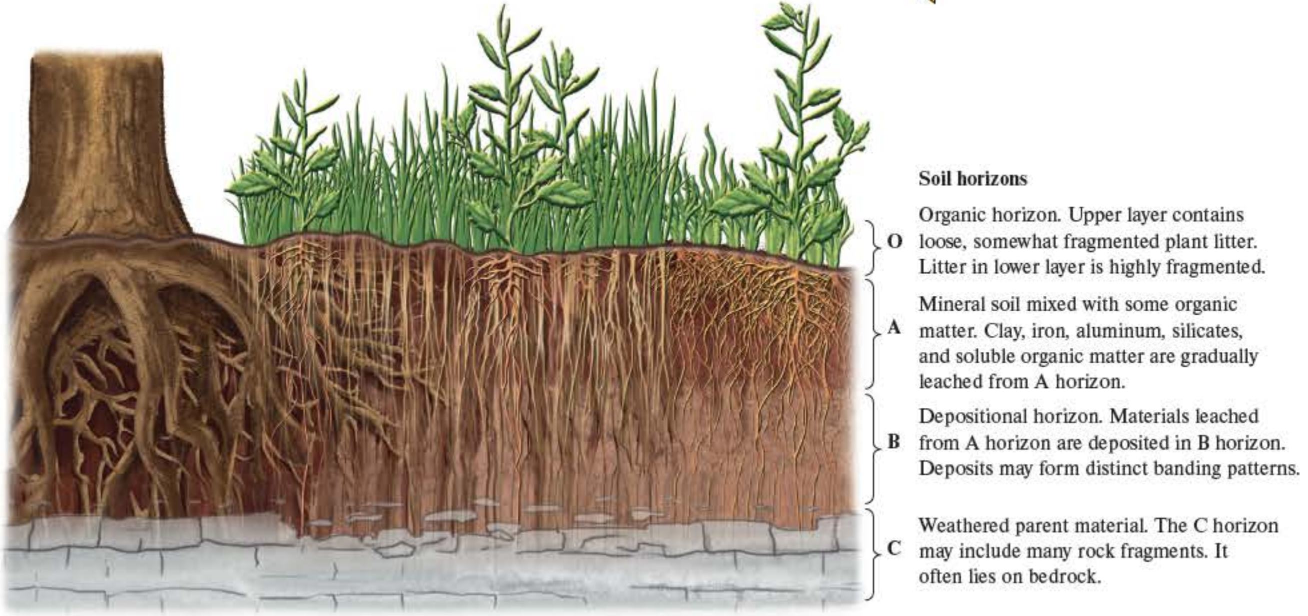
Conifer forest is favored when there are both moisture and cool temperatures, here due to high elevation.

Only the highest peaks will be cold enough to have tundra at this latitude.

Temperate deciduous forest and conifer forest occur on the west slope of the Sierra Nevada mountains …

… whereas due to the rain shadow effect, desert and open conifer woodland are found on the east slope.

Figure 2.8 In the western United States, mountain ranges can include several different biomes, determined by both temperature and precipitation (fig. 2.1*b*), which can be influenced by the mountains themselves (fig. 2.7) (data from Thompson and Anderson 2000).



Soil horizons

O Organic horizon. Upper layer contains loose, somewhat fragmented plant litter. Litter in lower layer is highly fragmented.

A Mineral soil mixed with some organic matter. Clay, iron, aluminum, silicates, and soluble organic matter are gradually leached from A horizon.

B Depositional horizon. Materials leached from A horizon are deposited in B horizon. Deposits may form distinct banding patterns.

C Weathered parent material. The C horizon may include many rock fragments. It often lies on bedrock.

Figure 2.9 Generalized soil profile, showing O, A, B, and C horizons.

with increasing depth. Fragmentation and decomposition of the organic matter in this horizon are mainly due to the activities of soil organisms, including bacteria, fungi, and animals ranging from nematodes and mites to burrowing mammals. This horizon is usually absent in agricultural soils and deserts. At its deepest levels, the O horizon merges gradually with the A horizon.

The **A horizon** contains a mixture of mineral materials, such as clay, silt, and sand, and incorporated organic material derived from the O horizon. Burrowing animals, such as earthworms, mix organic matter from the O horizon into the A horizon. The A horizon is generally rich in mineral nutrients. It is gradually leached of clays, iron, aluminum, silicates, and humus, which is partially decomposed organic matter. These substances slowly move down through the soil profile until they are deposited in the B horizon.

The **B horizon** contains the clays, humus, and other materials that have been transported by water from the A horizon. The deposition of these materials often gives the B horizon a distinctive color and banding pattern. The B horizon gradually merges with the C horizon.

The **C horizon** is the deepest layer in our soil pit and the only one not typically dominated by plant roots. It consists of the weathered parent material, which has been worked by the actions of frost, water, and the deeper penetrating roots of plants. Because weathering is incomplete and less intense than in the A and B horizons, the C horizon may contain many rock fragments. Under the C horizon, we find unweathered parent material, which is often bedrock.

The soil profile gives us a snapshot of soil structure. However, soil structure is in a constant state of flux as a consequence of several influences. Those influences were summarized by Hans Jenny (1980) as climate, organisms, topography, parent material, and time. Climate affects the rate of weathering of parent materials, the rate of leaching of organic and inorganic substances, the rate of erosion and transport of mineral particles, and the rate of decomposition of organic matter. Living organisms, which as we know are also affected by climate, influence the quantity and quality of organic matter added to soil and the rate of soil mixing by burrowing animals. Topography affects the rates and direction of water flow and patterns of erosion. Meanwhile, parent materials, such as granite, volcanic rock, and wind- or water-transported sand, set the stage for all other influences. Last is the matter of time. Soil age influences soil structure.

As with many aspects of ecology, it is often difficult to separate organisms from their environment. The biome discussions that follow provide additional information on soils by including aspects of soil structure and chemistry characteristic of each biome.

Concept 2.2 Review

1. The organic horizon is generally absent from agricultural soils because tilling (e.g., plowing), buries organic matter. Why is an organic horizon generally absent from desert soils?

2.3 Natural History and Geography of Biomes

LEARNING OUTCOMES

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

2.10 List the major terrestrial biomes.
2.11 Describe the climatic differences among the biomes.
2.12 Contrast the soils typical of the terrestrial biomes.
2.13 Describe the types of vegetation, animals, and other organisms characteristic of the terrestrial biomes.
2.14 Explain variation in human presence in the various terrestrial biomes.

Environmental conditions shape each biome's characteristic biology. Early in the twentieth century, many plant ecologists studied how climate and soils influence the distribution of vegetation. Later ecologists concentrated on other aspects of plant ecology. Today, as we face the prospect of global warming (see chapter 23), ecologists are once again studying climatic influences on the distribution of vegetation. International teams of ecologists, geographers, and climatologists are exploring the influences of climate on vegetation with renewed interest and with much more powerful analytical tools. Ecologist Osvaldo Sala and others created a predictive model (for more on models, see Investigating the Evidence 1 in Appendix A) using biological and environmental data from each biome to determine where biodiversity is at the most risk. While deserts and tundra were not expected to change much over the next century, Mediterranean and grassland biomes were found to be highly sensitive to anticipated human-caused changes to the environment, including but not limited to climate change (Sala et al. 2000).

In this section, we discuss the climate, soils, and organisms of the earth's major biomes and how they have been influenced by humans.

Tropical Rain Forest

Tropical rain forest is nature's most extravagant garden (fig. 2.10). Beyond its tangled edge, a rain forest opens into a surprisingly

Figure 2.10 Tropical rain forest in Ecuador. More species live within the three-dimensional framework of tropical rain forests than in any other terrestrial biome. Elena Kalistratova/Vetta/Getty Images

spacious interior, illuminated by dim, greenish light shining through a ceiling of leaves. The architecture of rain forests, with their vaulted ceilings and spires, has invited comparisons to cathedrals and mansions. However, this cathedral is alive from ceiling to floor, perhaps more alive than any other biome on the planet. In the rain forest, the sounds of evening and morning, the brilliant flashes of color, and rich scents carried on moist night air speak of abundant life, in seemingly endless variety.

Geography

Tropical rain forests straddle the equator in three major regions: Southeast Asia, West Africa, and South America (fig. 2.11). Most rain forest occurs within 10° of latitude north or south of the equator. Outside this equatorial band are the rain forests of Central America and Mexico, southeastern Brazil, eastern Madagascar, southern India, and northeastern Australia.

Climate

The global distribution of rain forests corresponds to areas where conditions are warm and wet year-round (see fig. 2.11). Temperatures in tropical rain forests vary little from month to month and often change as much in a day as they do over the entire year. Average temperatures are about 25°C to 27°C, lower than average maximum summer temperatures in many deserts and temperate regions. Annual rainfall ranges from about 2,000 to 4,000 mm, and some rain forests receive even more precipitation. In a rain forest, a month with less than 100 mm of rain is considered dry.

Soils

Heavy rains gradually leach nutrients from rain forest soils and rapid decomposition in the warm, moist rain forest climate keeps the quantity of soil organic matter low. Consequently, rain forest soils are often nutrient-poor, acidic, thin, and low in organic matter. In many rain forests, more nutrients are tied up in living tissue than in soil. Some rain forests, however, occur where soils are very fertile such as along rivers. Fungi, bacteria, and soil animals, such as mites and springtails, rapidly scavenge nutrients from plant litter (leaves, flowers, etc.) and animal wastes, further tightening the nutrient economy in tropical ecosystems.

Biology

Trees dominate the rain forest landscape and average about 40 m in height but some reach 80 m. These rain forest giants are often supported by well-developed buttresses. The diversity of rain forest trees is also impressive. One hectare (100 m × 100 m) of temperate forest may contain a few dozen tree species; 1 ha of tropical rain forest may contain up to 300 tree species.

Primary production in tropical rain forests is the highest of all terrestrial ecosystems, not only from the trees but also because the three-dimensional framework formed by rain forest trees is festooned with other plant growth forms. The trees are trellises for climbing vines and growing sites for epiphytes, plants that grow on other plants (fig. 2.12). This vast amount of converted energy supports a great biological richness of consumers as well. A single rain forest tree may support several thousand species of insects, many of which have not been described by scientists.

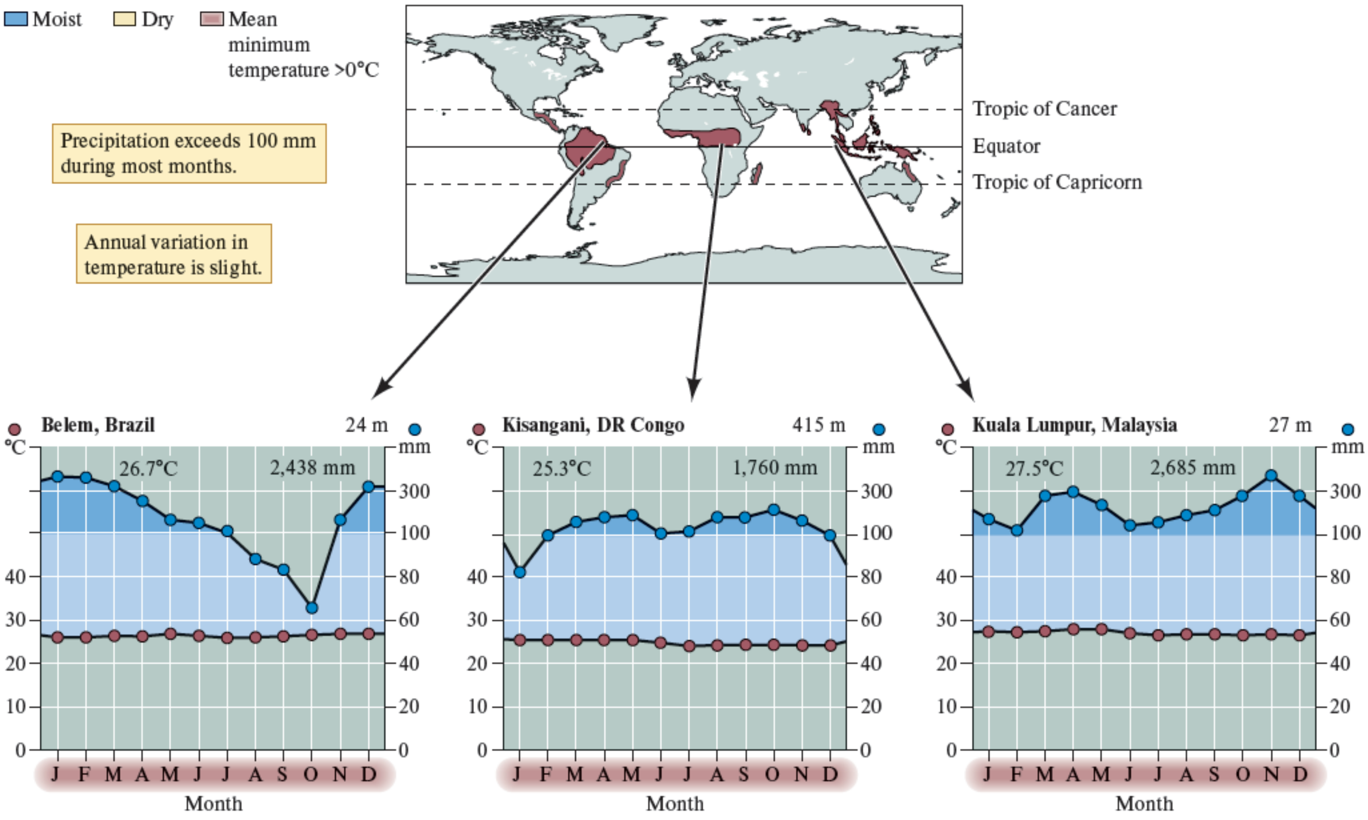


Figure 2.11 Tropical rain forest geography and climate.

