

The background of the cover is a photograph of a mountain range. The mountains are rugged and covered in patches of snow, with some rocky outcrops visible. In the foreground, there is a dense forest of evergreen trees, likely spruce or fir, which are dark green. The sky is a clear, bright blue. The overall scene is a typical representation of a North American mountain landscape.

ECOLOGY of NORTH AMERICA

SECOND EDITION

Brian R. Chapman and Eric G. Bolen

WILEY Blackwell

Foreword

As a professor, scientist, and student of wildlife for over four decades, I cannot think of a more important body of work to understand than ecology. This field of science is the basis for all natural history professions including anything that involves flora and fauna in its native habitat. It would be hard to impossible to understand, conserve, or manage coastal areas, deserts, forests and woodlands, grasslands, or tundra (essentially the landscapes that contribute to habitats for wildlife) and the plants and animals that occupy them without a solid understanding of ecology. Brian Chapman and Eric Bolen have brought these systems and others to life in this new edition of *Ecology of North America*.

Eric Bolen published the first edition of the book in 1998. This new edition is not just a makeover of Bolen's earlier work. Chapters were updated where needed and new information was added, including a new chapter on coastal environments to round out the landscapes examined. Another exciting addition is the inclusion of information boxes that call out special individuals and events in ecology that will be of interest to readers. Individuals highlighted include the "Fathers" of animal ecology, ecosystem science, grassland ecology, wildlife management, and prominent movers and shakers in the field such as Samuel Hearne, Rachel Carson, E. Lucy Braun, and John Muir. There are 18 information boxes scattered throughout the book with intriguing titles that are engaging, interesting to read, and informative, including: "The elk that saved a forest", "Spirit bear, the other white bear", and "Agave, margaritas, and bats". Not only are they interesting, but these selected

topics are written in such a way as to make the reader to want to know more.

This book is not the typical ecology text that only gives a cursory treatment to the important landforms of North America. It is unique in that it briefly describes the basics of ecology in the first chapter, and then delves into the ecology of the major landscapes of our continent in detail. College students and layman alike can easily understand the descriptions. The writing is clear and interesting, and would be of value to anyone interested in the places they live or new places they will be visiting. For example, I have taken many visitors with me during my studies in the deserts of North America, and often hear statements like "Wow, there is nothing here - no wonder they call it a desert". It is only after visitors spend time looking at the vast amount of life and signs of life that their tunes change to one of wonder. The authors believe that people will have a much better appreciation for the landscapes they occupy - from the fragile cryptogamic soils in deserts to freezing frogs in tundra - by reading this book prior to visiting new areas (biomes). This new volume is chock-full of interesting information including how alligators create habitat with "gator holes", introducing the reader to forests in the ocean, the importance of "scuzz" in enriching forests on land, and how *Lagerstätten* fossils and packrat middens can help humans understand their past. The writing brings together the interactions of plants, animals, and habitats (as ecology should), such as the explanations of how brown bears, salmon, and forests interact, or uses birds and thousand-year-old pines or cicadas to introduce ecological terms to readers.

The advent of computers and models has greatly changed the way students are taught and how they learn in North American universities and colleges. As more flora and fauna are reduced from living, breathing organisms to

pixels on a computer screen, there seems to be less attention devoted to actual field study. Some universities even have labs in the natural sciences online. I cannot imagine learning something as basic, yet complex, as ecology from a computer, and that is clearly not the intent here. Brian Chapman and Eric Bolen bring the fascinating landscapes humans share with flora and fauna to life and also explain how mankind influences these systems.

The authors are well-known ecologists with a long history together; both have dedicated their lives to understanding ecology around the United States and passing on that knowledge to others. Because of their long-term association, the writing is seamless as though written by a single author. The book will certainly give budding ecologists and natural resource professionals a sense and better understanding of “place”. The authors had a goal of following Leopold’s example of emphasizing the importance of landscapes to the biologic community and to the human spirit. *Comme il faut!*

Paul R. Krausman
Certified Wildlife Biologist®
Fellow and Past-president of The Wildlife Society
Emeritus Professor of Wildlife Ecology,
University of Arizona
Boone and Crockett Professor of Wildlife
Conservation,
University of Montana

Preface

About this book

Ecology of North America stems from our belief that many college students – and non-students – lack much awareness about the natural world in which they live. Thanks to the effects of mass media, some may indeed deplore the destruction of far-off tropical rain forests or the plight of whales; however, too few are acquainted with the all-but-vanished inland sea of tallgrass prairie, the ‘gator holes of the Everglades, or the enigmatic population cycles of lynx (and other) animals in the spruce-fir forests of North America here at home. Our conviction rests, collectively, on more than 60 years of college teaching and countless public presentations. Moreover, until the first edition appeared no single text designed for classroom use had attempted to survey the ecological diversity of North America’s vast landscape. The first edition of *Ecology of North America*, drafted while one of us (EGB) taught a course of the same name, was therefore conceived and eventually born as a tool fashioned for undergraduate instruction.

