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.

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

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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.

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

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.

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.

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.

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

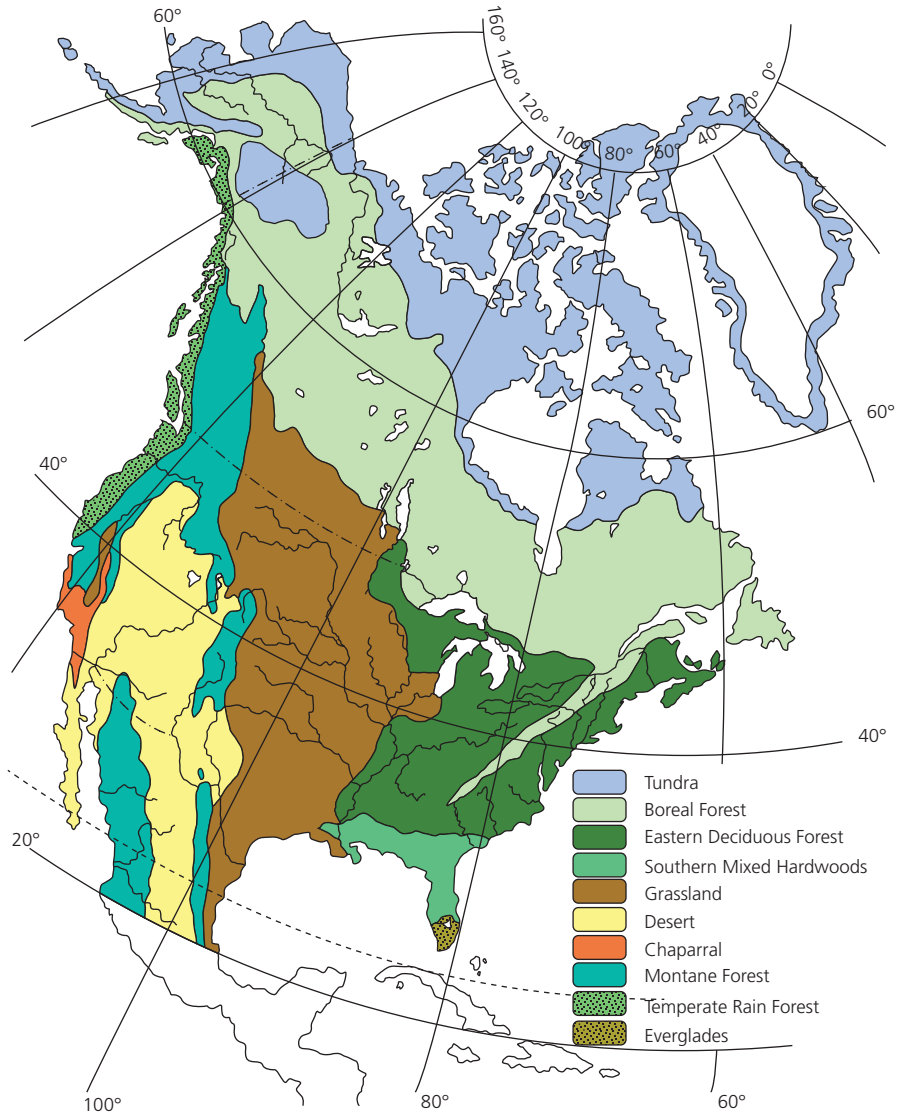


Figure 1.3 The predominately east–west distribution of major biomes in North America is determined largely by precipitation. In contrast, the north–south arrangement of major plant associations in the middle and southern regions of the continent result more from interactions of temperature, evaporation,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

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 regrowth 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.

Climax vegetation, once established, should not be viewed as static. Instead, it experiences a state of dynamic equilibrium, that is, it continually replaces itself. A climax community will maintain its composition so long as the climate remains stable and there are no major disturbances such as fire that return the community to an earlier stage of development. In some places, fire recurs often enough to inhibit the development of a climax community; such a setting is said to be a **subclimax** community.