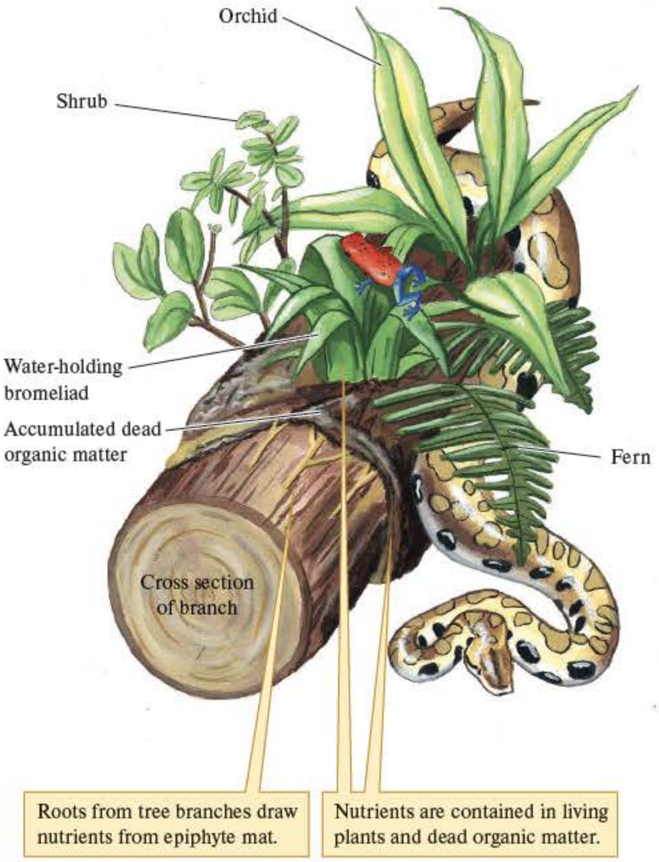


Figure 2.12 An epiphyte mat in the tropical rain forest canopy. Epiphyte mats store a substantial fraction of the nutrients in tropical rain forests and support a high diversity of plant and animal species.

The rain forest is not, however, just a warehouse for a large number of dissociated species. Rain forest ecology is marked by intricate, complex relationships between species. In the tropical rain forest, there are plants that cannot live without particular species of fungi, which help them absorb nutrients (called **mycorrhizae**), the hummingbirds or insects that pollinate their flowers, and the animals that disperse their seeds.

Human Influences

People from all over the globe owe more to the tropics than is generally realized. Many of the world's staple foods, including maize (called corn in North America and Australia), rice, bananas, and sugarcane, and approximately 25% of all prescription drugs were originally derived from tropical plants. Many more species, directly useful to humans, may await discovery. Unfortunately, tropical rain forests are fast disappearing. According to data collected by scientists at the University of Maryland, in 2019 an astonishing 11.9 million hectares of tropical forest cover was lost; this is equal to a football field-sized area every 8.25 minutes (www.globalforestwatch.org). This loss diminishes our chances of understanding the extent and dynamics of biological diversity.

Tropical Dry Forest

During the dry season, the **tropical dry forest** is all earth tones; in the rainy season, it's an emerald tangle (fig. 2.13). Life in the tropical dry forest responds to the rhythms of the annual solar cycle, which drives the oscillation between wet and dry seasons. During the dry season, most trees in the tropical dry forest are dormant. Then, as the rains approach, trees flower and insects appear to pollinate them. Eventually, as the first storms of the wet season arrive, the trees produce their leaves and transform the landscape.

Geography

Tropical dry forests make up approximately 42% of tropical and sub-tropical forest area (Hasnat and Hossain 2020) (fig. 2.14). In Africa, tropical dry forests are found both north and south of the central African rain forests. In the Americas, tropical dry forests are the natural vegetation of extensive areas south and north of the Amazon rain forest. Tropical dry forests also extend up the west coast of Central America and into North America along the west coast of Mexico. In Asia, tropical dry forests are the natural vegetation of most of India and the Indochina peninsula. Australian tropical dry forests form a continuous band across the northern and northeastern portions of the continent.

Figure 2.13 Tropical dry forest during the wet and dry seasons. Created by Tomas Zrna/Getty Images; Ralph Lee Hopkins/Science Source

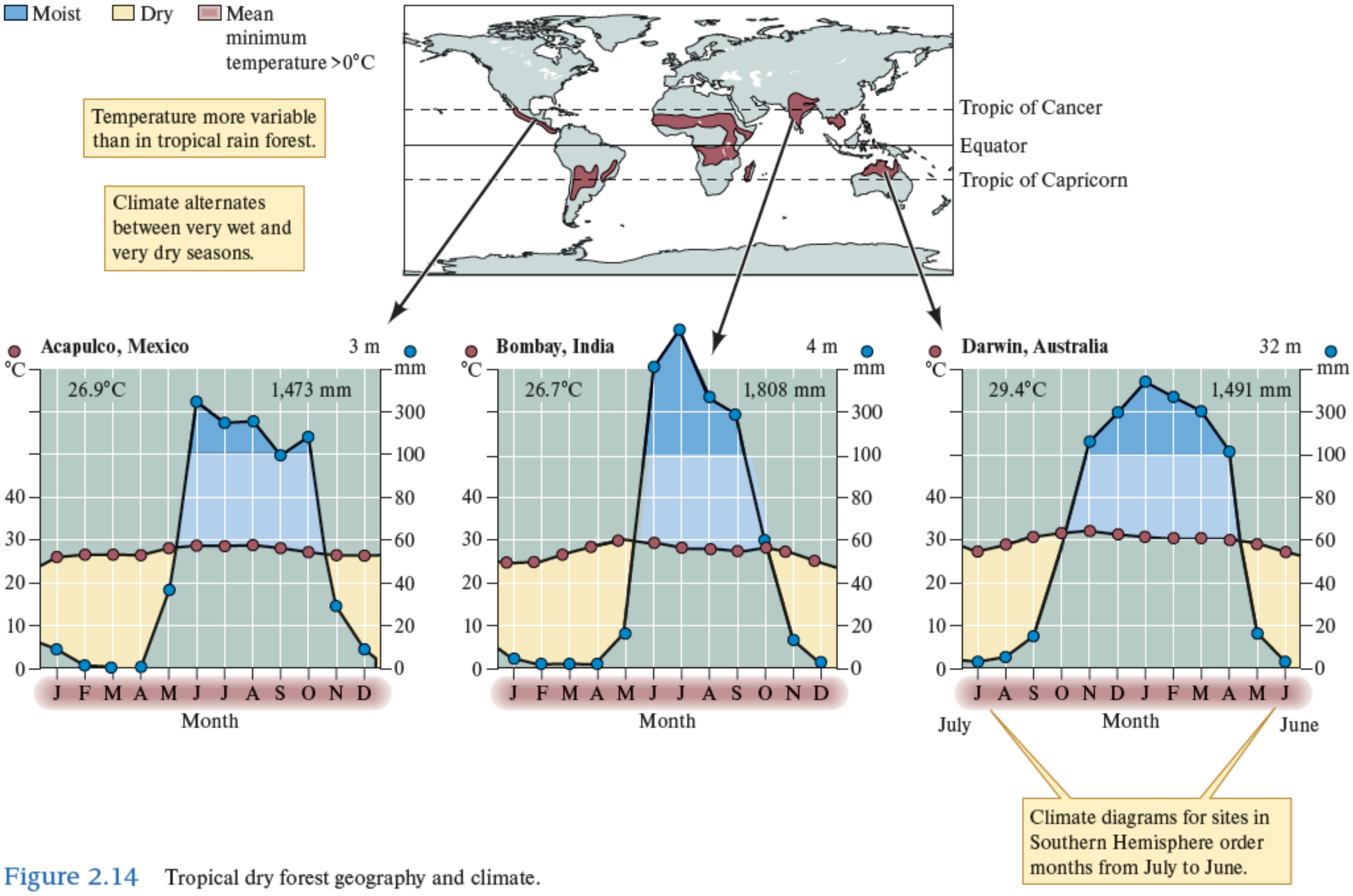


Figure 2.14 Tropical dry forest geography and climate.

Climate

The climate of tropical dry forests is more seasonal than that of tropical rain forests. The three climate diagrams shown in figure 2.14, for example, show a dry season lasting for 6–7 months, followed by a season of abundant rainfall, lasting 5–6 months. The climate diagrams also indicate more seasonal variation in temperature compared to tropical rain forest.

Soils

The soils of many tropical dry forests are of great age, particularly those in the parts of Africa, Australia, India, and Brazil that were once part of the ancient southern continent of Gondwana. The soils of tropical dry forests tend to be less acidic than those of rain forests and are generally richer in nutrients. However, the annual pulses of torrential rain make the soils of tropical dry forest highly vulnerable to erosion.

Biology

The plants of the tropical dry forest are strongly influenced by physical factors. For example, the height of the dry forest is highly correlated with average precipitation. Trees are tallest in the wettest areas. In the driest habitats, all trees drop their leaves during the dry season; in wetter areas over 50% may be evergreen. As in the tropical rain forest, many plants produce animal-dispersed seeds. However, wind-dispersed seeds are also common. Many dry forest birds, mammals, and even insects make seasonal migrations to wetter habitats along rivers or to the nearest rain forest.

Human Influences

Heavy human settlement has devastated the tropical dry forest. While the world's attention has been focused on the plight of rain forests, tropical dry forests have been quietly disappearing, including in so-called protected areas. The relatively fertile soil of tropical dry forests has attracted agricultural development, including cattle ranches, grain farms, and cotton fields. Tropical dry forests are more easily converted to agriculture compared to rain forests, since the dry season makes them more accessible and easier to burn. Using remote sensing data that spanned 40 years, Binita Kumari and colleagues found that areas of a reserve in eastern India that had more human settlements also had higher rates of deforestation (Kumari et al. 2020; fig. 2.15). In other areas, protections seem to be working; in Ghana, researchers found that rates of deforestation had decreased in recent years and new trees are colonizing in some areas (Janssen et al. 2018).

The loss of the dry forest is significant because, while rain forests may support a somewhat greater number of species, many dry forest species are found nowhere else, as many as 40% of the tree and shrub species found there are endemic (Hasnat and Hossain 2020).

Tropical Savanna

Stand in the middle of a savanna, a tropical grassland dotted with scattered trees, and your eye will be drawn to the horizon for the approach of thunderstorms or wandering herds of wildlife (fig. 2.16). The **tropical savanna** is the kingdom of

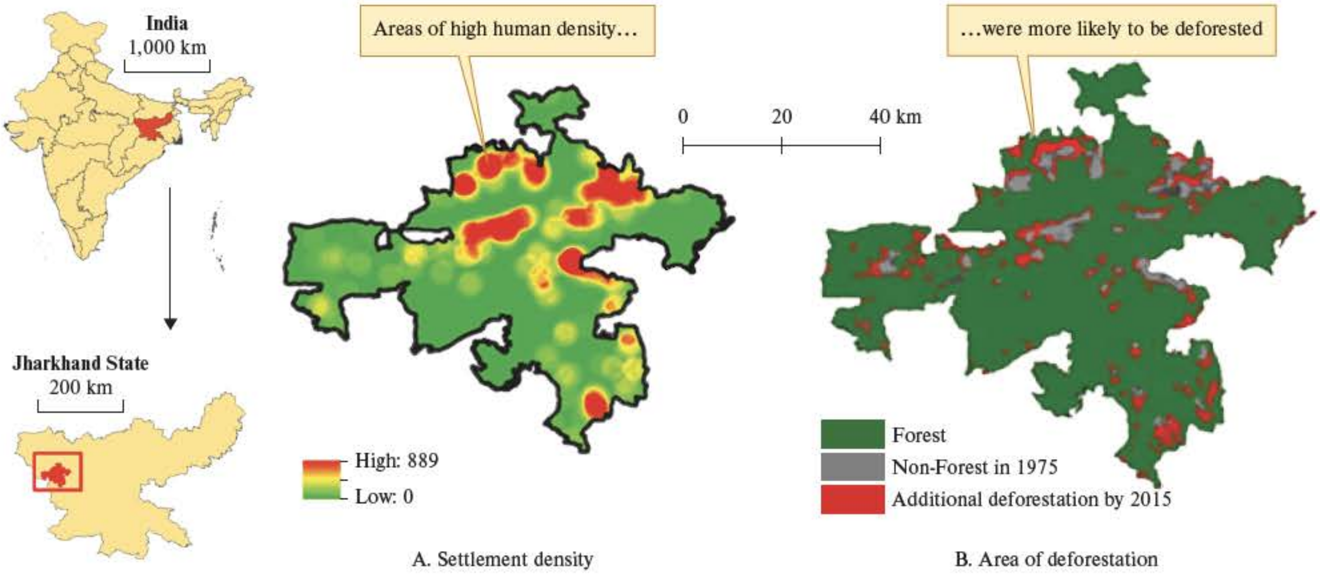


Figure 2.15 A comparison of human settlement density (A) and deforestation (B) at the Palamau Tiger Reserve, the latter using satellite imagery. Authors found that loss of forest cover over time was greatest in the central and northern regions, where population densities were highest (based on data from Kumari et al. 2020).

Figure 2.16 Tropical savanna and herbivores in East Africa. This ecosystem is characterized by a dominance of grasses with a few woody species. Anna Sher

the farsighted, the stealthy, and the swift and is the birthplace of humankind. It was from here that we eventually moved out into every biome. Though most humans live away from this first home, the fascination continues.

Geography

Most tropical savannas occur north and south of tropical dry forests within 10–20° of the equator. In Africa south of the Sahara Desert, tropical savannas extend from the west to the east coasts, cut a north–south swath across the East African highlands, and reappear in south-central Africa (fig. 2.17). In South America, tropical savannas occur in south-central Brazil and cover a great deal of Venezuela and Colombia. Tropical savannas are also the natural vegetation of much of northern Australia in the region just south of the tropical dry forest. Savanna is also the natural vegetation of an area in southern Asia just east of the Indus River in eastern Pakistan and northwestern India.