Shortly after the first edition appeared preparation began for a second edition, but various circumstances precluded its completion (not least EGB’s retirement). Hence, if a new edition was to materialize, a coauthor was needed to revitalize the work. BRC then entered the scene when, after careers at other universities, he joined the faculty at UNCW as provost and professor of biology. Notably, his teaching and research experiences paralleled the basic themes expressed in *Ecology of North America*, and a marriage of interests thereafter followed. Our association

in fact began decades ago when BRC was completing his doctoral work at Texas Tech University, where EGB was then serving on the faculty and as a member of his advisory committee. This edition is therefore the result of a long-standing partnership founded on both a deeply shared interest in plant and animal ecology and a collegial and personal friendship.

As in the previous edition, the geographical coverage begins in the far north (the frigid tundra), continues southward into boreal and deciduous forests, swings westward into the interior grasslands and deserts, and continues to the western mountains before traveling onward to chaparral and temperate rain forests. Sites along North America's long and varied coastline conclude our regional tour. We present a selection of unique areas (e.g., the Grand Canyon), expanded in this edition to include the fossil history offered by the La Brea tar pits and Burgess Shale. We also visit far-flung locations such as the Polar Ice Cap, Mississippi River, and Florida Keys, as well as stopping to investigate pitcher plant bogs and other habitats of interest on the way. As appropriate to a new edition, we have supplemented and updated the previous text with a variety of subjects ranging from cicada cycles and the moth-eating habits of bears, to the mysterious disease now devastating bat populations and the havoc wrought to the Everglades by introduced pythons.

Some entirely new features highlight the second edition including a chapter dedicated to coastal environments, among them seagrass communities, tide pools, and barrier islands, and ecological portraits of Chesapeake Bay and the Laguna Madre. The new chapter also describes phenomena such as the vital relationship between horseshoe crabs and migrant shorebirds. "Infoboxes" likewise appear for the first time; these present stand-alone descriptions, including biographies, as disparate as spirit bears, Lucy Braun, and

the conservation successes of gray whales and Maine's puffin colonies. To our delight, color photos now complement the gallery of black and white images.

Each chapter ends with "Readings and references," some of which present basic descriptions of community structure. These appeared early in the development of ecology, yet still provide an essential foundation for many readers. Other sources which have been published more recently represent new discoveries and refinements of previous concepts, such as: revelations about the hunting success of spirit bears; evidence of inbreeding depression in Isle Royale's isolated wolf population; the biotic community in the canopy of towering redwoods; and expanding knowledge of the beneficial impacts of nutrients derived from salmon carcasses. We also list works of greater scope for those seeking deeper insight into the subjects at hand.

Our focus

This edition, updated with both new and expanded coverage, broadly targets an audience of both undergraduate students and the general public. In doing so, we continue writing in a "user-friendly" format that appends Latin taxa and literature sources instead of embedding these within the text in the style of scientific journals. Understandably, some professional biologists may fault our format, but we aim to hold the attention of readers who may place higher priorities on the primary message of the book. For the same reason, we shied from marching lockstep through a catalog of species, soil types, and weather regimes for every unit; these are provided only when they seem important. Otherwise, our steady focus is on key or at least interesting plants and animals and their interactions.

Finally, we were guided by the thoughts of Aldo Leopold who, in *Sand County Almanac* (1949), entwined three thoughts into a common theme: “land is a community” that forms the fabric of ecology; land should be cherished and respected as an “extension of ethics”; and “land yields a cultural harvest.” Leopold wedded science, ethics, and aesthetics. In doing so, he established an understanding of nature that we, in our own small way, have tried to nourish.

Brian R. Chapman, Huntsville, Texas

Eric G. Bolen, Wilmington, North Carolina

Acknowledgments

Our task would surely have foundered without the generous advice, knowledge, and contributions of many colleagues. Merely to list their names seems far too superficial, but we are nonetheless indebted to all, including anyone we have inadvertently omitted.