Succession and species abundance

The number of species in a community increases steadily as succession progresses. Because of their harsh environment, pioneer communities typically contain only a few species but in large numbers. A barren field, for example, receives the full impact of solar radiation during the day creating surface temperatures ill-suited to, or even fatal for, many organisms, but at night the barren field cools rapidly due to a lack of both solar radiation and an insulating blanket of vegetation. The bare soil is also exposed to the full force of wind and rain, often creating unstable conditions (e.g., erosion). Consequently, only a limited number of species are suited to such environments and those few form the pioneer community. Indeed, pioneer communities are sometimes monotypic in their composition.

Physical conditions become less harsh after pioneer vegetation gains a foothold. The herbaceous blanket ameliorates extremes in temperature, reduces runoff, and discourages wind erosion, enabling the soil to hold more moisture. Other plants find suitable conditions and the number of species, including insects, rodents, and other animals, steadily increases during the middle stages of succession.

While it is tempting to conclude that climax communities contain a maximum number of species, the peak is reached slightly before the climax reaches its full development. This relationship results from heightened biological competition, that is, some less-competitive species (e.g., goldenrod) are eliminated when the dominant climax species (e.g., oaks) reach their fullest development. The relative degree of species reduction at climax is somewhat greater in forests and other mesic communities than in communities where the physical conditions are limiting (e.g., Arctic Tundra).

The biome concept

Climax vegetation with similar characteristics develops in broad areas throughout the world. Although the species may vary, the vegetation over a large region exhibits a common appearance and structure (i.e., **physiognomy**) in response to analogous physical environments. Because of their similarities, climax vegetation throughout the world may be grouped into one of several ecological units, each known as a **biome.** Thus, the grasslands in North America (Great Plains), Eurasia (steppes), South America (pampas), and Africa (veld) are united in the Grassland Biome. Similarly, the northern evergreen forests that form a band across North America and Eurasia form the Boreal Forest Biome. Of the ten terrestrial biomes that are generally recognized worldwide, the only other biomes represented in North America include Desert, Temperate Deciduous Forest, Temperate Rain Forest, and Tundra. Despite the primary focus on their respective climax communities, however, each biome is best viewed as a mosaic that includes areas of early and mid-successional communities resulting from various types of disturbances. For example, stands of longleaf pine, although clearly not representative of broad-leafed deciduous trees, represent a significant subclimax community within the Eastern Deciduous Forest.

Animals should of course not be overlooked when considering biomes but, by tradition, biomes are named to reflect their dominant vegetation. In the past, "Spruce–Moose" was proposed to identify the Boreal Forest Biome, thereby including a major animal in the name, but this and similar designations never gained acceptance. Moreover, biomes are named for climax species, which is not the case for moose (as noted in Chapter 3).

Biodiversity

Biodiversity is shorthand for biological diversity and refers to the number of species that naturally occurs in a defined space or ecological unit, taking into account the relative population size of each species. **Species richness** is a similar term, although it does not account for the relative abundance of each species. The ever-growing human population and accompanying consumption of resources place increasing pressure on the world's fauna and flora. As a result, biodiversity is declining. Cities and other developed areas are obvious examples of locations where biodiversity has become severely limited. The destruction of tropical rain forests eliminates large

numbers of species, but many other human activities (e.g., acid rain) also reduce biodiversity in places where concrete, bulldozers, or chainsaws are not in evidence.