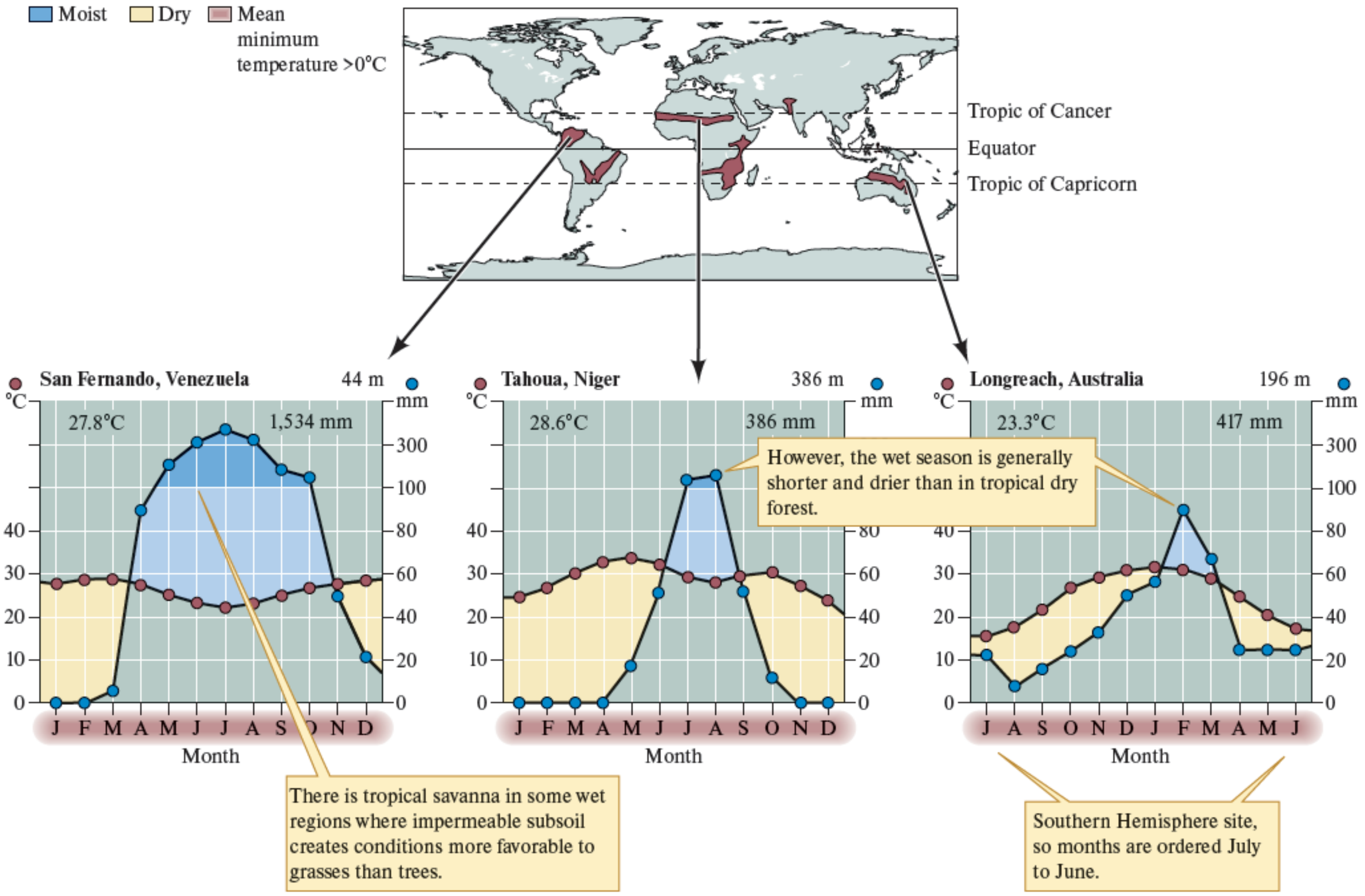
Climate

As in the tropical dry forest, life on the savanna cycles to the rhythms of alternating dry and wet seasons (see fig. 2.17). Here, however, seasonal drought combines with another important physical factor, fire. The rains come in summer and are accompanied by intense lightning. This lightning often starts fires, particularly at the beginning of the wet season when the savanna is tinder dry. These fires kill young trees while the grasses survive and quickly resprout. Consequently, fires help maintain the tropical savanna as a landscape of grassland and scattered trees.

The savanna climate is generally drier than that of tropical dry forest. However, San Fernando, Venezuela (see fig. 2.17), receives as much rainfall as a tropical dry forest. Other savannas occur in areas that are as dry as deserts. What keeps the wet savannas near San Fernando from being replaced by forest and how can savannas persist under desertlike conditions? The answer lies deep in the savanna soils.

Soils

Soil layers with low permeability to water play a key role in maintaining many tropical savannas. For instance, because a dense, impermeable subsoil retains water near the surface, savannas occur in areas of southwestern Africa that would otherwise support only desert. Impermeable soils also help savannas persist in wet areas, particularly in South America. Trees do not move onto savannas where an impermeable subsoil keeps surface soils waterlogged during the wet season. In these landscapes, scattered trees occur only where soils are well drained.



However, the wet season is generally shorter and drier than in tropical dry forest.

There is tropical savanna in some wet regions where impermeable subsoil creates conditions more favorable to grasses than trees.

Southern Hemisphere site, so months are ordered July to June.

Figure 2.17 Tropical savanna geography and climate.

Biology

Even though savannas don't support many trees, their total primary production across the globe is second only to tropical rain forest; a greater proportion of the biological activity on the savanna simply takes place near ground level, primarily in grasses. Frequent fires have selected for fire resistance in the savanna flora. The few tree species on the savanna resist fire well enough to be unaffected by low-intensity fires.

The tropical savanna is populated by wandering animals that move in response to seasonal and year-to-year variations in rainfall and food availability. The wandering consumers of the Australian savannas include kangaroos, large flocks of birds, and, for about 50,000 years, humans. During droughts, some of these Australian species travel thousands of kilometers in search of suitable conditions. The African savanna is also home to a host of well-known mobile consumers, such as elephants, wildebeest, giraffes, zebras, lions, and, again, humans (see fig. 2.16).

Human Influences

Humans are, in some measure, a product of the savanna and the savanna, in turn, has been influenced by human activity. One of the factors that forged an indelible link between us and this biome is fire. Long before the appearance of hominids, fire played a role in the ecology of the tropical savanna. Later, the savanna was the classroom where early humans observed and learned to use, control, and make fire. Eventually, humans began to purposely set fire to the savanna, which, in turn, helped to maintain and spread the savanna itself. We had begun to manipulate nature on a large scale.

Originally, humans subsisted on the savanna by hunting and gathering. In time, they shifted from hunting to pastoralism, replacing wild game with domestic grazers and browsers. Today, livestock ranching is the main source of livelihood in all the savanna regions. In Africa, livestock raising has coexisted with wildlife for millennia. In modern-day sub-Saharan Africa, however, the combination of growing human populations, high density of livestock, and drought has devastated much of the region known as the Sahel (fig. 2.18).

Figure 2.18 Domestic livestock, such as these cattle on an African savanna, have had a major impact on tropical savannas around the world. Syda Productions/Shutterstock

Desert

In the spare **desert** landscape, sculpted by wind and water, the ecologist grows to appreciate geology, hydrology, and climate as much as organisms (fig. 2.19). The often repeated description of life in the desert as "life on the edge" betrays an outsider's view. Although primary production is lower than that of other biomes, it does not follow that living conditions there are necessarily harsh. In their own way, many desert organisms flourish on meager rations of water, high temperatures, and saline soils. To understand life in the desert, the ecologist must see it from the perspective of its natural inhabitants.

Geography

Deserts occupy about 20% of the land surface of the earth. Two bands of deserts ring the globe, one at about 30° N latitude and one at about 30° S (fig. 2.20). These bands correspond to latitudes where dry subtropical air descends (see fig. 2.4), drying the landscape as it spreads north and south. Other deserts are found either deep in the interior of continents, for example, or in the rain shadow of mountains, such as the Great Basin Desert of North America as shown in figure 2.8. Still others are found along the cool western coasts of continents, for example, the Atacama of South America and the Namib of southwestern Africa, where air circulating across a cool ocean delivers a great deal of fog to the coast but little rain.

Climate

Environmental conditions vary considerably from one desert to another. Some, such as the Atacama and central Sahara, receive very little rainfall and fit the stereotype of deserts as extremely dry places. Other deserts, such as some parts of the Sonoran Desert of North America, may receive nearly 300 mm of rainfall annually. Whatever their mean annual rainfall, however, water loss in deserts due to evaporation and transpiration by plants exceeds precipitation during most of the year.

Figure 2.20 includes the climate diagrams of two hot deserts. Notice that drought conditions prevail during all months and that during some months average temperatures exceed 30°C. Shade temperatures greater than 56°C have been recorded in the deserts of North Africa and western North America. However, some deserts can be bitterly cold. For example, average winter temperatures at Dzamiin Uuded, Mongolia, in the Gobi Desert of central Asia sometimes fall to −20°C (see fig. 2.20).

Soils

Desert plants and animals can turn this landscape into a mosaic of diverse soils. Desert soils are generally so low in organic matter that they are sometimes classified as **lithosols,** which means stone or mineral soil. However, the soils under desert shrubs often contain large amounts of organic matter and form islands of fertility. Desert animals can also affect soil properties. For example, in North America, kangaroo rats change the texture and elevate the nutrient content of surface soils by burrowing and hoarding seeds. In Middle Eastern deserts, blind mole rats and isopods have been shown to strongly influence soil properties.

Figure 2.19 Life on the edge. Sparse desert vegetation stabilizes a patch of soil at the edge of a field of giant dunes in the Namib Desert in southwestern Africa. Getty Images

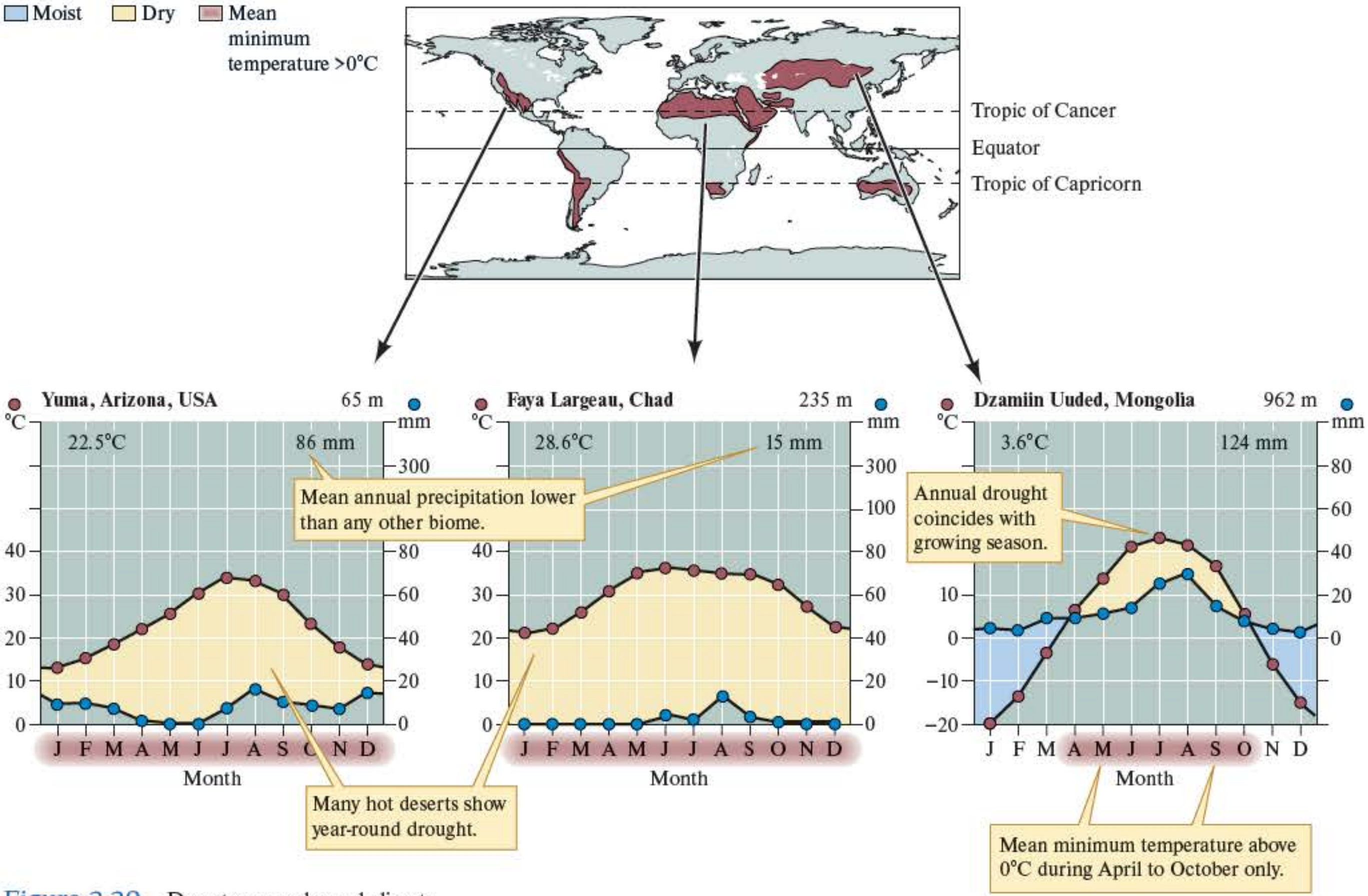


Figure 2.20 Desert geography and climate.

Desert soils, particularly those in poorly drained valleys and lowlands, may contain high concentrations of salts. Salts accumulate in these soils as water evaporates from the soil surface, leaving behind any salts that were dissolved in the water. Salt accumulation increases the aridity of the desert environment by making it harder for plants to extract water from the soils. As desert soils age they tend to form a calcium carbonate–rich hardpan horizon called **caliche.** The extent of caliche formation has proved a useful tool for aging these soils.

Biology

The desert landscape presents an unfamiliar face to the visitor from moist climates. Plant cover is absent from many places, exposing soils and other geologic features. Where there is plant cover, it is sparse. The plants themselves look unfamiliar. Desert vegetation often cloaks the landscape in a gray-green mantle. This is because many desert plants protect their photosynthetic surfaces from intense sunlight and reduce evaporative water losses with a dense covering of plant hairs. Other plant adaptations to drought include small leaves, producing leaves only in response to rainfall and then dropping them during intervening dry periods, or having no leaves at all (fig. 2.21). Some desert plants avoid drought almost entirely by remaining dormant in the soil as seeds that germinate and grow only during infrequent wet periods.

In deserts, animal abundance tends to be low but diversity can be high. Most desert animals use behavior to avoid environmental extremes. In summer, many avoid the heat of the day by being active at dusk and dawn or at night. In winter, the same species may be active during the day. Animals (as well as plants) use body orientation to minimize heat gain in the summer.