Our continued thanks are extended to those who contributed to the first edition (and in some cases, this edition as well): C. Davidson Ankney, Michael J. Armbruster, Stephen F. Arno, Guy A. Baldassarre, Thomas C. Barr, Jr, Mark Blumenthal, Carlton M. Britton, Lincoln P. Brower, C. Alexander Brownlow III, Dana C. Bryan, George C. Carroll, Donald D. Clark, Robert T. Coupland, John A. Crawford, James E. Deacon, Leonard F. DeBano, Ronald I. Dorn, Harold E. Dregne, Christine S. Dutton, Ellen Faurot-Daniels, Maeton C. Freel, Peter M. Frenzen, Ron R. George, Paul L. Gersper, Paul N. Gray, Lance H. Gunderson, Craig A. Harper, Wendy Hodgson, John R. Holsinger, Jon E. Keely, Fritz L. Knopf, Paul R. Krausman, Melissa Kreighbaum, Douglas W. Larson, Gordon S. Lind, Erik Lindquist, Glenn Longley, Charles Lowe, Richard Mack, John Mangimeli, Paul S. Martin, Roger Martin, Joseph R. McAuliffe, Burruss McDaniel, Robert W. Mitchell, Robert. H. Mohlenbrock, Elizabeth M. Morgan, Fritz P. Mueller, Richard Murzin, Nalini M. Nadkarni, S. Kim Nelson, David J. Odz, Karl A. Perry, James Petterson, Linda Pin, Donald Pinkava, Thomas L. Poulson, Donald R. Progulske, William O. Pruitt, Jr, John Riley, William L. Robinson, William H. Romme, Donald H. Rusch, Susan Shultz, John G. Sidle, John C.F. Tedrow, Jack W. Thomas, Walter M. Tovell, Merlin D. Tuttle, Gary Valentine, Thomas R. Van Devender, B.J. Verts, Doug Waid, Frederic H. Wagner, John R. Watson, Ronald R. Weeden,

Nathaniel R. Whitney, Edward O. Wilson, M. Eugene Wright, Paul J. Young, and Paul Zedler.

For their contributions to the second edition, we also thank Kathy L. Allen, Donna Anstey, Angie Babbit, Candice Bressler, Sanford Brown, Lisa D. Chapman, William R. Clark, Sherry Cosper, Tara Cuvelier, Pamela Dibble, John Dokken, Catherine Evans, Debbie R. Folklets, W. Mark Ford, Eric Hallerman, Richard W. Halsey, Thomas Henry, Susan Jacobson, Rick Kesterman, Jack L. Kindinger, Roel Lopez, Jim Lovett, D. A. Mascarelli, Joyce Maschinski, Vincente Mata, Laurie McBurnie, Danny L. McDonald, Thomas C. Michot, Thomas E. Moore, William F. Moore, Ashley R. Morgan, Paige A. Najvar, T. J. Pernas, Luis Prado, Kristen Quarles, T.P. Quinn, W. Scott Richardson, Celia Rozen, Charles H. Smith, Mike Smith, Autumn J. Smith-Herron, Clyde Sorenson, Nancy P. Stewart, James Stubbendieck, Orly (Chip) Taylor, Monte L. Thies, Nancy Thompson, Jace Tunnell, David Welch, Josh Westerhold, Don White, Jr, Richard Whyte, and Kathy S. Williams.

Colleagues at the University of North Carolina at Wilmington generously provided advice and assistance as one or both of the editions of the book were being prepared. Special mention goes to W. Franklin Ainsley, Walter J. Biggs, Thomas F. Britt, Lawrence B. Cahoon, Troy M. Clites, Mike Durako, D. Wilson Freshwater, Jocelyn Gaudet, Gilbert S. Grant, Melissa Grey, Neil F. Hadley, William B. Harris, Paul E. Hosier, John R. Huntsman, Stephen T. Kinsey, David L. LaVere, David G. Lindquist, John J. Manock, R.D. McCall, Ian A. McLaren, William McLellan, Daniel W. Noland, D. Ann Pabst, David E. Padgett, Beth A. Pardini, James F. Parnell, Joseph R. Pawlik, Martin H. Posey, David J. Sieren, Amanda Southwood, Peter N. Thomas, Carmelo Tomas, W. David Webster, and Barbara L. Wilson. The staff at the Randall Library at UNCW

expertly – and patiently – accommodated requests for often obscure bibliographic information and materials.

Associates at Sam Houston State University, the University of Houston-Downtown, and colleagues at several other universities thoughtfully provided essential information, assistance with photographic needs, and various kinds of advice and support during preparation of the second edition. Among these, special thanks go to Loren K. Ammerman, Jerry L. Cook, Quenton R. Dokken, Richard Eglsaer, Jaimie L. Herbert, David R. Hoffpauir, William I. Lutterschmidt, Lisa A. Shipley, Melissa S. Sisson, and John W. Tunnell, Jr. Sandra S. Chapman painstakingly proofread the manuscript, and we appreciate her keen eye and invaluable suggestions.

Persons and/or agencies providing photographs are acknowledged in the appropriate figure captions, as are the artists who prepared maps and line drawings; special thanks go to Tamara R. Sayre. Many of her illustrations appear again in the second edition as testimony to her talent and, certainly, to the importance of her work to the content of the book.

We benefitted from constructive comments provided by colleagues who reviewed the first edition as well as those who examined draft chapters prepared for the second edition, among them Leonard A. Brennan, Paul R. Krausmann, Bruce D. Leopold, Joyce Maschinski, Eric Ribbins, Fred E. Smeins, and an anonymous reviewer.

We are especially indebted to Paul R. Krausman who provided advice and constructive suggestions during the preparation of both editions, and who graciously wrote the Foreword for the second edition.