The "species richness gradient"

The correlation between number of species and latitude is one of the more intriguing features of biogeography. Alfred Russell Wallace (1823–1913), who discovered **natural selection** independently of Charles Darwin (1809–1882), was among the first to highlight that "animal life is, on the whole, far more abundant and varied within the tropics than in any other part of the globe." This pattern, which applies equally to both plants and animals, begins with the incredible number of species in the tropical rain forests at the equator. North or south of the equator, species richness gradually declines toward the poles, where biotic communities consist of a rather small number of species. In the Northern Hemisphere, a steady reduction in the number of nesting birds is reflected at intervals along a gradient northward from the tropics: Columbia (1400 species); Panama (1100); Guatemala (470); New York (195); Newfoundland (81); and Greenland (56 species). A gradient of similar magnitude occurs in the biota of the Southern Hemisphere, reaching an extreme in Antarctica where terrestrial vertebrates and vascular plants are completely absent.

What might explain this pattern? Some short answers follow, but the debate continues. First, tropical climates are relatively stable year round and offer favorable conditions for life (i.e., warm and humid), whereas seasonal differences become steadily more apparent at higher latitudes. Tropical regions are also relatively free of dramatic disturbances. Conversely, disturbances such as drought and hard winters and, over the long term, glaciations occur with greater frequency in the middle and higher latitudes. Such disturbances hinder the course of diversification. While the influence of abiotic factors is lessened in a stable climate, biotic interactions – especially competition, herbivory, and predation – increase in importance. Under these conditions, tropical regions become a "diversity pump" where resources are partitioned, **speciation** increases, and **extinction** decreases. For example, as predation increases, the number of individuals in a prey population decreases, which enables a greater number of other species to coexist. At higher latitudes, however, the highly variable physical environment limits specialization and results in fewer species.

Time is the second factor to interact with climatic stability. Because diversity is the product of **evolution**, greater diversity results when and where evolution can proceed uninterrupted for long periods of time. Long periods of stability provide areas such as tropical rain forests and coral reefs with adequate time to produce rich biotas. Elsewhere, however, the regions today occupied by Tundra and Boreal Forest biomes only recently (from a geological perspective) emerged from a glacial blanket and have had much less time to evolve a mature biota.

Abundance and availability of food also contributes to species richness along a latitudinal gradient. In tropical regions, for example, plants of one kind or another bear fruit all year round, thereby providing an abundant and consistently available food source for **frugivorous** species. These in turn become the food base for various predators and scavengers. Conversely, fruiting is markedly seasonal in temperate regions, and there are fewer frugivores. Such a relationship is evident when the species diversity of bat fauna is compared by latitude. In temperate areas, bats feed on insects and must either migrate or hibernate when winter limits their food supply; in tropical areas, where both fruit and insects are abundant and available all year round, bats can specialize and more species have evolved. A correlated factor is the increase in primary productivity along a gradient from pole to equator; as solar radiation increases, so does plant production. Consequently, more consumers can exist which encourages competition and other biological interactions (see above). Interestingly, the latitudinal pattern for terrestrial species is reversed for marine mammals, but nonetheless remains based on food abundance. Species diversity of baleen whales and carnivorous pinnipeds (e.g., seals) is greater at higher latitudes where the abundance of their prey is directly or indirectly related to an immense base of planktonic foods.

The pattern in which food or other resources is distributed within a landscape, referred to as patchiness, also seems to be involved. Greater patchiness, typical in the tropics but much less so in the Boreal Forest or Arctic Tundra, may increase diversity by accelerating the development of subspecies and species among isolated populations. Habitat patches promote isolation, and isolation promotes speciation.

To summarize, terrestrial species diversity shows a global pattern of increase from the poles to the equator. In terms of the North American biota, a band stretching from Labrador to Alaska contains far fewer species than a band of the same width stretching from Virginia to California. Various factors contribute to this relationship including environmental stability, biological interactions, solar energy, and patchiness.