Human Influences

Desert peoples have flourished where nature is stingiest. Compared to true desert species, however, humans are profligate water users. Consequently, human populations in deserts concentrate at oases and in river valleys. Many desert landscapes that once supported irrigated agriculture now grow little as a result of salt accumulation in their soils (Wang et al. 2019).

The desert is the one biome that, because of human activity, is increasing in area. Humanity's challenge is to stop the spread of deserts that comes at the expense of other biomes and to establish a balanced use of deserts that safeguards their inhabitants, human and nonhuman alike.

(a)

(b)

Figure 2.21 Similar environments have selected for nearly identical traits in unrelated desert plants: (*a*) cactus in North America, (*b*) *Euphorbia* in Africa. (*a*) Lucky-photographer/Shutterstock; (*b*) Natphotos/Digital Vision/Getty Images

Woodland and Shrubland

Woodlands and shrublands occur widely in temperate regions. Some are found in the interior of continents and others in coastal regions (see fig. 2.1a). Within the woodland/shrubland biome is a particular climate called Mediterranean, although it can be found in many different regions of the globe. The **Mediterranean woodland and shrubland** climate was the climate of the classical Greeks and the coastal Native American tribes of Old California. The mild temperate climate experienced by these cultures was accompanied by high biological richness (fig. 2.22). The richness of the Mediterranean woodland flora is captured by a folk song from the Mediterranean region that begins: "Spring has already arrived. All the countryside will bloom; a feast of color!" To this visual feast, Mediterranean woodlands and shrublands add a chorus of birdsong and the smells of aromatic plants, including rosemary, thyme, and laurel.

Figure 2.22 A Mediterranean woodland in southern Italy. Manuel C. Molles

Geography

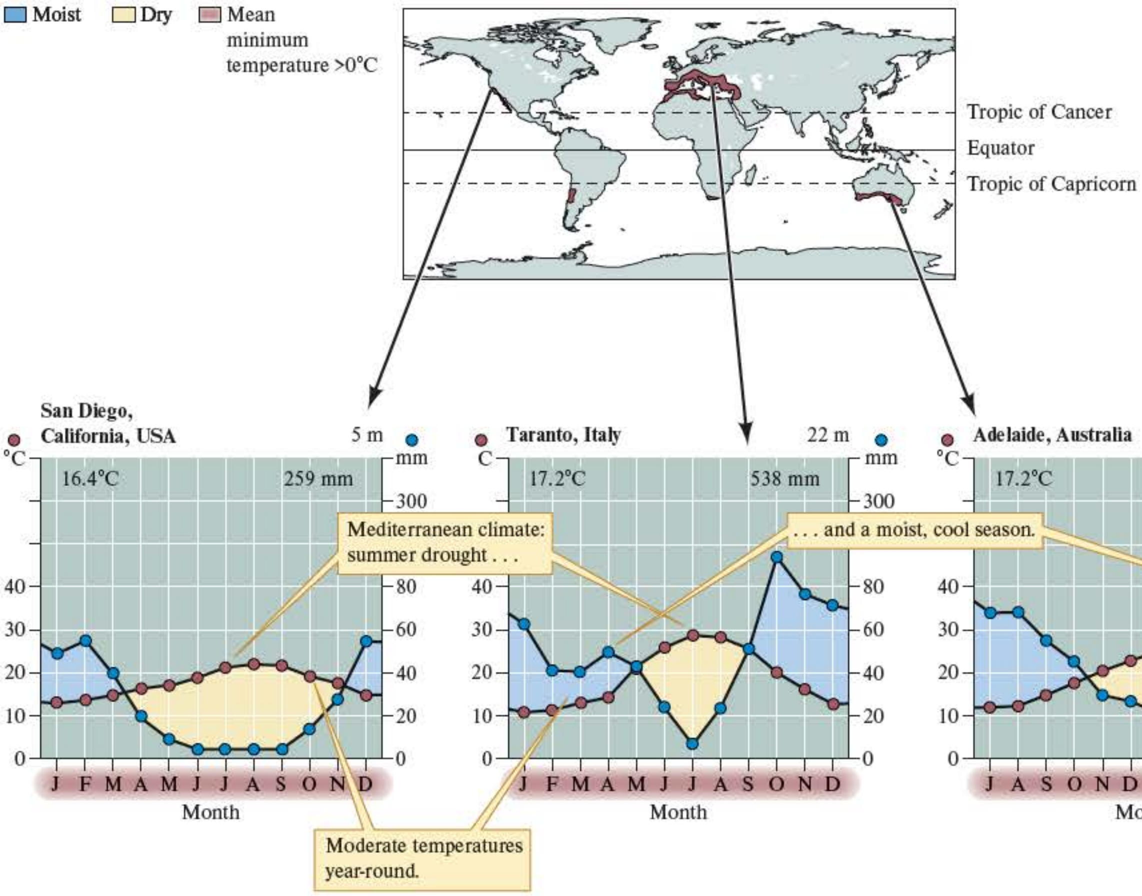
Mediterranean woodlands and shrublands occur on all the continents except Antarctica (fig. 2.23). They are most extensive around the Mediterranean Sea and in North America, where they extend from California into northern Mexico. They are also found in central Chile, southern Australia, and southern Africa. Under present climatic conditions, Mediterranean woodlands and shrublands grow between about 30° and 40° latitude. This position places the majority of this biome north of the subtropical deserts in the Northern Hemisphere, and south of them in the Southern Hemisphere. The far-flung geographic distribution of Mediterranean woodland and shrubland is reflected in the diversity of its names. In western North America, it is called *chaparral.* In Spain, the most common name for Mediterranean woodland and shrubland is *matorral.* Farther east in the Mediterranean basin the biome is referred to as *garrigue.* Meanwhile, South Africans call it *fynbos,* while Australians refer to at least one form of it as *mallee.* Although the names for this biome vary widely, its climate does not.

Climate

The Mediterranean woodland and shrubland climate is cool and moist during fall, winter, and spring, whereas summers are hot and dry (see fig. 2.23). The danger of frost varies considerably from one Mediterranean woodland and shrubland region to another. When they do occur, however, frosts are usually not severe. The combination of dry summers and dense vegetation, rich in essential oils, creates ideal conditions for frequent and intense fires.

Soils

The soils of Mediterranean woodlands and shrublands have generally low to moderate fertility and are considered fragile. Some soils, such as those of the South African fynbos, have exceptionally low fertility. Soil erosion can be severe. Fire coupled with overgrazing has stripped the soil from some



Mediterranean climate: summer drought . . .

. . . and a moist, cool season.

Moderate temperatures year-round.

Figure 2.23 Mediterranean woodland and shrubland geography and climate.

Mediterranean landscapes. Elsewhere, these landscapes, under careful stewardship, have maintained their integrity for thousands of years.

Biology

The plants and animals of Mediterranean woodlands and shrublands are highly diverse and, like their desert neighbors, show several adaptations to drought. Trees and shrubs are typically evergreen and have small, tough leaves, which conserve both water and nutrients (fig. 2.24). Many plants of Mediterranean woodlands and shrublands have well-developed, mutualistic relationships with microbes that fix atmospheric nitrogen.

The process of decomposition is greatly slowed during the dry summer and then started again with the coming of fall and winter rains. Curiously, this intermittent decomposition may speed the process sufficiently so that average rates of decomposition are comparable to those in temperate forests.

Fire, a common occurrence in Mediterranean woodlands and shrublands, has selected for fire-resistant plants. Many Mediterranean woodland trees have thick, fire-resistant bark. In contrast, many shrubs in Mediterranean woodlands are rich in oils and burn readily but resprout rapidly. Most herbaceous plants grow during the cool, moist season and then die back in summer, thus avoiding both drought and fire.

Human Influences

Human activity has had a substantial influence on the structure of landscapes in Mediterranean woodlands and shrublands. For example, the open oak woodlands of southern Spain and Portugal are the product of an agricultural management system that is thousands of years old. In this system, cattle graze on grasses, pigs consume acorns produced by the oaks, and cork is harvested from cork oaks as a cash crop. Selected areas are planted in wheat once every 5 to 6 years and allowed to lie fallow the remainder of the time. This system of agriculture, which emphasizes low-intensity cultivation and long-term sustainability, may offer clues for sustainable agriculture in other regions.

Figure 2.24 These shrubs found in South Africa's fynbos have the characteristic leaves that help prevent water loss from this Mediterranean-type climate. Anna Sher

High population densities coupled with a long history of human occupation have left an indelible mark on Mediterranean woodlands and shrublands. Early human impacts included clearing forests for agriculture, setting fires to control woody species and encourage grass, harvesting brush for fuel, and grazing and browsing by domestic livestock. Today, Mediterranean woodlands and shrublands around the world are being covered by human habitations.

Temperate Grassland

In their original state, **temperate grasslands** extended unbroken over vast areas (fig. 2.25). Standing in the middle of

Figure 2.25 Bison, native grazers of the temperate grasslands of North America. MedioImages/PunchStock

unobstructed prairie under a dome of blue sky evokes a feeling similar to that of being on a small boat in the open ocean. It is no accident that early visitors from forested Europe and eastern North America often referred to the prairie in the American Midwest as a "sea of grass" and to the wagons that crossed them as "prairie schooners." Prairies were the home of the bison and pronghorn and of the nomadic cultures of Eurasia and North America.

Geography

Temperate grassland is the largest biome in North America, extending from 30° to 55° latitude. These grasslands are even more extensive in Eurasia (fig. 2.26). In North America, the prairies of the Great Plains extend from southern Canada to the Gulf of Mexico and from the Rocky Mountains to the deciduous forests of the east. Additional grasslands are found on the Palouse prairies of Idaho and Washington and in the central valley and surrounding foothills of California. In Eurasia, the temperate grassland biome forms a virtually unbroken band from eastern Europe all the way to eastern China. In the Southern Hemisphere, temperate grassland occurs in Argentina, Uruguay, southern Brazil, and New Zealand.

Climate

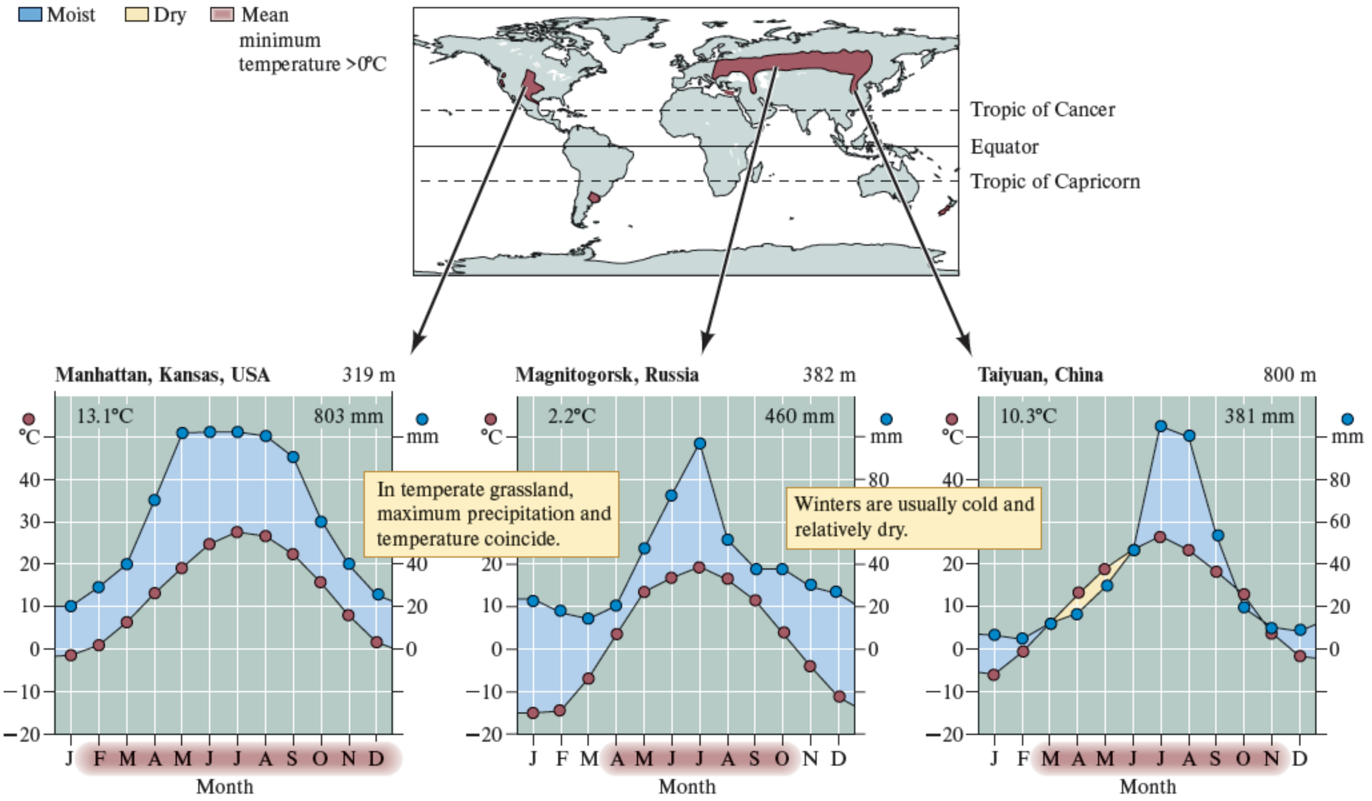
Temperate grasslands receive between 300 and 1,000 mm of precipitation annually. Though wetter than deserts, temperate grasslands do experience drought, and droughts may persist for several years. The maximum precipitation usually occurs in summer during the height of the growing season (see fig. 2.26). Winters in temperate grasslands are generally cold and summers are hot.

Soils

Temperate grassland soils are derived from a wide variety of parent materials. The best temperate grassland soils are deep, basic or neutral, and fertile and contain large quantities of organic matter. The black prairie soils of North America and Eurasia, famous for their fertility, contain the greatest amount of organic matter. The brown soils of the more arid grasslands contain less organic matter.

