Rangeland Ecosystems of the Western US

RANGELAND ECOSYSTEMS OF THE WESTERN US

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Synecology

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Introduction

The author of this textbook, in collaboration with Oregon State University Ecampus, has created a suite of interactive learning tools to foster critical thinking skills for understanding and analyzing the ecological structure and function of shrublands, deserts, and woodland savannas of the western United States. The suite of learning tools includes this textbook, *Rangeland Ecosystems of the Western US*, an interactive ecosystem mapping tool, and a species database. The textbook is written to convey fundamentals of autecology and synecology and general information about the primary ecosystems covered. Its structure will provide a framework that can be applied to understand and analyze any arid shrubland, desert, or woodland savanna. Students are expected to leverage the information conveyed in the textbook to craft ecosystem profiles using the accompanying interactive ecosystem mapping and species database tools.

Autecology

Ecosystem Biogeography

Have you ever wondered why deserts are geographically located in one area and forests or grasslands in another?

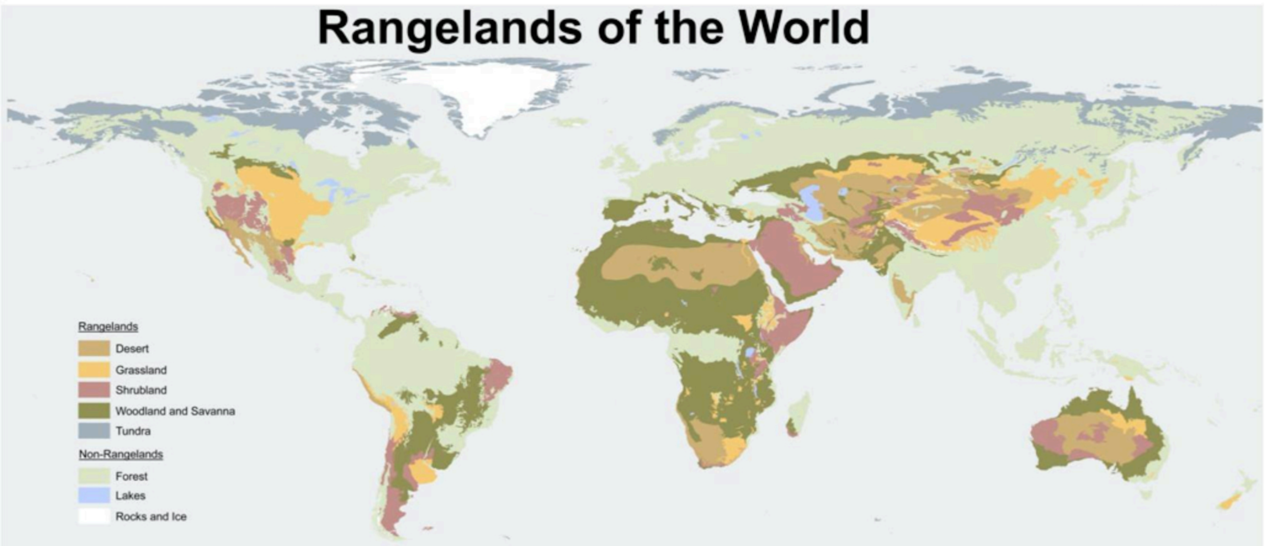


Figure 1.1

Have you noticed that vegetation changes as you drive from a valley up a mountain and over to the other side?