Biodiversity "hotspots"

Biodiversity is widely regarded as a global resource, yet extinction rates soar as the march of expanding human populations steadily degrades natural habitats. Some conservationists estimate a species is lost every day while others believe the rate is nearly one per hour. To help stem this destruction, some 25 areas around the world with important but endangered environments – notably those with large numbers of **endemic** species – have been designated as biodiversity hotspots. Each hotspot



Figure 1.4 Madrean pine–oak woodlands, which occur in deep canyons and remote sky-islands in the rugged mountains of northern Mexico and the southwestern United States, represent sites with an amazing diversity of flora and fauna. Usually surrounded by arid habitats, these isolated hotspots – this one in Hell's Canyon in the Davis Mountains, Texas – illustrate an insular type of distribution. Photo courtesy of Brian R. Chapman.

(a) contains vegetation that includes at least 0.5% (or alternately 1500) species of endemic vascular plants; and (b) has already experienced a significant loss of biodiversity.

Two regions in North America meet these criteria: the California Floristic Province, a broad strip lying between the Sierra Nevada Range and the Pacific Coast and extending from southern Oregon to northern Mexico, contains about 3500 species of flowering plants of which approximately 61% are endemic; and the Madrean Pine–Oak Woodland features a series of unique habitats in the rugged mountain ranges and deep canyons in southern Arizona, southwestern Texas, and northern Mexico (Fig. 1.4). Unfortunately, only a small percentage of the land within each of these hotspots is currently protected, but national and international conservation organizations, including The Nature Conservancy and Sierra Club, are actively working to protect additional habitats in both regions.

Patterns of distribution

Organisms are not randomly distributed but instead show more-or-less distinctive distributional patterns. Those with restricted distributions are said to be endemic to the area (e.g., pronghorns are endemic to western North America). Conversely, the patterns for some organisms are more complex and often difficult to explain. Discontinuous distributions, for example, are characterized by the presence of a single species in two or more widely separated areas. The range of wood ducks covers eastern North America, then skips the western plains and Rocky Mountains, but resumes along the northern Pacific coastline (California, Oregon, Washington, and southern British Columbia).

Continental patterns

The discontinuous distribution of some organisms involves even greater distances, which may even span parts of two or more continents. A few of the more common distributional patterns are briefly described below and, although they are traditionally applied to animals, they characterize plant distributions just as well.

Organisms whose distributions occur exclusively in North America are known as **Nearctic** species; prairie dogs and Gila monsters are good examples, as are pronghorns and wild turkeys. For comparison, **Palearctic** species occur in Eurasia. Organisms found only in the Northern hemisphere – Nearctic and Palearctic together – are said to have **Holarctic** distributions.

Holarctic distributions are most obvious in species associated with the boreal forest (e.g., lynx). Physical linkages between segments of boreal forest in North America and Eurasia are virtually absent, however, and thereby preclude movement of organisms between these regions. Lacking contact, these populations have varying degrees of reproductive isolation and progress towards speciation. Thus, Holarctic species are often distinguished by one or more subspecies (e.g., caribou and elk in the Nearctic and their Palearctic counterparts, reindeer and red deer). In other cases, however, closely related species may represent Holarctic distributions (e.g., two species of beaver, one in North America and another in Europe).

Late in the 18th century, Holarctic species contributed to a transoceanic debate between Thomas Jefferson (1743–1826) and French naturalist Georges-Louis Buffon (1707–1788). Buffon, a scientific giant of his century, steadfastly maintained that the biota of North America was a degenerate and smaller counterpart of life in Europe. Jefferson, a champion of scientific rigor and America's equality, responded by measuring specimens

from both continents, which revealed no disparity in size. In order to avoid his data being challenged, the resourceful Jefferson sent Buffon a North American representative of a Holarctic species: the remains of a fully grown bull moose!

Typical **Neotropical** species are endemic to Central and South America (e.g., sloths and anteaters). Sometimes included in this group, however, are species that migrate to the tropical areas of the Western Hemisphere (= New World). For example, several species of migratory birds, among them tanagers and wood warblers, breed in North America and overwinter in the tropical climes of Central and South America. A few Neotropical species have expanded their distribution range by moving into North America (the armadillo is a prime example). Some groups of organisms (e.g., monkeys) occur in tropical zones around the world; these exhibit a pattern known as a pantropical distribution.