Biology

Temperate grassland is thoroughly dominated by herbaceous vegetation. Drought and high summer temperatures encourage fire. As in tropical savannas, fire helps exclude woody vegetation from temperate grasslands, where trees and shrubs are often limited to the margins of streams and rivers. In addition to grasses, there can be a striking diversity of other herbaceous vegetation. Spring graces temperate grasslands with showy anemones, ranunculus, iris, and other wildflowers; up to 70 species can bloom simultaneously on the species-rich North American prairie. The height of grassland vegetation varies from about 5 cm in dry, short-grass prairies to over 200 cm in the wetter, tall-grass prairies. The root systems of grasses and forbs (herbaceous plants that are not grasses) form a dense network of sod that resists invasion by both trees and the plow.



In temperate grassland, maximum precipitation and temperature coincide.

Winters are usually cold and relatively dry.

Figure 2.26 Temperate grassland geography and climate.

Temperate grasslands once supported huge herds of roving herbivores: bison and pronghorns in North America (see fig. 2.25) and wild horses and Saiga antelope in Eurasia. As in the open sea, the herbivores of the open grassland banded together in social groups, as did their attendant predators, the steppe and prairie wolves. The smaller, inconspicuous animals, such as grasshoppers and mice, were even more numerous than the large herbivores.

Human Influences

The first human populations on temperate grasslands were nomadic hunters. Next came the nomadic herders. Later, with their plows, came the farmers, who broke the sod and tapped into fertile soils built up over thousands of years. Under the plow, temperate grasslands have produced some of the most fertile farmlands on earth and fed much of the world (fig. 2.27). However, much of this primary production depends on substantial additions of inorganic fertilizers, and we are "mining" the fertility of prairie soils. Amy Molotoks and colleagues used a world soil database combined with land cover maps from satellite imagery plus data collected in the field to determine that 59% of soil organic carbon is lost when grassland is converted to cropland (Molotoks et al. 2018). In addition, the more arid grasslands, with their frequent droughts, do not appear capable of supporting sustainable farming.

Temperate Forest

For many, nothing epitomizes "nature" as do the diverse and majestic deciduous trees that characterize **temperate forest** (fig. 2.28). In the subdued light of this cool, moist realm, a world of mushrooms and decaying leaves, you can stand beside the giants of the biosphere.

Geography

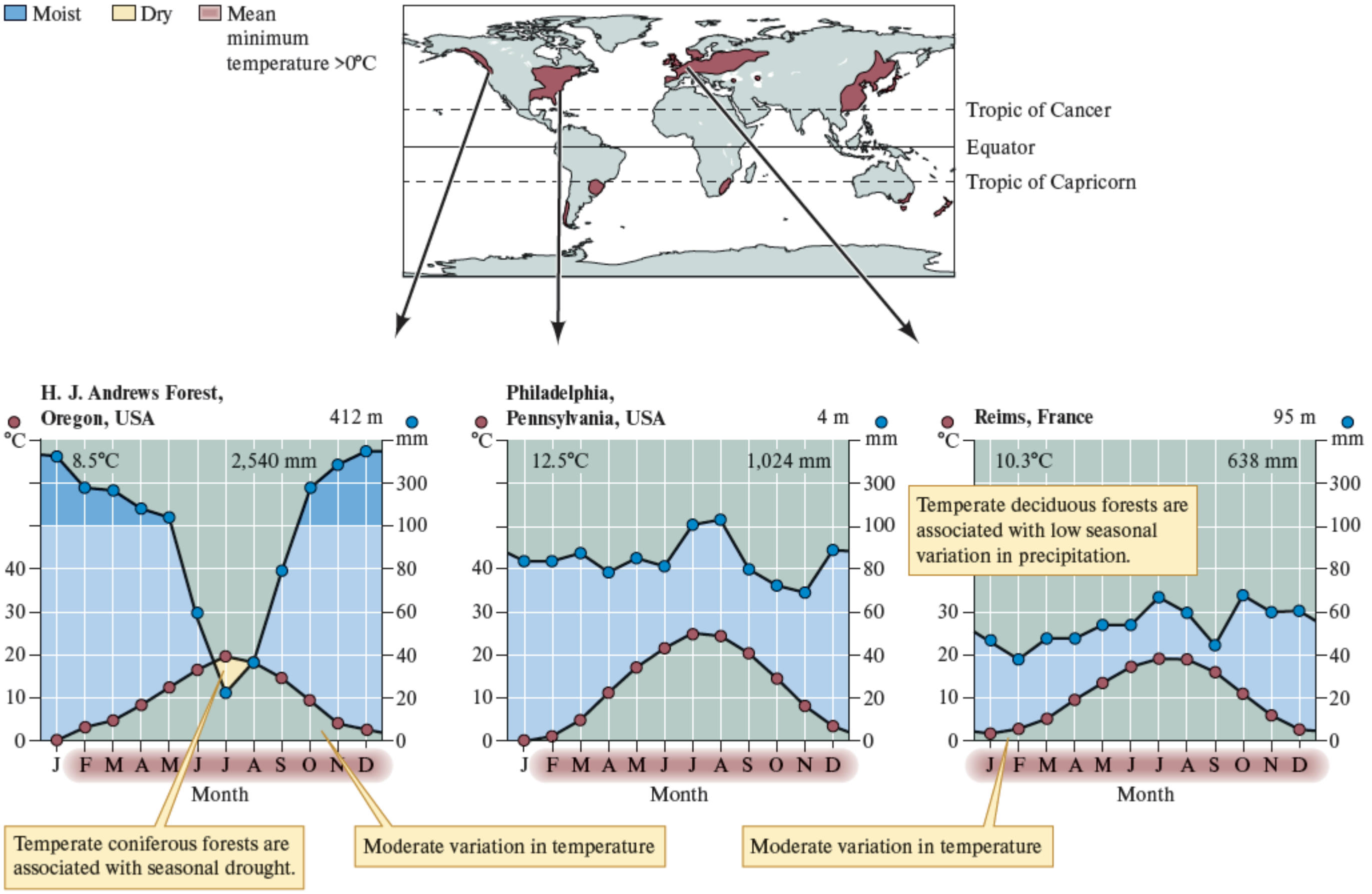
Temperate forest can be found between 30° and 55° latitude. However, the majority of this biome lies between 40° and 50° (fig. 2.29). In Asia, temperate forest originally covered much of Japan, eastern China, Korea, and eastern Siberia. In western Europe, temperate forests extended from southern Scandinavia to northwestern Iberia and from the British Isles through eastern Europe. North American temperate forests are found from the Atlantic seacoast to the Great Plains and reappear on the West Coast as temperate coniferous forests that extend from northern California through southeastern Alaska. In the Southern Hemisphere, temperate forests are found in southern Chile, New Zealand, South Africa, and southern Australia.

Figure 2.27 Once the most extensive biome on earth, temperate grasslands have been largely converted to agriculture.
Dave Reede/Getty Images

Climate

Temperate forests, which may be either coniferous or deciduous, occur where temperatures are not extreme and where annual precipitation averages anywhere from about 650 mm to over 3,000 mm (see fig. 2.29). These forests generally receive more winter precipitation than temperate grasslands. Deciduous trees usually dominate temperate forests, where the growing season is moist and at least 4 months long. In deciduous forests, winters last from 3 to 4 months. Though snowfall may be heavy, winters in deciduous forests are relatively mild. Where winters are more severe or the summers drier, conifers are more abundant than deciduous trees. The temperate coniferous forests of the Pacific Coast of North America receive most of their precipitation during fall, winter, and spring and are subject to summer drought. Summer drought is shown clearly in the climate diagram for the H. J. Andrews Forest of Oregon (see fig. 2.29). The few deciduous trees in these coniferous forests are largely restricted to streamside environments, where water remains abundant during the drought-prone growing season.

Figure 2.28 A mixed deciduous and coniferous temperate forest in New England. This temperate forest in early autumn gives just a hint of the dramatic display of color that occurs each autumn in the New England countryside, where farms and towns occupy areas cleared of forest. Songquan Deng/Shutterstock



Temperate deciduous forests are associated with low seasonal variation in precipitation.

Temperate coniferous forests are associated with seasonal drought.

Moderate variation in temperature

Moderate variation in temperature

Figure 2.29 Temperate forest geography and climate.

Soils

Temperate forest soils are usually fertile. The most fertile soils in this biome develop under deciduous forests, where they are generally neutral or slightly acidic and rich in both organic matter and inorganic nutrients. Rich soils may develop under coniferous forests, but conifers are also able to grow on poorer, acidic soils. Nutrient movement between soil and vegetation tends to be slower and more conservative in coniferous forests; nutrient movement within deciduous forests is generally more dynamic.

Biology

Primary production in temperate forests is less than tropical forests, but can be very high, especially where young trees are getting established. Furthermore, while the diversity of trees found in temperate forests is lower than that of tropical forests, temperate forest biomass can be as great or greater. Like tropical rain forests, temperate forests are vertically stratified. The lowest layer of vegetation, the herb layer, is followed by a layer of shrubs, then shade-tolerant understory trees, and finally the canopy, formed by the largest trees. The height of this canopy varies from approximately 40 m to over 100 m. Birds, mammals, and insects make use of all layers of the forest from beneath the forest floor through the canopy. Some of the most important consumers are the fungi and bacteria, which, along with a diversity of microscopic invertebrate animals, consume the large quantities of wood stored on the floor of old-growth temperate forest (fig. 2.30). The activities of these organisms recycle nutrients, a process upon which the health of the entire forest depends.

Human Influences

What, besides being large cities, do Tokyo, Beijing, Moscow, Warsaw, Berlin, Paris, London, New York, Washington, D.C., Boston, Toronto, Chicago, and Seattle have in common? They are all built on lands that once supported a temperate forest. The first human settlements in temperate forests were concentrated along forest margins, usually along streams and rivers. Eventually, agriculture was practiced in these forest clearings, and animals and plant products were harvested from the surrounding forest. This was the circumstance several thousand years ago, in Europe, Asia, and North America. Since those times, most of the ancient forests have fallen to ax and saw. Few tracts of the virgin deciduous forest that once covered most of the eastern half of North America remain, and disparate interests struggle over the fate of the remaining 1% to 2% of old-growth forests in western North America.

Boreal Forest

The **boreal forest,** or **taiga,** is a world of wood and water that covers over 11% of the earth's land area (fig. 2.31). On the surface, the boreal forest is the essence of monotony. However, if you pay attention you are rewarded with plenty of variety. Forests

Figure 2.30 Key decomposers in temperate forests. The massive wood deposited on the floor of temperate forests is broken down by fungi, which are essential to the addition of organic matter to forest soils and to the cycling of nutrients in forest ecosystems. Photo 24/Stockbyte/Brand X Pictures/Getty Images

Figure 2.31 Boreal forests, such as this one in Alaska, are dominated by a few species of conifer trees. AlxYago/Shutterstock

of different ages, shaped by wind, fire, and other environmental forces, host diverse communities of insects, birds, rodents, and other animals. The understory may be open, with patches of fruit-bearing shrubs, or dense with young saplings. The summer forest is colored green, gray, and brown; the autumn adds brilliant splashes of yellow and red; and the long northern winter turns the boreal forest into a land of white solitude.

Geography

Boreal comes from the Greek word for north, reflecting the fact that boreal forests are confined to the Northern Hemisphere. Boreal forests extend from Scandinavia, through European Russia, across Siberia, to central Alaska, and across central Canada in a band between 50° and 65° N latitude (fig. 2.32). These forests are bounded in the south by either temperate forests or temperate grasslands and in the north by tundra. Fingers of boreal forest follow the Rocky Mountains south along the spine of North America, and patches of boreal forest reappear on the mountain slopes of south-central Europe and Asia.

Climate

Boreal forest is found where winters are too long, usually longer than 6 months, and the summers too short to support temperate forest (see fig. 2.32). The boreal forest zone includes some fairly moderate climates, such as that at Umeå, Sweden, where the climate is moderated by the nearby Baltic Sea. However, boreal forests are also found in some of the most variable climates on earth. For instance, the temperature at Verkhoyansk, Russia, in central Siberia, ranges from about −70°C in winter to over 30°C in summer, an annual temperature range of over 100°C! Precipitation in the boreal forest is moderate, ranging from about 200 to 600 mm. Yet, because of low temperatures and long winters, evaporation rates are low, and drought is infrequent. During droughts, however, forest fires can devastate vast areas of boreal forest.