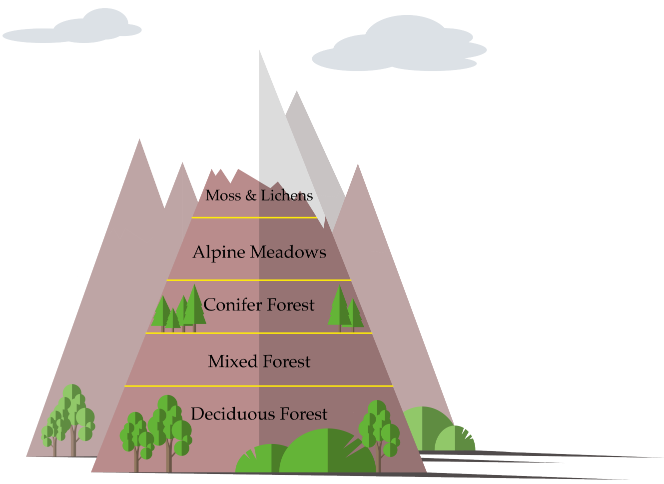


Figure 1.2

To answer these questions we need to develop an understanding of biogeography that is rooted (no pun intended) in four basic factors: solar radiation, climate, water, and soil.

In this chapter, we will look at how each factor influences the geographic distribution of ecosystems and the structure and function of those systems.

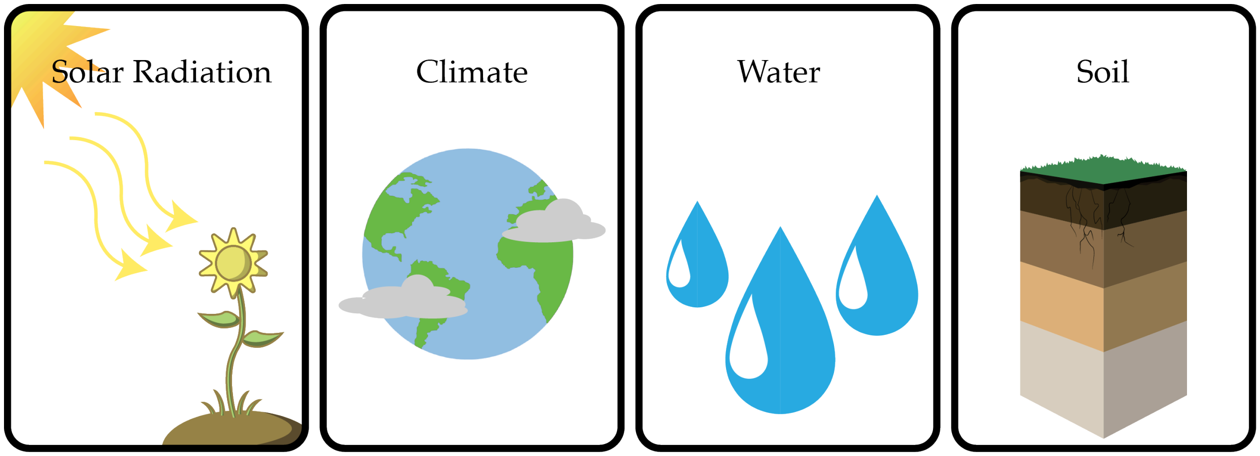


Figure 1.3

Section 1: Solar Radiation

Solar radiation is the energy radiated from the sun that reaches the Earth's atmosphere and surface. In one way or another, solar radiation is the origin of all energy on Earth. It is captured by plants and by a variety of technologies and then converted into forms of energy useful for living organisms. However, solar radiation is not evenly distributed across the Earth's surface: the amount of available energy varies around the globe. This uneven distribution of solar radiation underlies not only the distribution of ecosystems but also the distribution of climate, soil types, species, and land uses.

The distribution of solar radiation across the globe is influenced by a number of factors:

1. Distance from the sun
2. Declination of the sun
3. Latitude
4. Slop
5. Length of day
6. Time of day
7. Atmospheric conditions

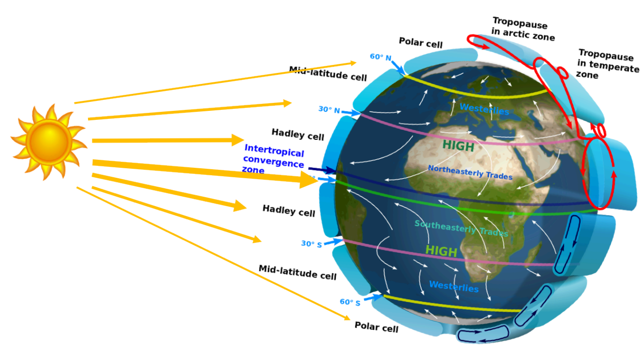


Figure 1.4

Distribution of Solar Radiation: Distance from the Sun and Latitude

The Earth rotates on a tilted axis, and therefore only the equator is at a direct ninety-degree angle to the sun;

the equator thus receives the most solar radiation. Intensity of solar radiation decreases as latitude increases, both north and south, because solar radiation is spread across a greater area.