Rachael Ballard, Executive Commissioning Editor at John Wiley and Sons, unhesitatingly authorized this project, and

we enjoyed working with her and Delia Sandford, Managing Editor. We also thank Fiona Seymour, Senior Project Editor, and Audrie Tan, Project Editor, who guided the manuscript through the start-to-finish maze of production. We owe a special debt of gratitude to our copyeditor, Elaine Rowan, whose thoughtful improvements made what we were attempting to say far more intelligible.

Clearly, many have contributed, but we alone remain responsible for any errors that escaped unnoticed.

Finally, our wives, Sandy and Elizabeth, endured more neglect than we care to admit while this project inched toward completion. We marvel at our good fortune to find such wonderful, loving, and supportive partners. To them, we dedicate this book (albeit that it seems so little in return for so much).

CHAPTER 1

Introduction

In all things of nature there is something of the marvelous.

Aristotle

Think big for a moment. Imagine a transect running north to south, stretching across the midpoint of pristine North America in the year 1500. We will use the 100th meridian, which traces the right-hand edge of the Texas Panhandle, as our line of travel. At its northern end – the North Pole – the transect begins in a desolate cap of ice and snow and then crosses a vast Arctic landscape of tundra before traversing a wide band of spruce and fir known as the Boreal Forest. Wolves howl in the distance; the scattered remains of their most recent kill – a sickly moose – lie still fresh atop the deep snow. South of these dark forests spread the plains, grasslands grazed by millions of bison and even larger numbers of prairie dogs. After leaving the plains, our excursion takes us across the narrow, clear rivers and low hills of the Edwards Plateau before dropping into a region studded with low, thorny trees. The transect ends, for our purposes, when it reaches northern Mexico and the yucca-spiked Chihuahuan Desert.

A similar transect running east to west across the waist of North America at first encounters the sandy beaches and dunes of the Atlantic seashore. Here, at the latitude of Virginia, the transect crosses what once was an immense forest of oak and hickory ([Fig. 1.1](#)). According to folklore, an ambitious squirrel could have journeyed from the Atlantic seaboard to the Mississippi River 300 years ago without the necessity of ground travel, false testimony to

the idyllic notion that an unbroken canopy of deciduous forest once stretched across more than a third of North America.



Figure 1.1 A vast expanse of eastern deciduous forest once covered much of North America east of the Mississippi River, but the romantic notion of an unbroken canopy 300 years ago is inaccurate. Indeed, Native Americans and natural processes, such as fire, periodically cleared many areas, some quite large, within the primordial forest. A mountaintop bald, visible atop the Smoky Mountain ridge (right), represents a natural opening described in more detail in [Chapter 3](#). Photo courtesy of Brian R. Chapman.

Westward, with the Appalachians, Cumberland Plateau, and Mississippi River behind us, the forest gradually thins and our transect enters the grasslands. Our trek skirts the southern edge of the Prairie Pothole Region - North America's famed "duck factories" - and pushes onward toward the plains. As we cross our north-south transect in western Kansas, courting prairie chickens dance and boom

in the background and black-tailed jackrabbits crouch, ears lowered, to escape our notice. Still farther west rise the Rocky Mountains with their rather distinctive zones of vegetation, after which we enter into a desolate terrain of sagebrush in the Great Basin. In the distance loom the peaks of the Sierra Nevada where the largest of trees, the giant sequoia, almost defy description. In a quiet grove of these immense trees, we might allow our imagination to behold the ghost of John Muir (1838–1914), the hard-trekking Scot who championed wilderness preservation.

By the time we reach the rocky seashore of the Pacific Ocean, our transect will have dropped into the Central Valley of California and then risen upward to cross the Coastal Range that rims the western edge of the continent. Offshore, frisky sea otters float above submerged kelp forests. North of where we stand are the old-growth forests of Sitka spruce and western hemlock, heavily draped with epiphytes, replete with spotted owls and maples. On the Alaskan coast, vulnerable hoards of migrating salmon attract giant bears to the rushing streams each year. To the south are chaparral-covered hills, and beyond these are the beckoning Joshua trees in the Mojave Desert. Still farther south at a small site in the mountains of Mexico are firs cloaked each winter with millions of slumbering butterflies. Our telescoped journey across North America has been brief to be sure, but perhaps it is long enough to preview the contents of this book.

A brief overview of ecology

Ecology is the branch of biology that investigates the interrelationships between organisms and their environment. The original name *oekologie*, based on the Greek word *oikos* meaning “home”, was coined in 1866 by German zoologist Ernst Haeckel (1834–1919). An

ecological study of any species involves a detailed examination of an organism's life history and biological requirements, the physical environment in which the organism lives, and its interactions with the other species that occupy the same area. Physical features of the environment (e.g., temperature, soil type, and moisture) influence the distribution and abundance of organisms, but all living things process materials from the environment and transform energy as they grow and reproduce.