Soils

Boreal forest soils tend to be of low fertility, thin, and acidic. Low temperatures and low pH impede decomposition of plant litter and slow the rate of soil building. As a consequence, nutrients are largely tied up in a thick layer of plant litter that

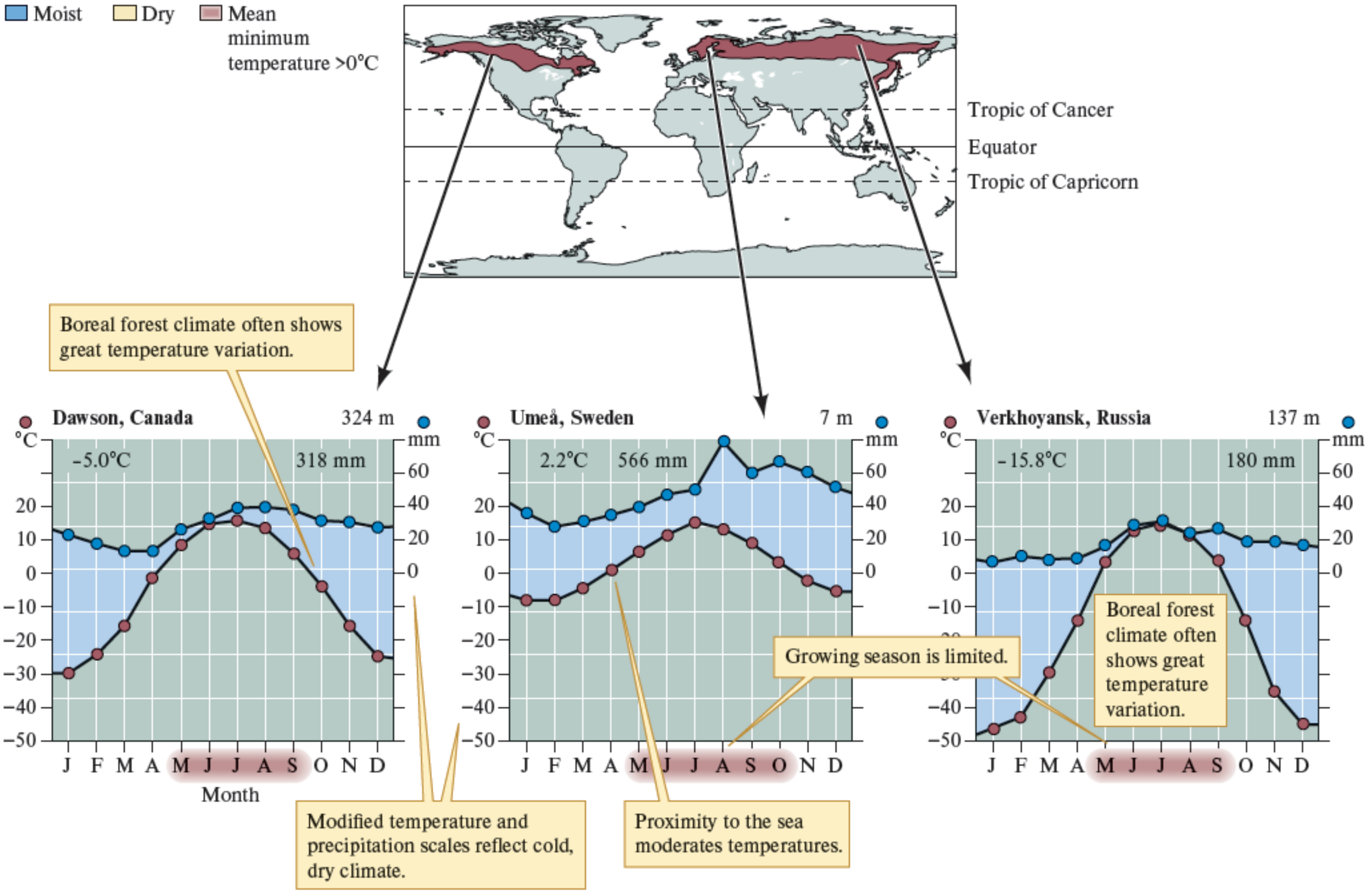


Figure 2.32 Boreal forest geography and climate.

carpets the forest floor. In turn, most trees in boreal forests have a dense network of shallow roots that, along with associated mycorrhizal fungi, tap directly into the nutrients bound up in this litter layer. The topsoil, which underlies the litter layer, is thin. In the more extreme boreal forest climates, the subsoil is permanently frozen in a layer of "permafrost" that may be several meters thick.

Biology

Boreal forest is generally dominated by evergreen conifers such as spruce, fir, and, in some places, pines. Larch, a deciduous conifer, dominates in the most extreme Siberian climates. Deciduous aspen and birch trees grow here and there in mature conifer forests and may dominate the boreal forest during the early stages of recovery following forest fires. Willows grow along the shores of rivers and lakes. There is little herbaceous vegetation under the thick forest canopy, but small shrubs such as blueberry and shrubby junipers are common.

Boreal forest is home to many animals, including migratory caribou and reindeer in winter and moose and woodland bison year-round. The wolf is the major predator of the boreal forest. This biome is also inhabited by black bears and grizzly bears in North America and the brown bear in Eurasia. A variety of smaller mammals such as lynx, wolverine, snowshoe hare, porcupines, and red squirrels also live in boreal forests. Boreal forest is the nesting habitat for many birds, such as the American redstart (see fig. 1.4), that migrate from the tropics each spring and the year-round home of other birds such as crossbills and spruce grouse.

Our survey of the biosphere has taken us far from the rain forest, where we started. Let's reflect back on the tropical rain forest and where we've come. What has changed? Well, we're still in forest but a very different one. In the rain forest, a single hectare could contain over 300 species of trees; here, in the boreal forest, you can count the dominant trees on one hand. What about epiphytes and vines? The vines are gone and the epiphytes are limited to lichens and some mistletoe. In addition, many of the intricate relationships between species that we saw in the rain forest are absent. All the trees are wind-pollinated, and none produce fleshy fruits like bananas or papayas. Now listen to the two forests at night. Tropical rain forest echoes with a rich chorus of sounds. In contrast, the silence of the boreal forest is broken by few animal voices—the howl of a wolf, the hoot of an owl, the cry of the loon, soloists of the northern forest—accompanied by incessant wind through the trees.

Human Influences

Ancient cave paintings in southern France and northern Spain, made during the last ice age when the climate was much colder, reveal that humans have lived off boreal forest animals, for tens of thousands of years. In Eurasia, hunting of reindeer eventually gave way to domestication and herding. In northern Canada and Alaska, some Native Americans still rely on wild caribou for much of their food, and northern peoples have long harvested the berries that grow in boreal forests.

For most of history, human intrusion in the boreal forest was relatively light. More recently, however, harvesting of both animals and plants has become intense. In a review of the current literature, Tähti Pohjanmies and her colleagues found that research consistently shows that logging in boreal forests has long-reaching ecological impacts, including changing climate (Pohjanmies et al. 2017). For example, boreal forests strongly affect global climate by sequestering carbon in the soil; this carbon can be released into the atmosphere when soils are disturbed during logging (fig 2.33).

Figure 2.33 Deforestation in boreal forest. Comstock Images/Alamy Stock Photo

Tundra

Follow the caribou north as they leave their winter home in the boreal forest and you eventually reach an open landscape of mosses, lichens, and dwarf willows, dotted with small ponds and laced with clear streams (fig. 2.34). This is the **tundra.** If it is summer and surface soils have thawed, your progress will be cushioned by a spongy mat of lichens and mosses and punctuated by sinking into soggy accumulations of peat. The air will be filled with the cries of nesting birds that have come north to take advantage of the brief summer abundance of their plant

Figure 2.34 Alaskan tundra. Tundra vegetation is mostly low-growing mosses, lichens, perennial herbaceous plants, and dwarf willows and birches. ajliikala/Getty Images

and animal prey. After the long winter, the midnight sun signals a celebration of light and life.

Geography

Like the boreal forest, arctic tundra rings the top of the globe, covering most of the lands north of the Arctic Circle at approximately 66.5° N latitude (fig. 2.35). The tundra extends from northernmost Scandinavia, across northern European Russia, through northern Siberia, and right across northern Alaska and Canada. It reaches far south of the Arctic Circle in the Hudson Bay region of Canada and is also found in patches on the coast of Greenland and in northern Iceland.

Climate

The tundra climate is typically cold and dry. However, temperatures are not quite as extreme as in the boreal forest. Though winter temperatures are less severe, the summers are shorter (see fig. 2.35). Precipitation on the tundra varies from less than 200 mm to a little over 600 mm. Still, because average annual temperatures are so low, precipitation exceeds evaporation. As a consequence, the short summers are soggy and the tundra landscape is alive with ponds and streams.

Soils

Soil building is slow in the cold tundra climate. Because rates of decomposition are low, organic matter accumulates in deposits of peat and humus. Surface soils thaw each summer but are generally underlain by a layer of permafrost that may be many meters thick. The annual freezing and thawing of surface soil combine with the actions of water and gravity to produce a variety of surface processes that are largely limited to the tundra. One of these processes, **solifluction,** slowly moves soils down slopes. In addition, freezing and thawing bring stones to the surface of the soil, forming a netlike, or polygonal, pattern on the surface of tundra soils (fig. 2.36).

Biology

The open tundra landscape is dominated by a richly textured patchwork of perennial herbaceous plants, especially grasses, sedges, mosses, and lichens. The lichens, associations of fungi and algae, are eagerly eaten by reindeer and caribou. The woody vegetation of the tundra consists of dwarf willows and birches along with a variety of low-growing shrubs.

The tundra is one of the last biomes on earth that still support substantial numbers of large native mammals, including caribou, reindeer, musk ox, bear, and wolves. Small mammals such as arctic foxes, weasels, lemmings, and ground squirrels are also abundant. Resident birds such as the ptarmigan and snowy owl are joined each summer by a host of migratory bird species. Insects, though not as diverse as in biomes farther south, are very abundant. Each summer, swarms of mosquitoes and black flies emerge from the many tundra ponds and streams.

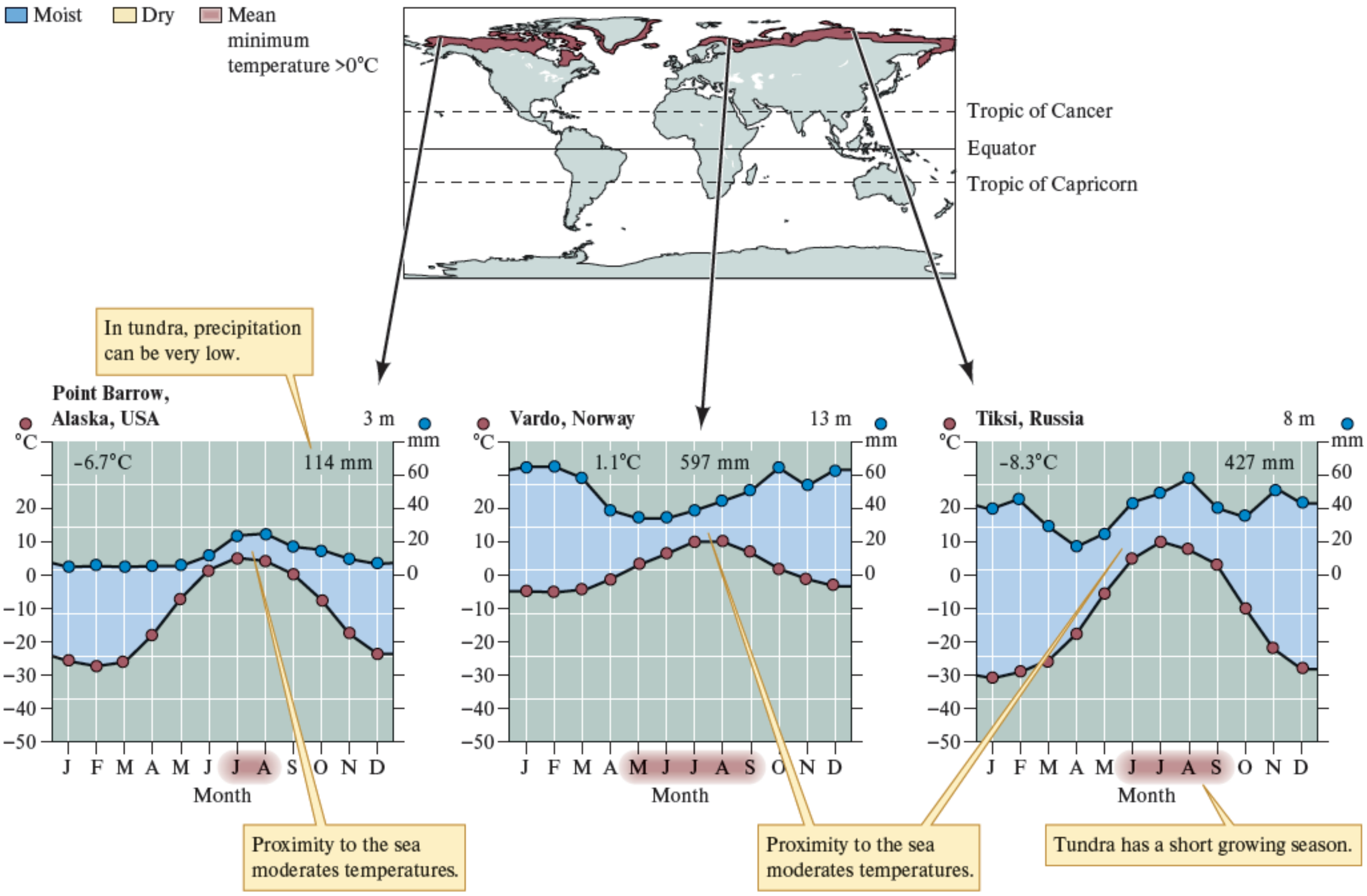


Figure 2.35 Tundra geography and climate.

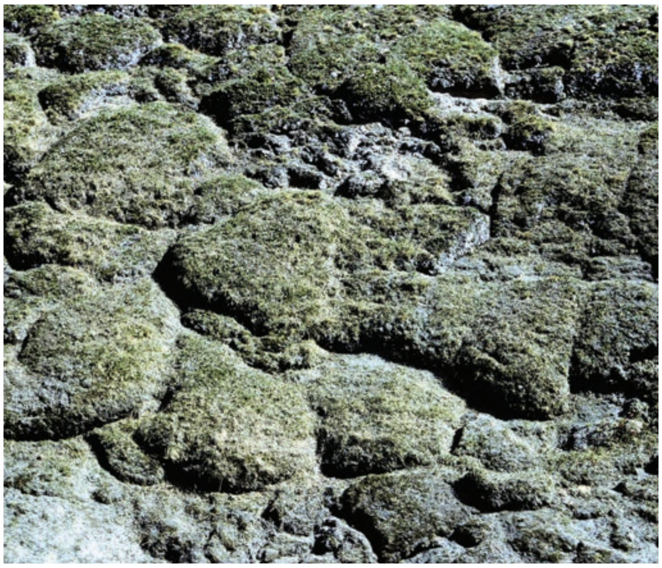


Figure 2.36 Freezing and thawing form netlike polygons on the surface of the tundra as seen here in an aerial photo of Alaska. Fletcher & Baylis/Science Source

Human Influences

Until recently, human presence in the tundra was largely limited to small populations of hunters and nomadic herders. As a consequence, the tundra has been viewed as one of the last pristine areas of the planet. Recently, however, human intrusion has increased markedly. This biome has been the focus of intense oil exploration and extraction. Airborne pesticides and radionuclides, which originate in distant human population centers, have been deposited on the tundra, sometimes with devastating results. Mercury, an element that is highly toxic to people and other animals, has increased dramatically in arctic lakes in recent years due to industrial pollution. This Hg can accumulate in fish, making it toxic to eat (Hudelson et al. 2019); this includes species that are eaten locally as well as for export. Such revelations have shattered the illusion of the tundra as an isolated biome and the last earthly refuge from human disturbance.

Mountains: A Diversity of Biomes

We now shift our attention to mountains, which are not a biome. As we explained earlier in this chapter, because of the environmental changes that occur with altitude, several biomes may be found on a single mountain, depending on elevation and which side of the mountain one is on. We include mountains here because they often introduce unique environmental conditions and organisms to regions around the globe.