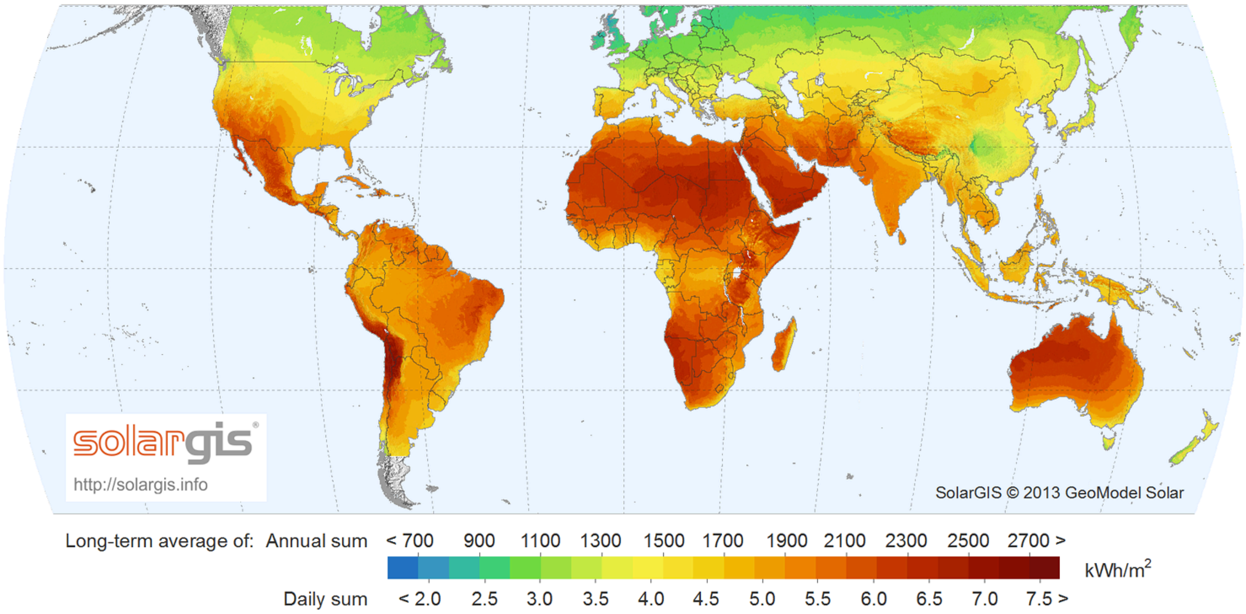


Figure 1.5

The amount of solar radiation reaching the Earth's surface at any given time is called insolation and is measured in Wm^2 (watts per meter-squared).

Distribution of Solar Radiation: Declination of the Sun

The Earth's elliptical orbit around the sun and the declination of the Earth (relative position of the sun with respect to the equator) shifts from 23.45 degrees north to 23.45 degrees south throughout a single year. It is this shift in declination that underlies the variations in climate that we refer to as seasons.

Distribution of Solar Radiation: Slope

What does "north face" mean? Yes, it's a clothing line—one named after the north aspect of a mountain. The north side of any area of elevated topography receives less solar radiation than its other aspects; such areas are therefore colder and tend to have wetter soils with lower densities of soil organisms, less integration of soil organic matter into the soil profile, and more acidity.

Distribution of Solar Radiation: Length and Time of Day

As latitude increases, the length and intensity of the photoperiod (hours of light within the 24-hour period of light and dark) decrease. This variation in photoperiod and intensity is determined by the latitude's distance from the sun and by the declination. Photoperiod influences both the growing season and the duration of daytime photosynthesis.