The ecosystem

In 1935, English botanist Arthur G. Tansley (1871–1955) proposed the term **ecosystem** to characterize the flow of energy and matter through a network of **food chains** collectively known as a **food web**. Energy passes through a series of **trophic levels** (i.e., feeding levels), the functional parts of an ecosystem. These rest on a foundation of non-living matter, the **abiotic level**, which consists of air, soil, and water. When fueled by sunlight, the abiotic level provides the fundamental components required for **photosynthesis** by species known as **primary producers**, which are represented by green plants such as algae, grasses, and trees and first in the series of trophic levels. **Primary consumers** – rabbits, deer, or other **herbivores** that consume the energy and matter bound in green plants – represent the next trophic level, followed by **secondary consumers**; the latter are predators such as foxes or hawks. **Tertiary consumers**, sometimes known as apex predators, are represented by animals such as polar bears or mountain lions. The final trophic level, **decomposers**, is populated by scavengers, bacteria, and fungi that return the tissues of dead plants and animals to their elemental form ([Fig. 1.2](#)). An ecosystem is therefore an area or volume in which energy and matter are exchanged between its living and non-living parts.



Figure 1.2 In forests decomposition is commonly thought to originate with logs, but it often begins when a dead tree remains upright as a snag. The bracket fungi on this snag possess enzymes that break down lignin and other complex chemicals found in wood, and the fungi absorb the nutrients for their growth and reproduction. When the snag eventually falls, other decomposers on the forest floor will return its elements to the soil. Photo courtesy of Brian R. Chapman.

Abiotic limits

Many environmental influences – such as moisture, temperature, the availability of nutrients, wind, and fire – limit the kinds and abundances of organisms that populate an ecosystem. In 1840, German organic chemist Justus von Liebig (1803–1873) was the first to recognize the role of abiotic limitations in nature. After studying the relationships between surface soils and agricultural plants, Leibig concluded: “The crops of a field diminish or increase in exact proportion to the diminution or increase of the mineral substances conveyed to it in nature.” Liebig recognized that each plant requires not only certain minerals, but each must also be present in the proper quantity for the plant to flourish. If a required nutrient is absent, the plant will not survive. Moreover, if the essential food substance is present only in a minimal amount, the plant’s growth will be correspondingly minimal. In later years, this concept became known as the **law of the minimum**.

Later studies indicated that the growth and survival of living organisms also may be limited by an overabundance of a required substance (e.g., terrestrial plants require moisture, but die when waterlogged for a prolonged period). Plants and animals are successful only when they live in an environmental range between too much and too

little, that is, within their limits of tolerance. Victor E. Shelford (1877-1968; [Infobox 1.1](#)) incorporated the concept of maximum and minimum limits on environmental condition into the **law of tolerance** in 1913. Some organisms are capable of living within wide ranges of conditions of one or more environmental factors, whereas others have narrow limits of tolerance. Certain species are capable of acclimatizing to different environmental limits as seasons or conditions change.

Infobox 1.1 Victor E. Shelford (1877-1968), Father of animal ecology

The scientific career of Victor Shelford began in 1899 when he enrolled at West Virginia University where his uncle, the assistant state entomologist, influenced his lifelong interest in insects. In 1901, however, the president of the university moved to the University of Chicago where he offered a scholarship to Shelford who accepted and eventually earned a Ph.D. (in 1907) dealing with tiger beetles and dune vegetation on the shores of Lake Michigan. Likely for the first time, this study associated animals with the successional changes in a plant community, a concept pioneered by his academic mentor Henry C. Cowles (1869-1939). Shelford thereafter joined the faculty at Chicago but moved to the University of Illinois in 1914, where he spent the remainder of his academic career.

In 1913, Shelford published his first book, *Animal Communities in Temperate America*, a landmark of its day. He helped found the Ecological Society of America and, in 1916, became its first president.

Along with his university duties, Shelford served as the laboratory supervisor for the Illinois Natural History Survey during 1914-1929 and, during alternate summers between 1914 and 1930, as director of marine ecology at the Puget Sound Biological Station. His research interests included topics ranging from benthic communities in both freshwater and marine environments to lemming populations in Arctic tundra. His experiments covered the physiological and

behavioral responses of animals to temperature and other variables in climate-controlled chambers. In the field, he used photoelectric cells to determine light penetration into seawater. His research, which often employed novel equipment, led to a manual entitled *Laboratory and Field Ecology* (1929). On the practical side, Shelford also studied termites and other insect pests, as well as the response of fishes to sewage treatment. He eventually reduced his lab work in favor of spending more time on field studies, especially those that concerned food chains, structure, and other analyses of natural communities.

In the 1930s, Shelford began collaborating with Frederic E. Clements (1874-1945), a prominent plant ecologist. Their relationship was cordial but strained at times as, much to Shelford's dismay, Clements harbored reservations about the role animals played in vegetational development. Nonetheless, in 1939 the two produced *Bio-Ecology*, a book that integrated plants and animals into the formation of communities.