Mountains capture the imagination as places of geological, biological, and climatic diversity (fig. 2.37). Mountains have long offered refuge for distinctive flora and fauna and humans alike. Like oceanic islands, they offer unique insights into evolutionary and ecological processes.

Figure 2.37 Mount Kilimanjaro, East Africa, where environmental conditions vary from tropical savanna at the base of the mountain to ice fields at its peak. Getty Images

Geography

Mountains are built by geological processes, such as volcanism and movements of the earth's crust that elevate and fold the earth's surface. These processes operate with greater intensity in some places than others, and so mountains are concentrated in belts where these geological forces have been at work (fig. 2.38). In the Western Hemisphere, these forces have been particularly active on the western sides of both North and South America, where a chain of mountain ranges extends from northern Alaska across western North America to Tierra del Fuego at the tip of South America. Ancient low mountain ranges occupy the eastern sides of both continents. In Africa, the major mountain ranges are the Atlas Mountains of northwest Africa and the mountains of East Africa that run like beads on a string from the highlands of Ethiopia to southern Africa. In Australia, the flattest of the continents, mountains extend down the eastern side of the continent. Eurasian mountain ranges, which generally extend east to west, include the Pyrenees, the Alps, the Caucasus, and, of course, the Himalayas, the highest of them all.

Climate

On mountains, climates change from low to high altitude, but the specific changes are different at different latitudes. On mountains at middle latitudes, the climate is generally cooler and wetter at higher altitudes (fig. 2.39). In contrast, there is less precipitation at the higher elevations of polar mountains and on some tropical mountains. In other tropical regions, precipitation increases up to some middle elevation and then decreases higher up the mountain. On high tropical mountains, warm days are followed by freezing nights. The organisms on these mountains experience summer temperatures every day and winter temperatures every night. The changes in climate that occur up the sides of mountains have profound influences on the distribution of mountain organisms.

Soils

Mountain soils change with elevation and have a great deal in common with the various soils we've already discussed. However, some special features are worth noting. First, because of the steeper topography, mountain soils are generally well drained and tend to be thin and vulnerable to erosion. Second, persistent winds blowing from the lowlands deposit soil particles and organic matter on mountains, materials that can make a significant contribution to local soil building. In some locations in the southern Rocky Mountains, coniferous trees draw the bulk of their nutrition from materials carried by winds from the valleys below, not from local bedrock.

Biology

Climb any mountain that is high enough and you will notice biological and climatic changes. Whatever the vegetation at the base of a mountain, that vegetation will change as you climb and the air becomes cooler. The sequence of vegetation up the side of a mountain may remind you of the biomes we encountered on our journey from the equator to the poles. In the cool highlands of desert mountains in the southwestern United States, you can hike through spruce and fir forests much like those we encountered far to the north. However, what you see on these desert mountains differs substantially from boreal forests. These mountain populations have been isolated from the main body of the boreal forest for over 10,000 years; in the interim, some populations have become extinct, some teeter on the verge of extinction, while others have evolved sufficiently to be

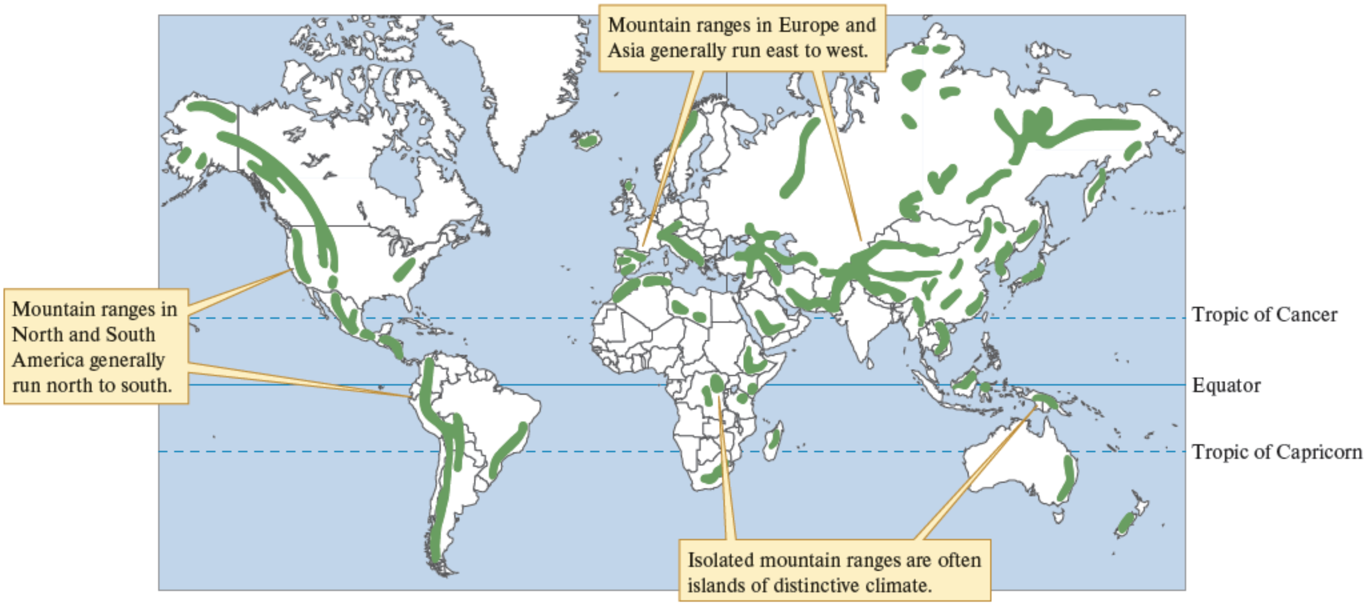


Figure 2.38 Mountain geography. Note that the shape of the continents is different in this map than in figure 2.35 and elsewhere in this chapter; that is because there is no perfect way to represent a round globe in two dimensions. Here, the Mercator map is shown, which exaggerates the Northern hemisphere so as to represent nautical distances correctly, whereas figure 2.35 is what is called the Robinson map. You can find many other types of maps on the Internet.

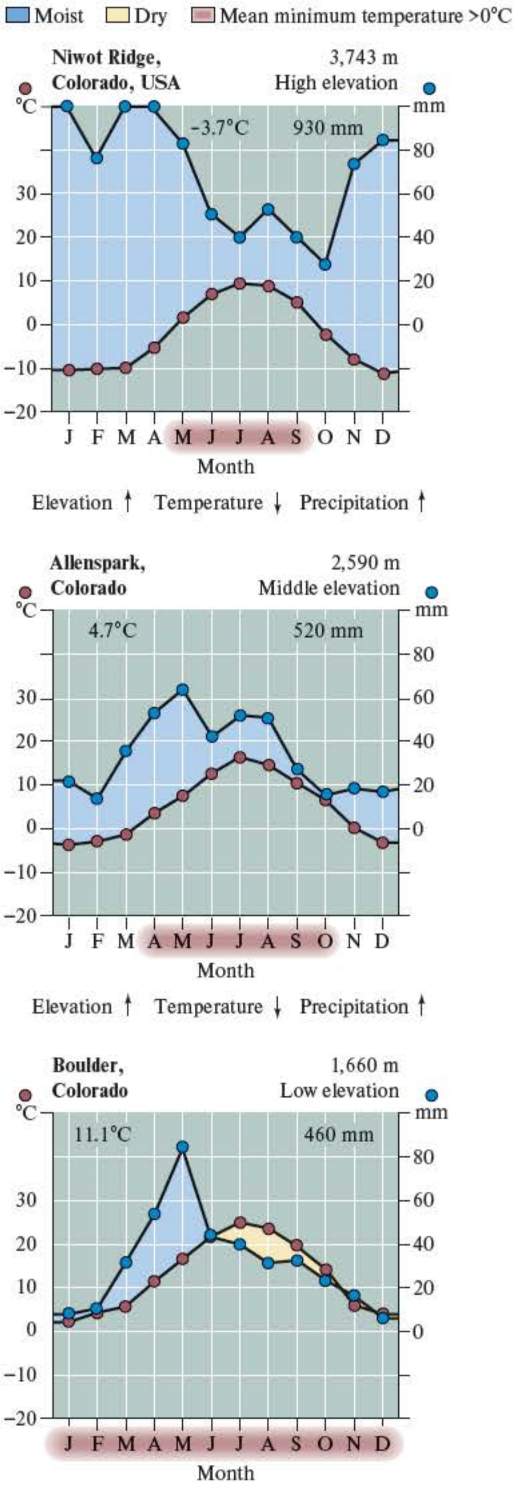


Figure 2.39 Mountain climates along an elevational gradient in the Colorado Rockies. Temperatures decrease and precipitation increases from low to high elevations in these midlatitude mountains.

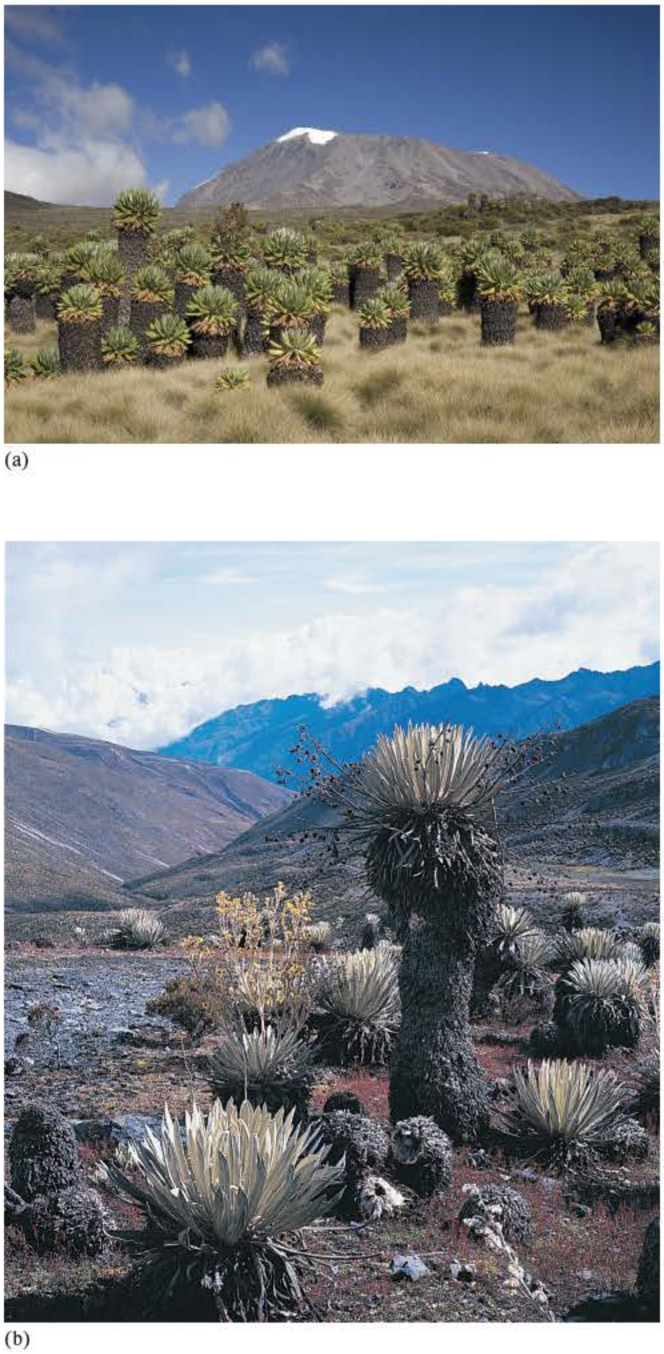


Figure 2.40 Convergence among tropical alpine plants: (*a*) *Senecio* trees on Mount Kilimanjaro, Africa; (*b*) *Espeletia* in the Andes of South America. (*a*) Avatar_023/Shutterstock; (*b*) Francois Gohier/Science Source

recognized as separate species or subspecies. On these mountains, time and isolation have forged distinctive gene pools and mixes of species.

The species on high equatorial mountains are even more isolated. Think for a moment of the geography of high tropical mountains: some in Africa, some in the highlands of Asia, and the Andes of South America. The high-altitude communities of Africa, South America, and Asia share very few species. On the other hand, despite differences in species composition, there are structural similarities among the organisms on these mountains (fig. 2.40). These similarities demonstrate the power of matching evolutionary forces—such as the selective pressures of freezing nights followed by warm days.

Human Influences

Because mountains differ in climate, geology, and biota (plants and animals) from the surrounding lowlands, they have been useful as a source of raw materials such as wood, forage for animals, medicinal plants, and minerals. Some of these uses, such as livestock grazing, are highly seasonal. In temperate regions, livestock are taken to mountain pastures during the summer and back down to the lowlands in winter. Human exploitation of mountains has produced ecological degradation in many places and surprising balance in others. Increased human pressure on mountain environments has sometimes created conflict between competing economic interests, between recreation seekers and between livestock ranchers. Because of their compressed climatic gradients and biological diversity, mountains offer living laboratories for the study of ecological and evolutionary responses to climatic variation.

Concept 2.3 Review

1. Why do regions that include high mountains (in tropical, desert, or temperate biomes) tend to have greater biological diversity compared to lowland regions in the same biomes?
2. Why would the soils in tropical rain forests generally be depleted of their nutrients more rapidly compared to the nutrients in temperate forest soils?

Applications

Finer Scale Climatic Variation over Time and Space

LEARNING OUTCOMES

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

2.15 Describe some ways that climate diagrams may oversimplify the conditions that organisms actually experience.
2.16 Interpret temporal and spatial representations of the Palmer Drought Severity Index.

In this chapter, we've used the biome concept and climate diagrams to represent the diversity of environmental selective pressure and resulting diversity of life on earth. However, both of these useful tools oversimplify what is actually occurring.

Here we explore a climatic index, the **Palmer Drought Severity Index,** which can be used to characterize climatic variation. First, what is a drought? A **drought** can be defined as an extended period of dry weather during which precipitation is reduced sufficiently to damage crops, impair the functioning of natural ecosystems, or cause water shortages for human populations. While such a definition may be sufficient for some needs, climatologists created quantitative indices of drought. The Palmer Drought Severity Index, or PDSI, is such an index. The PDSI uses temperature and precipitation to calculate moisture conditions relative to long-term averages for a particular region at a particular time. Negative values of the PDSI reflect drought conditions, while positive values indicate relatively moist periods. Values near zero indicate approximately average conditions in a particular region.