Distribution of Solar Radiation: Atmosphere

Atmospheric composition, density, and distribution have a substantial effect on the amount and timing of solar radiation reaching the surface of the Earth. The primary gases in the Earth's atmosphere (water, oxygen, carbon dioxide, and ozone) all absorb and reflect solar radiation.

Far red: Elongation of internodes, seed germination, and photoperiod response

Red: Absorbed by chlorophyll for photosynthesis, germination, and photoperiod response

Green: Reflected (it's why plants are green)

Blue: Absorbed by chlorophyll for photosynthesis

Ultraviolet: Damaging

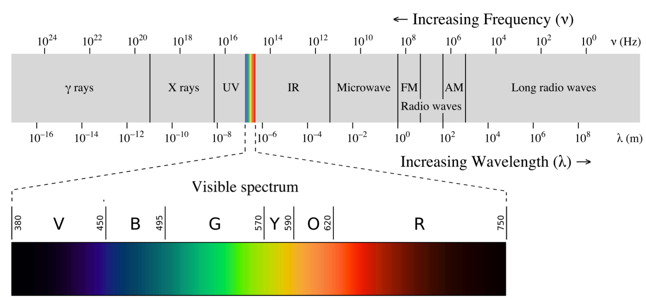


Figure 1.6

Section 2: Climate

In a moment we will connect solar radiation to climate, but before we do that, let's differentiate between weather and climate. Weather is the day-to-day, hour-to-hour state of the atmosphere; it is what meteorologists predict based on atmospheric conditions. Climate consists of patterns of precipitation, temperature, humidity, barometric pressure, and wind over time. For example, a Mediterranean climate is characterized by cool, wet winters and hot, dry summers. Weather is a driving factor in determining the degree of vegetation growth in a given season. Climate is a driving factor in determining biome type.

The primary drivers of climate are solar radiation, the atmosphere surrounding the Earth that holds in or releases solar radiation, and topography. Solar radiation from the sun hitting the Earth's surface and heating it drives wind patterns and the water cycle, which in turn influence the distribution of weather patterns across the globe.

Precipitation

Precipitation is the primary factor determining vegetation production and, concomitantly, ecosystem function and dynamics. For example, the Pacific Northwest has high precipitation and is well known for producing the conifer forests that provide much of the country's pine and cedar lumber. Most arid and semiarid ecosystems covered in this course have low precipitation and some degree of drought. Referring to Whittaker's biome graph, we see that deserts, shrublands, and woodland savannas average annual precipitation of less than 100 cm. Although rain is generally the first form of precipitation to come to mind, snow is a significant form of precipitation in some of these ecosystems.

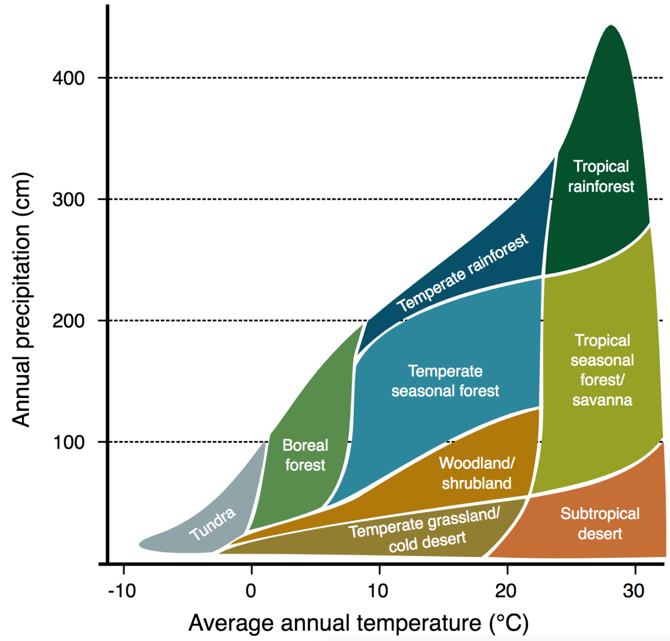


Figure 1.7

Timing and Intensity of Precipitation: Deserts

Hot deserts in the far western United States generally receive winter precipitation from ocean-borne storms driven by global wind patterns that push moisture inland and up against the southern Sierra Nevada. These storms then track east or northeast across the southwestern United States. These precipitation events generally cover a wide area and are of long duration and low intensity. The desert systems can thus absorb and store the precipitation.