Shelford's marathon field trips were legendary experiences for students; some included several weeks of camping while visiting prairie, forest, desert, or tundra. Indeed, he wanted his students to study first hand every major biome in North America. Reelfoot Lake in Tennessee, created by a cataclysm of earthquakes in the winter of 1811-1812, was a regular stop for many years; the site included opportunities to study oxbow lakes, cypress sloughs, and floodplain forests. Wherever they went, however, Shelford steadfastly donned shirt and tie in the field. Shelford's career represented a major link in a chain of renowned ecologists that began with Cowles and continued with Shelford, followed by his student S. Charles Kendeigh (1904-1986) and, in turn, the latter's student Eugene P.

Odum (1913–2002), who is regarded as the founder of modern ecology.

Shelford retired from university life in 1946, but he hardly remained inactive. His passion for preserving natural areas with fully intact communities initiated the Ecologist's Union, which evolved into *The Nature Conservancy* whose mission is now global in scope. His association with Clements helped Shelford develop his appreciation for the concept of biomes and, after years of work, resulted in a monumental treatise, *Ecology of North America* (1963), the inspiration and namesake for the book at hand.

Soon after Shelford completed his graduate studies at Chicago, he was advised by a prominent scientist to “discontinue this field of ecology” and instead pursue biology with a traditional focus on individual organisms. Fortunately, Victor E. Shelford chose otherwise.

To complicate things further, an organism may tolerate a wide range of conditions for one environmental factor, but be restricted by a narrow range for another. In the latter case, the distributional range of the species will be restricted by the condition for which it possesses the narrowest tolerance.

Climate and topography

The climatic conditions of any region are determined by many factors, including latitude, seasonal temperature ranges, the amount and periodicity of rainfall, and location on the continent (e.g., interior versus coastal).

Geographical features, such as proximity to mountain ranges or bodies of water, can alter local conditions enough to influence the type of plant associations that can exist.

Thus, vegetation maps of North America ([Fig. 1.3](#)) illustrate

the influence of climate. The northern region of North America has two broad, east-west belts of natural vegetation: tundra and boreal coniferous forest. These follow a gradient correlated with temperature patterns, but the vegetative zones on the remainder of the continent are more closely associated with the availability of moisture. Precipitation decreases from east to west while evaporation, which is largely influenced by temperature, increases; this interaction results in a series of north and south vegetation bands. Along the coasts, regions of higher humidity support forests. The broadest zone of forest is on the eastern half of the continent where rainfall exceeds evaporation.