The distribution of some species forms a more-or-less circular pattern around the North Pole. These are known as **circumpolar** species, and their ranges lie along the northern zones of North America and Eurasia. The distribution of some circumpolar species also includes the polar icecap itself. Continental land masses are in close proximity in the far north, where pack ice enables the movements and genetic mingling of cold-adapted species across the expanse of Arctic environments. Arctic foxes and polar bears are circumpolar, as are walruses, beluga whales, and several other species of marine mammals. With the exception of marine organisms, species associated with the Arctic Tundra offer some of the best examples of circumpolar distributions. These species include mammals, especially lemmings, and resident birds such as willow ptarmigan and snowy owls. Circumpolar distributions also include the breeding ranges of migrant birds such as ruddy turnstones and lesser golden plovers.

Included among **cosmopolitan** species are organisms whose geographical distributions are essentially worldwide (excluding Antarctica and sometimes Australia in practice). Peregrine falcons and ospreys are each cosmopolitan species and the 11 species of barn owls exemplify a cosmopolitan family (in this case, including representatives in Australia). A grass known as common cane is an example of a cosmopolitan plant.

Geographical and ecological distribution

Plant and animal taxa (Infobox 1.2) have rather well-known geographical distributions that are often shown as shaded areas on maps but, within the confines of the mapped distributional range, a species may occupy only certain habitat types. Pronghorn, sometimes known as pronghorn antelope, is a species whose geographical distribution occurs only in western North America. Within this large area, however, pronghorn are specifically associated with grasslands and desert communities; they are noticeably absent elsewhere in western North America (e.g., forest communities and mountainous terrain). Within the larger context of their geographical distribution, pronghorn have a smaller, habitat-specific ecological distribution. Wild turkeys also occur widely in North America, and one race – the eastern wild turkey – has an ecological distribution associated with eastern deciduous forests.

Some ecological concepts

Niches

In everyday use, a niche is a recess in a church wall where a religious icon rests securely in a place of its own. Such a site-specific relationship mirrors the concept of **niche** as an ecological term. In ecology, a niche represents the role played by an organism in its environment. Some herbivores occupy grazing niches in grasslands; other species fill grazing niches in forests, deserts, or aquatic environments (e.g., sea urchins graze on kelp). It is therefore useful to describe an organism's niche in terms of its habitat as well as its role in that habitat. Accordingly, niches are sometimes defined as the "job and address" of an organism.

Niches can be narrow and highly specialized, as in the case of a plant or animal that survives only in a limited range of conditions. Snail kites, described in Chapter 12, prey only on a single kind of food. Although snail kites may forage over a large area of open wetland, their niche as a wetland predator is actually quite narrow. A single tree may contain several feeding niches, as determined for five species of warblers in the Boreal Forest (Chapter 3). Organisms with narrow niches, that is, niche specialists, often have evolved physical features that "match" their niches (e.g., birds with uniquely shaped bills represent adaptations for obtaining specific foods). Conversely, niches may be wide as is the case for raccoons, opossums, and white-tailed deer, which occur in many types of environments and consume a variety of foods (i.e., they are generalists).

As described more fully in Chapter 9, some organisms can tolerate a broad set of conditions but competition from other organisms limits them to a narrower range. Indoor experiments with potted plants, for example, have demonstrated that some species of plants grow equally well in both saline and non-saline soils. In nature, however, the same plants grow only in saline soils because species of plants with greater competitive abilities but less tolerance for salt exclude them from other locations. In short, niches sometimes must be