Figure 2.41 shows how drought can vary over both space and time. To ease interpretation, negative values of the Palmer Drought Severity Index are shaded red, indicating drought. Periods during which the index was positive are shaded blue, indicating moist conditions.

Figure 2.41*a* maps values of the Palmer Drought Severity Index across the United States for a single month in 2020. Notice that during this period, moisture conditions varied widely across this portion of the North American continent.

Extreme summer drought conditions in Colorado and elsewhere in the West set the stage for historical, devastating wildfires in 2020, while other areas in the East experienced hurricanes and flooding that same summer. Climate is varying not only in space but also in time. The area of Kansas from which the climate data are plotted in figure 2.41*b* falls within the temperate grassland biome. What does figure 2.41*b* suggest about moisture availability in the region around Manhattan, Kansas? One of the most apparent characteristics of this area is its great variability; the availability of water in the region is far from constant. Now compare figure 2.41*b* with the representation of climate for Manhattan, Kansas, shown in figure 2.26. How do the two figures compare? While the climate diagram and the PDSI represent climate from the same geographic location, the climate diagram, because it draws our attention to average climatic conditions, seems to suggest climatic stability. Meanwhile, the PDSI shows that the climate around Manhattan, Kansas, is in fact highly variable.

Note that variability in the short term reflects **weather,** whereas *climate* refers to conditions considered over longer time periods. For example, an analysis of temperature and precipitation in Kansas over the past century reveals that Kansas has become warmer on average, western Kansas has been getting drier, and eastern Kansas has increasing frequency of large rain events (Rahmani and Harrington 2019, https://www.epa.gov/climate-indicators/). This is an example of **climate change.** In this chapter, we have seen how climate shapes ecosystems; given this, it is not surprising that climate change can be a driver of evolution and other, significant ecological changes (see chapters 4, 5, 23, and elsewhere). Ecologists study the relationships between organisms and environment. As these examples show, in the study of those relationships both averages and variation in environmental factors need to be considered.

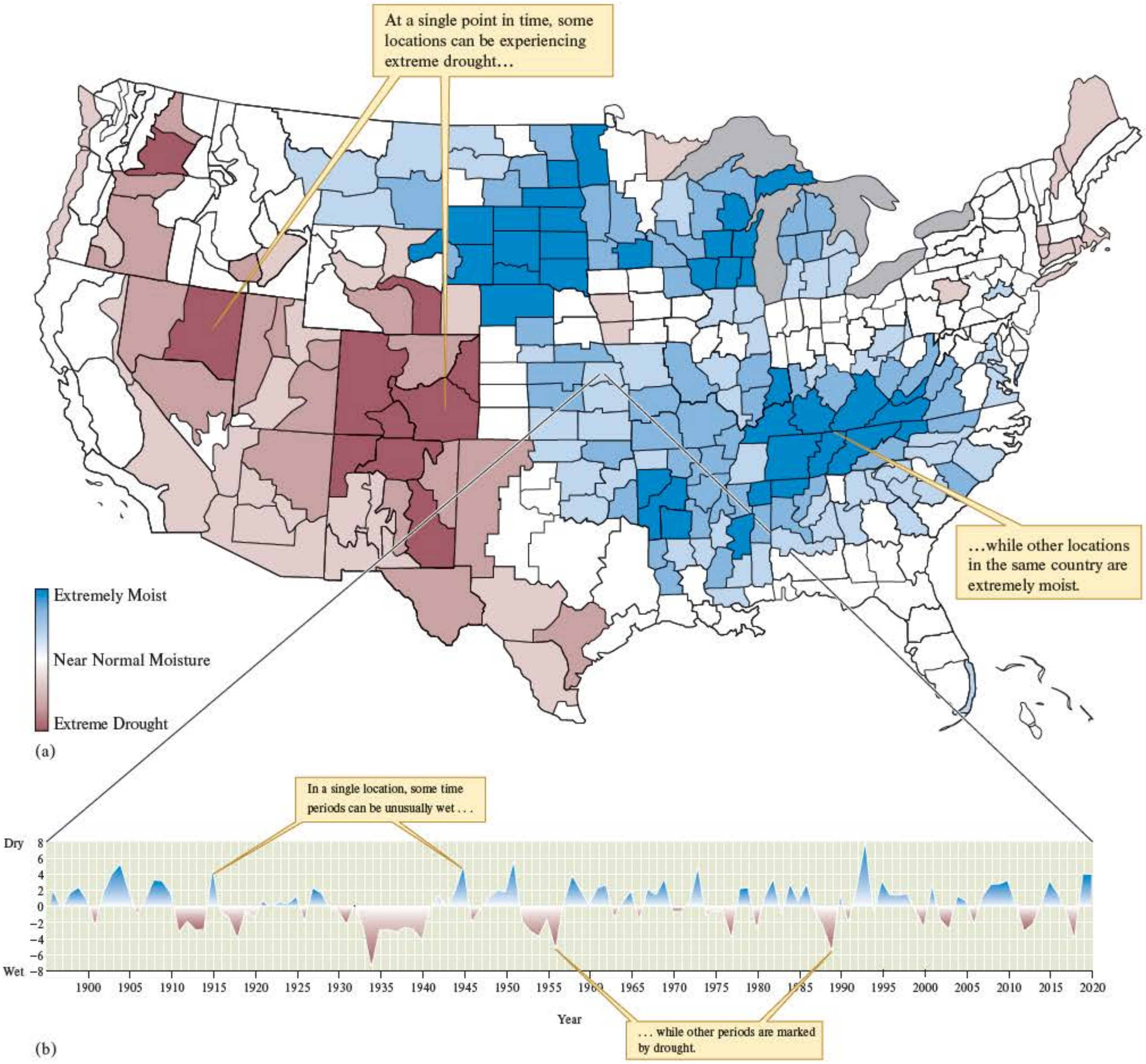


Figure 2.41 Like any feature of climate, drought can vary significantly over both space and time. (*a*) Regional variation in moisture conditions for the month of July, 2020, as indicated by the Palmer Drought Severity Index (data from NOAA 2020, www.cpc.ncep.noaa.gov). (*b*) Variation in the Palmer Drought Severity Index for Kansas region 3 near Manhattan, Kansas, plotted for the years 1895 to 2020 (data from NOAA 2020, cpc.ncep.noaa.gov).

Summary

We can understand the diversity of life on our planet in terms of the distributions of types of plant communities, called biomes. Biomes are characterized by particular functional traits of the plants, shaped by selective pressure from the environment. Because plants make sun energy available to the rest of the ecosystem, the types of plants will have profound influences on the rest of the ecosystem. The environmental influence that determines differences between biomes is primarily climate.

Uneven heating of the earth's surface by the sun and the tilt of the earth combine to produce predictable latitudinal and

seasonal variation in climate. Because the earth is a sphere, the sun's rays are most concentrated at the latitude where the sun is directly overhead. This latitude changes with the seasons because the earth's axis of rotation is not perpendicular to its plane of orbit about the sun but is tilted approximately 23.5° away from the perpendicular. The sun is directly overhead at the tropic of Cancer, at 23.5° N latitude during the northern summer solstice. During the northern winter solstice the sun is directly overhead at the tropic of Capricorn, at 23.5° S latitude. The sun is directly overhead at the equator during the spring and autumnal equinoxes. During the northern summer the Northern Hemisphere is tilted toward the sun and receives more solar energy than the Southern Hemisphere. During the northern winter, the Northern Hemisphere is tilted away from the sun and the Southern Hemisphere receives more solar energy.

Heating of the earth's surface and atmosphere drives atmospheric circulation and influences global patterns of precipitation. As the sun heats air at the equator, it expands and rises, spreading northward and southward at high altitudes. This high-altitude air cools as it spreads toward the poles, eventually sinking back to the earth's surface. Rotation of the earth on its axis breaks up atmospheric circulation into six major cells, three in the Northern Hemisphere and three in the Southern Hemisphere. These six circulation cells correspond to the trade winds north and south of the equator, the westerlies between 30° and 60° N or S latitude, and the polar easterlies above 60° latitude. These prevailing winds do not blow directly south because of the Coriolis effect.

As air rises at the tropics, it cools, and the water vapor it contains condenses and forms clouds. Precipitation from these clouds produces the abundant rains of the tropics. Dry air blowing across the lands at about 30° latitude produces the great deserts that ring the globe. When warm, moist air flowing toward the poles meets cold, polar air, it rises and cools, forming clouds that produce the precipitation associated with temperate environments. Complicated differences in average climate can be summarized using a climate diagram.

While terrestrial biome distribution is strongly associated with latitude, biomes are also influenced by microclimate and soil type. Biomes do not exist in simple bands determined solely by latitude; this is because topography and geology also play a role. Mountain ranges create different temperature zones based on elevation as well as microclimates due to the rain shadow effect. Just as rising air in the tropics induces precipitation, so too does moist air hitting the side of a mountain, resulting in forests on one side and desert on the other. Soil types can also dramatically affect distributions of plant types.

Terrestrial biomes are built upon a foundation of soil, a vertically stratified and complex mixture of living and nonliving material. Most terrestrial life depends on soil. Soils are generally divided into O, A, B, and C horizons. The O horizon is made up of freshly fallen organic matter, including leaves, twigs, and other plant parts. The A horizon contains a mixture of mineral materials and organic matter derived from the O horizon. The B horizon contains clays, humus, and other materials that have been transported from the A horizon. The C horizon consists of weathered parent material.

The geographic distribution of terrestrial biomes corresponds closely to variation in climate, especially prevailing temperature and precipitation. The major terrestrial biomes and climatic regimes are: *tropical rain forest:* warm; moist; low seasonality; infertile soils; exceptional biological diversity and intricate biological interactions. *Tropical dry forest:* warm and cool seasons; seasonally dry; biologically rich; as threatened as tropical rain forest. *Tropical savanna:* warm and cool seasons; pronounced dry and wet seasons; impermeable soil layers; fire important to maintaining dominance by grasses; still supports high numbers and diversity of large animals. *Desert:* hot or cold; dry; unpredictable precipitation; low primary production but often high diversity; organisms well adapted to climatic extremes. *Mediterranean woodland and shrubland:* cool, moist winters; hot, dry summers; low to moderate soil fertility; organisms adapted to seasonal drought and periodic fires. *Temperate grassland:* hot and cold seasons; peak rainfall coincides with growing season; droughts sometimes lasting several years; fertile soils; fire important to maintaining dominance by grasses; historically inhabited by roving bands of herbivores and predators. *Temperate forest:* moderate, moist winters; warm, moist growing season; fertile soils; high primary production and biomass; dominated by deciduous trees where growing seasons are moist, winters are mild, and soils fertile; otherwise dominated by conifers. *Boreal forest:* long, severe winters; climatic extremes; moderate precipitation; infertile soils; permafrost; occasional fire; extensive forest biome, dominated by conifers. *Tundra:* cold; low precipitation; short, soggy summers; poorly developed soils; permafrost; dominated by low vegetation and a variety of animals adapted to long, cold winters; migratory animals, especially birds, make seasonal use. *Mountains:* temperature, precipitation, soils, and organisms shift with elevation; mountains are climatic and biological islands.

Key Terms

A horizon 19
B horizon 19
biome 11
boreal forest (taiga) 32
caliche 27
C horizon 19
climate change 40
climate diagram 16
consumer 13
Coriolis effect 15
desert 25
drought 40
functional traits 13
lithosol 25
Mediterranean woodland and shrubland 27
microclimates 17
mycorrhizae 21
natural history 11
O (organic) horizon 17
Palmer Drought Severity Index 40
secondary producers 13
temperate forest 31

tropical rain forest 19
primary producers 13
selective pressure 13
temperate grassland 29
tropical savanna 22
rain shadow effect 17
solifluction 36
tropical dry forest 21
tundra 35
weather 40

Review Questions

1. Plants form the foundation of most terrestrial ecosystems. Pick a biome from this chapter and explain how the functional traits of plants from that biome could affect the evolution of other organisms in that biome.
2. Draw a typical soil profile, indicating the principal layers, or horizons. Describe the characteristics of each layer.
3. Describe global patterns of atmospheric heating and circulation. What mechanisms produce high precipitation in the tropics? What mechanisms produce high precipitation at temperate latitudes? What mechanisms produce low precipitation in the tropics?
4. Use what you know about atmospheric circulation and seasonal changes in the sun's orientation to earth to explain the highly seasonal rainfall in the tropical dry forest and tropical savanna biomes. (Hint: Why does the rainy season in these biomes come during the warmer months?)
5. We showed how the rain shadow effects biome distribution in the western United States Where else in the world can you see the impact of a rain shadow? Do you think that the height of the mountains creating it matters? Why or why not?
6. Some of the earliest studies of the geographic distribution of vegetation suggested a direct correspondence between latitudinal and altitudinal variation in climate, and our discussion in this chapter stressed the similarities in climatic changes with altitude and latitude. Now, what are some major climatic differences between high altitude at midlatitudes and high altitude at high latitudes?
7. How is the physical environment on mountains at midlatitudes similar to that in tropical alpine zones? How do these environments differ?
8. English and other European languages have terms for four seasons: spring, summer, autumn, and winter. This vocabulary summarizes much of the annual climatic variation at midlatitudes in temperate regions. Are these four seasons useful for summarizing annual climatic changes across the rest of the globe? Look back at the climate diagrams presented in this chapter. How many seasons would you propose for each of these environments? What would you call these seasons?
9. Biologists have observed much more similarity in species composition among boreal forests and among areas of tundra in Eurasia and North America than among tropical rain forests or among Mediterranean woodlands around the globe. Can you offer an explanation of this contrast based on the global distributions of these biomes shown in figures 2.11, 2.23, 2.32, and 2.35?
10. To date, which biomes have been the most heavily affected by humans? Which seem to be the most lightly affected? How would you assess human impact? How might these patterns change during this century? (You may need to consult the discussion of human population growth in the Applications section of chapter 11.)

Design elements: (Yellowstone thermal pool):©flickrRF/Getty Images