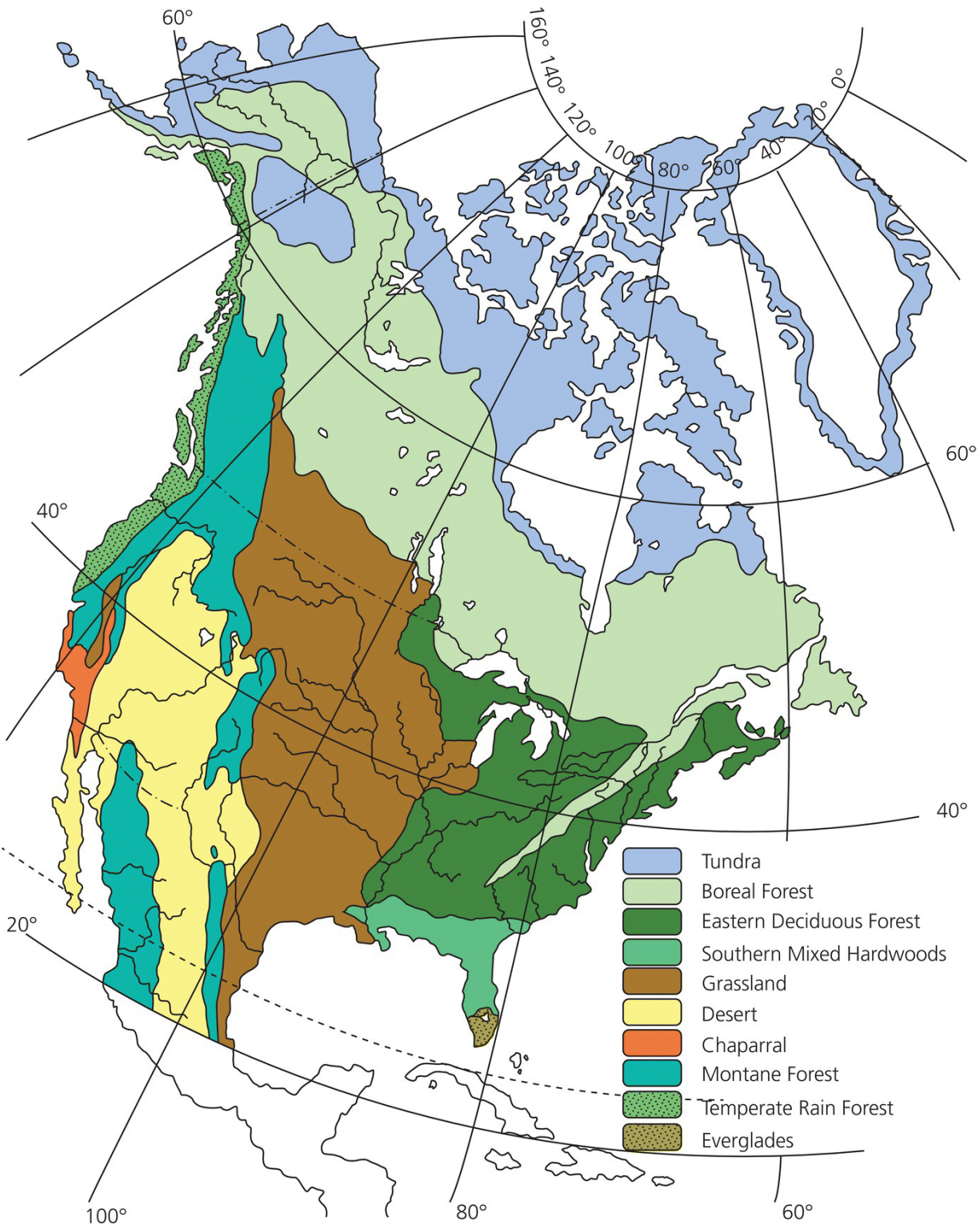


Figure 1.3 The predominately east-west distribution of major biomes in North America is determined largely by precipitation. In contrast, the north-south arrangement of major plant associations in the middle and southern regions of the continent result more from interactions of temperature, evaporation, and elevation. Illustration courtesy of Tamara R. Sayre and Brian R. Chapman, based on Brown et al. (2007).

Mountains intercept winds and directly influence regional climates. As winds ascend a mountain slope, the air mass cools and gradually becomes saturated; cool air holds less moisture than warm air. The windward sides of mountains usually receive rain at mid- to higher elevations as the moisture is, in effect, wrung out of the air. On the leeward side, descending cool dry air absorbs moisture from the soil and vegetation creating **rain shadow**, an area where evaporation greatly exceeds precipitation. The Great Basin Desert on the eastern (leeward) side of the Sierra Nevada Range illustrates the impact of a rain shadow, whereas the western slopes of the mountains support lush forests.

Topography and vegetation create local environmental conditions that can differ substantially from the overall climate of a region. For example, the **microclimate** under a dense clump of bushes does not share the same temperature, moisture, and wind conditions as may be found in an open area just a short distance away. Similarly, the north-facing slope on a mountain does not receive the same solar radiation as a south-facing slope. Because of the difference in exposure, the evaporation rate on north-facing slopes may be 50% lower, the temperature is lower, and soil moisture is higher. Thus, two sides of a mountain, even at the same elevation, are often occupied by different compositions of plant and animal species.

Soils and soil profiles

Climatic features, especially temperature and precipitation, influence the formation of soils. Soil is a complex mixture of minerals, organic matter, water, and air, forming a substrate harboring bacteria, fungi, and other small organisms. Minerals are derived from the weathering of parent material, usually rock, by chemical and physical processes. The microorganisms (e.g., decaying organisms) contribute to soil formation and development by breaking down organic matter, fixing atmospheric nitrogen, and contributing to nutrient cycling.

The US Department of Agriculture (USDA) recognizes twelve textural classes of soil based on various compositions of three particle sizes of minerals - clay, silt, and sand - but soil also may contain larger mineral particles ranging in size from pebbles to large fragments of rock. Of the textural classes, loam (composed of varying percentages of clay, silt, and sand) is the most valuable because it supports many agricultural crops. The USDA also developed a soil classification system that places all the soil types in the world into twelve **soil orders**. These soil groups are defined using a set of characteristics that includes texture as well as physical and chemical properties. The name of each soil order ends in *-sol*, which is derived from the Latin word *solum* meaning "soil". For example, about 16% of the world's surface is covered by entisols which have moderate to low fertility; mollisols, which are the most productive agricultural soils, only occur on about 7% of the Earth's surface.

Anyone who has dug a posthole or planted a tree knows that soils are organized into distinct layers or **horizons**, descending from the ground surface down to the bedrock. These layers form a **soil profile**, and are the product of weathering and the actions of vegetation, temperature, rainfall, and microorganisms acting for millennia on parent material in a specific locality. The organic material - leaf

litter and decaying plant and animal matter – on the ground surface forms the **O horizon**. The O horizon is generally thin or absent in deserts and grasslands, but may be quite deep in forests. The first layer of soil, the **A horizon**, is often called “topsoil” and is usually rich in **humus**, the dark-colored products of decomposed organic materials. The A horizon is absent in most deserts, but can be up to 1 m (3 feet) deep in the fertile wheat-growing prairies of Washington State. Progressively downward in the soil profile, the E, B, and C horizons represent zones where the vertical processes of leaching gradually reduce the organic content of each successive layer, thereby increasing the amount of mineral matter. Bedrock is reached at the R horizon, which typically represents parent material.