Infobox 1.2 Taxonomy and the binomial system

Plants and animals are organized in taxonomic hierarchies. The largest group is a kingdom, of which Animalia and Plantae are foremost in our discussions, with Fungi mentioned less often. Following, in ever-smaller groups, are phylum (for animals) and division (for plants), class, order, family, genus (plural genera), and species. Subspecies may be designated in cases where a species exhibits two or more slight but consistent variations, typically in body size or coloration; such forms occupy separate areas within the overall distribution of the species (e.g., the diminutive Key deer in Florida). Each of these groups – kingdom to subspecies – is known as a taxon (plural taxa). Beginning with phylum, the taxa for white-tailed deer include:

Phylum: Chordata
Class: Mammalia
Order: Artiodactyla
Family: Cervidae
Genus: *Odocoileus*
Species: *Odocoileus virginianus*

For animals, the family taxon always ends in –idae; for plants, -aceae. Other taxa, however, are not readily identified by a consistent suffix. Genus and species names are always italicized. The names are Latin (or latinized, as when Smith appears as *smithii*) as it is a "dead language" and therefore remains unchanging.

This arrangement, known as the binomial system of nomenclature, replaced a confusing hodge-podge of names. Until the mid-18th century, species were described with unwieldy strings of Latin adjectives (which were often altered at will by naturalists of the day). The common wild briar rose, for example, once was designated *Rosa sylvestris alba cum rubore, folio glabro*. Adoption of the binomial system resulted from the work of the Swede, Carolus Linnaeus (1707–1778), published for plants as *Species Plantarum* (in 1753) and for animals as *Systema Naturae* (the 10th edition appeared in 1758). Thanks to Linnaeus, the briar rose became *Rosa canina.*

Soon after publication of his seminal works, the names proposed by Linnaeus gained wide acceptance and, although many were later revised as taxonomic science improved, many others remain unchanged to the present time. Some taxonomists are regarded as "splitters", those who make finer distinctions between taxa, typically "splitting" a genus into more species, hereas "lumpers" consolidate similar species, thereby reducing the number of species within a genus. In any event, Carolus Linnaeus once and for all established the binomial system as the standard format for nomenclature, and he thereby is honored as the Father of Taxonomy.

Linnaeus, trained in medicine, held a professorship at Uppsala, where he expanded the university's botanical gardens. His interest in botany inspired a generation of students, several of whom were commissioned to explore various areas of the world in search of new species. Pehr (Peter) Kalm (1716–1779) was among these and spent three years traveling in America's northeastern colonies. The genus *Kalmia*, created by Linnaeus, recognizes Kalm's contributions to the botany of North America; the taxon includes mountain laurel (*K. latifolia*), today the state flower of both Pennsylvania and Connecticut.

Plants and animals are identified using keys in which one in a series of paired choices, called couplets, is selected to match the distinctive features of the specimen at hand (e.g., leaves with spines versus leaves lacking spines). The progression of choices steadily eliminates other possibilities until only one remains.

Classification, a discipline closely allied with taxonomy, determines relationships among taxa (e.g., uniting closely related species in the same genus or, conversely, assigning a species to another genus). DNA techniques are strong tools used in making these decisions. In sum, classification deals with kinship and taxonomy with nomenclature.

considered in terms of the influences exerted by other species in the community.

On occasion, certain niches may be considered "unoccupied." This is most noticeable on oceanic islands (e.g., Hawaii), where certain types of organisms cannot colonize from mainland areas. Large grazing animals and ground-dwelling predators are among those often missing from the fauna of oceanic islands. Indeed, the only mammals in the original fauna of some islands are bats. Unfortunately, humans often disrupt the biota of ocean islands by introducing cattle, goats, or pigs. This usually leads to the rapid deterioration of the native vegetation, which evolved without incorporating adaptations for suddenly coping with new influences. Similarly, native animals, often birds, are eliminated or vastly reduced in number after predators gain access to oceanic islands under human influences (e.g., rats escaping from ships at dock). Introduced species that fill an unoccupied niche typically exploit the new situation and increase rapidly. Thus the adage "Nature abhors a vacuum."