Hot desert areas that border Northern Mexico, the Great Plains, and the Gulf of Mexico receive summer rainfall in the form of monsoons driven by intense summer heating of the Earth's surface and concomitant large shifts in atmospheric circulation patterns. Cyclonic thunderstorms of short duration and high intensity form in the Gulf of Mexico and track west and northwest. These storm systems generally result in surface water run-off and soil erosion and are immediately followed by high evapotranspiration rates due to high summer temperatures.

Timing and Intensity of Precipitation: Shrublands and Woodlands

Whereas hot desert precipitation is largely driven by the heating of the Earth's surface and by atmospheric circulation patterns, in northern latitudes precipitation in shrubland and woodland systems is driven by topography, elevation, and geographic location. Further, while desert annual precipitation is primarily in the form of rain, shrubland and woodland systems receive a substantial portion of their annual precipitation in the form of snow.

Other Factors Influencing the Effectiveness of Precipitation

Regardless of the type of system, precipitation infiltration and ground storage are influenced by soil texture, slope, and vegetation cover.

The percentage of sand in soil correlates with its water-holding capacity: the higher the percent of sand, the lower the water-holding capacity. For clay in soil, the higher the percent of clay, the higher the water-holding capacity, to the degree that the ionic bonds in clay soils can limit soil water movement and availability to plants.

The greater the degree of slope, the greater the degree of surface water run-off, although this can be mitigated by the degree of vegetation canopy cover and vegetation basal area and distribution, both of which obstruct surface water flow. Other surface elements, such as gravel and rocks, can perform the same function.

Vegetation canopy intercepts precipitation and channels it to more slowly to the soil surface, increasing infiltration.

Temperature

While deserts, shrublands, and woodland savannas all have low average annual precipitation (below 100 cm), the temperature variance is much greater (below 0°C to over 30°C), as these systems span from approximately 30° north to 45° north. Not only is there variation across these systems, but there can also be substantial diurnal temperature variation, the difference between daily minimum and maximum temperatures. This variation in temperature influences evapotranspiration rates, growing degree-days, and likelihood of frost.

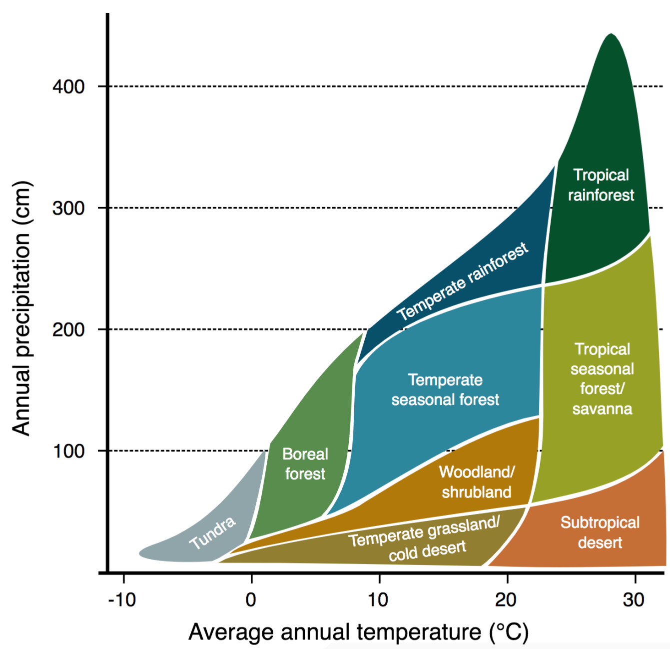


Figure 1.8

Looking across the United States at the average diurnal temperature variance in July (the height of the growing season for most vegetation), we see minimal diurnal temperature variation east of the

Rocky Mountains, but from the Rocky Mountains west, particularly in the intermountain region, we see up to a 45.5°F diurnal variation.