Biotic community

A **biotic community**, the living part of an ecosystem, is composed of many species, but the number of species and their relative abundance diminish “upward” through a food chain. More species of plants exist in the producer level than do herbivores functioning as primary consumers. Likewise, herbivores are more numerous than the carnivores in the upper trophic levels. These relationships result in a pyramid-shaped community, with numerous (both in species and abundance) green plants at its base, fewer herbivores, and fewer still **carnivores** at its apex (e.g., mountain lions). In [Chapter 3](#), we will describe a relatively simple pyramid of vegetation, moose, and wolves on Isle Royale.

Community succession

Plant **succession** is the relatively predictable sequence of vegetational development within a geographic region. The composition of the local fauna also changes as the

vegetation develops and, to express the full ecological impact, the process is best regarded as biotic succession (i.e., sequential changes in both plants and animals). In practice, ecologists usually refer to the concept simply as succession and use the term more in reference to plants than to animals.

Notions about succession are embedded in several 19th century sources, including discourses of Henry David Thoreau (1817-1862) who described the regrowth of forests near Concord, Massachusetts. The first ecologist (at least in North America) to describe succession was Henry C. Cowles (1869-1939), who based his observations on the changes in dune vegetation on the shores of Lake Michigan. Later, Frederic Clements (1874-1945) proposed a complex hierarchy to describe the development of vegetation over time, but only a few of his terms remain widely used today.

Succession is currently viewed as a process of multiple invasions. As certain species replace others because of their own particular **adaptations** (e.g., tolerance to shade in an early growth stage, or greater ability to disperse), the composition of the community changes. The process of succession is also strongly influenced by local environmental factors such as soil type and the availability of water or certain nutrients.

Plant succession: from pioneer to climax

To perceive succession visually, consider a cleared landscape such as an agricultural field in a region with a moderate climate. Left unplowed, the exposed soil is soon covered with so-called weeds - dandelions and asters are typical invaders in many areas - that represent **pioneer** vegetation. Such herbaceous immigrants have three general characteristics: (a) they thrive on disturbed soils

where they tolerate harsh conditions (e.g., high soil temperatures, limited moisture and, in many cases, few nutrients); (b) they produce large numbers of seeds with adaptations for widespread dispersal and rapid germination but, when necessary, their seeds can persist in the soil for long periods; and (c) they are commonly, but not always, annuals. Some ecologists regard these as “opportunistic species”, plants that quickly take advantage of opportunities to colonize (or re-colonize) sites where competitive species are absent. The pioneer community accordingly consists of relatively few species; recently abandoned fields, for example, are often covered by blankets of single species.

Eventually, the pioneers give way to perennial species, which include plants with established roots systems, storage organs, and defensive structures. These species are better competitors and they eliminate the pioneers. Broomsedge and goldenrod are representative species. Shrubs soon appear, to be replaced later by trees. In many locations, a pine forest develops first, followed by a forest of oaks or other deciduous hardwoods. Of course, the species in these sequences vary by region, soil type, and other factors, but the pattern is consistent.

The final stage in succession is known as the **climax**, a term ecologists use to characterize regional vegetation. Climax communities, such as the Oak-Hickory Association in the Eastern Deciduous Forest, are mature ecosystems consisting of characteristic plants as well as animals (e.g., wild turkeys and eastern gray squirrels). When compared to pioneer and other successional stages, climax communities are (a) neither as **hydric** (wet) or **xeric** (dry) as the earlier stages and instead represent **mesic** conditions; (b) more complex and better organized; they have complicated food webs and more interspecific relationships; (c) include more species, which tend to be

relatively large and long-lived and have low reproductive rates; and (d) comparatively stable (e.g., resistant to invading species).

Primary and secondary succession

Old-field succession on abandoned farmlands is a real-world event often described to illustrate the sequence of community replacements. Fallow fields, which were widely available in the late 1930s, are useful sites to study succession because fields in various stages of re-growth are available (i.e., the date of abandonment, and hence the “age” of each field, and its vegetation can be determined from court records). One of the earliest studies of old-field succession on an abandoned farm in the Piedmont region of North Carolina revealed a sequence of herbaceous pioneers such as aster and ragweed, followed by the arrival of pine between years 5 and 15, and then full development of an oak-hickory forest 150 years after the fields were last cultivated.

Old-field succession illustrates **secondary succession**, the recovery of a previously vegetated but disturbed site. Secondary succession also occurs after fires remove the previous vegetation. These sites generally have well-developed soils that can support a variety of plants. The abandoned fields in North Carolina described in the previous paragraph were later cleared of forest vegetation and cultivated for many years thereafter. **Primary succession**, in contrast, occurs at sites devoid of previous vegetation, examples of which include dunes, atolls, volcanic cones, and land exposed by retreating glaciers. Such sites typically lack mature soils and have few nutrients. Primary succession, because it usually requires soil building, spans long time periods before the climax stage is reached.