Ecological equivalents

Not uncommonly, an organism may have a counterpart in another community or biome where it functions in a similar niche. Such pairs of organisms, although not closely related, are known as **ecological equivalents**. Forests, for example, represent the typical habitat for most kinds of woodpeckers, which excavate cavities in tree boles for their nests. The Sonoran Desert lacks trees, but two species of woodpeckers nest there by chiseling cavities in giant saguaro, a cactus that reaches tree-sized proportions (see Chapter 7). At least in terms of woodpecker habitat, these large cacti function as trees in the desert and thereby illustrate the concept of ecological equivalents.

As a further example, the world's major grassland communities each include grazing species. Many of these animals are insects (e.g., grasshoppers), but the grazers usually include at least one large-bodied herbivore. Grazing species of North America include bison, elk, and pronghorn; a much larger number of grazing species exist on Africa's grasslands, however (e.g., gazelles and several other kinds of antelope, as well as zebras). These animals, continent by continent, also represent ecological equivalents. Not all of these are closely related, yet they share some common characteristics typical of large grazing animals: hooves, complex stomachs, good eyesight, and usually horns or antlers. They also run rapidly and move in herds. In Australia, some species of kangaroo occupy grazing niches and, although they lack most physical features typical of large grazing animals, kangaroos are the ecological equivalents of bison and gazelles in grassland ecosystems.

Bergmann's rule

Ecologists discovered long ago that body size increases in the cooler portions and diminishes in the warmer parts of each species' distributional range. This relationship, known as **Bergmann's rule**, applies only to **endothermic** animals. In general, "cooler" and "warmer" conditions equate to the northern and southern latitudes of North America, respectively. Differences in body size are therefore best shown in species with distributions covering large areas of the continent (e.g., white-tailed deer, which are larger-bodied in Maine and Michigan than in Florida or Texas).

Bergmann's rule is usually explained in terms of the ratio of volume to surface area. Larger-bodied animals have less surface area per unit of volume and, when compared to smaller-bodied animals, they lose proportionately less body heat because less of their surface is exposed. In the cooler (= northern) regions of North America, larger-bodied animals gain an advantage over smaller-bodied animals. At lower latitudes, where the climate is warmer (e.g., southern North America), the advantage is reversed and smaller-bodied animals are better matched to ambient temperatures. Natural selection steadily favors animals whose body sizes are best suited to each climatic regime, north to south, resulting in a corresponding gradient of body sizes. However, exceptions do exist. The large body mass of the African elephant may be resistant to a significant increase in core body temperature in the warm climates within its range.

Recall that Bergmann's rule generally concerns endotherms, but some studies indicate that a few species of **ectotherms** may also conform to the rule. The reverse of Bergmann's rule applies to most reptiles and other ectothermic animals, but many large-bodied snakes and



Figure 1.5 Two closely related species of dark geese with white cheek patches evolved from a common ancestor in North America. The larger of these – the Canada goose – subsequently differentiated into seven subspecies, three of which are shown in the bottom row. The smaller species – the cackling goose – evolved into four subspecies, of which one is shown at the top. The larger forms lose less heat relative to body size than smaller forms, and the limits of the winter distribution of the larger geese accordingly lie farther north in comparison to the smaller forms. The winter distribution of these related taxa reflects Bergmann's Rule. Photo courtesy of Victor E. Krantz and the National Museum of Natural History.

lizards that occur in tropical regions maintain a constant, relatively high body temperature because of their greater volume-to-surface ratio. This relationship, sometimes called **gigantothermy** or ectothermic heterothermy, allows leatherback sea turtles to retain the heat generated by muscular activity and exploit highly productive marine feeding habitats in the cold waters of high latitudes or great depths. Animals in Australia and elsewhere conform to Bergmann's rule, but some ecologists do not accept the traditional explanation of heat loss per unit of body size.

Nonetheless, an interesting example of Bergmann's rule occurs in Canada geese, which are represented by numerous subspecies in North America. The plumages of each subspecies show some distinctive features, but differences in body size are far more obvious (Fig. 1.5). Canada geese evolved as migratory birds and, after breeding, they fly south to spend the winter (the season when heat loss exerts its greatest influence on their survival) in warmer environments. Accordingly, body size emerges as a factor determining the northernmost limits of the winter distributions of each subspecies. A large-bodied subspecies winters as far north as Minnesota, but a small subspecies spends winter no farther north than Oklahoma. When heat losses were calculated for these two subspecies, the results indicated that the larger geese lost about 40% less heat per hour per unit body weight than the smaller birds. In other words, the smaller geese would more rapidly expend their energy reserves if they wintered as far north as the larger birds. Because of this potential energetic cost, the smaller geese overwinter where temperatures are milder. In this instance, Bergmann's rule applies to the *winter* distribution of Canada geese rather than to their summertime breeding ranges.

Allen's rule

The extremities of endotherms are relatively shorter in colder regions when compared to those of the same or related species living in warmer areas. For example, the ears of hares and rabbits living in the Arctic and sub-Arctic areas are much shorter than those of jackrabbits living in the warm regions of North America (Fig. 1.6).

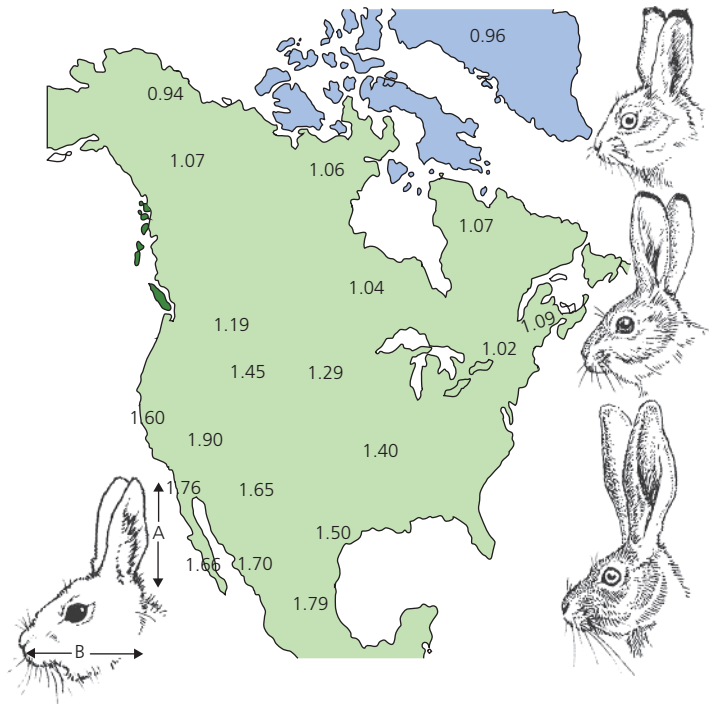


Figure 1.6 An example of Allen's Rule is shown in the ear lengths of rabbits and hares along a north–south temperature gradient across North America. The numbers are ratios determined by dividing ear length (A) by skull length (B), as shown lower left. Rabbits in warm regions have longer ears that readily dissipate excess body heat, whereas shorter ears help conserve body heat in cool areas. Illustrated by Tamara R. Sayre, based on Hesse (1928).

Thermoregulation is the underlying influence for this relationship. In warm areas, rabbits readily dissipate excess body heat from their large ears, whereas shorter ears help conserve body heat where the climate is colder. An anatomical explanation for **Allen's rule** is based on the relative amount of cartilage incorporated into the extremities. The growth rate of cartilage in developing endotherms is partially dependent upon temperature and blood flow. Young mammals raised in warmer regions of their range have more blood flowing to their warmer extremities during development and produce more cartilage, thus increasing the length of the body part. Bill sizes in 214 species of birds also follow the pattern predicted by Allen's rule.

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