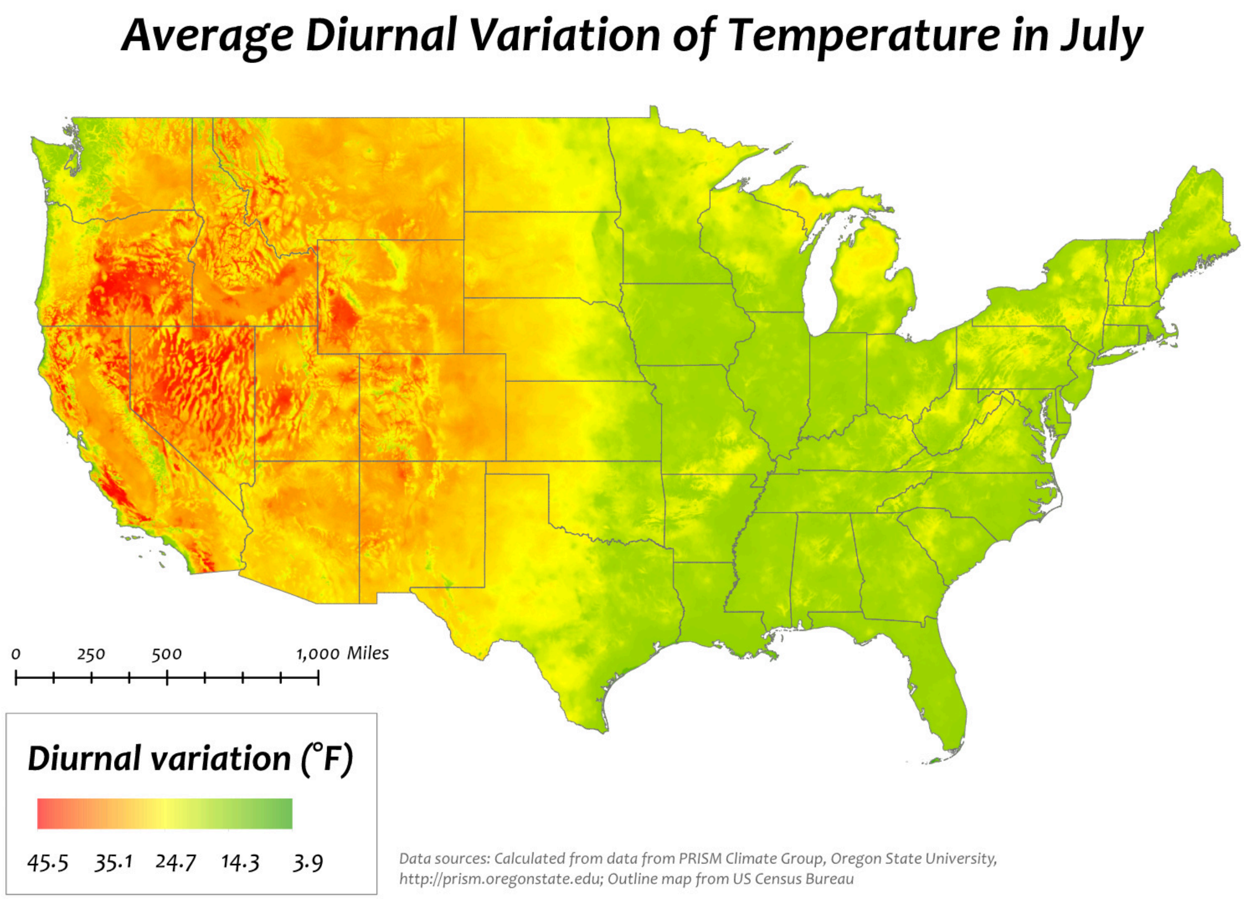


Figure 1.9

Evapotranspiration

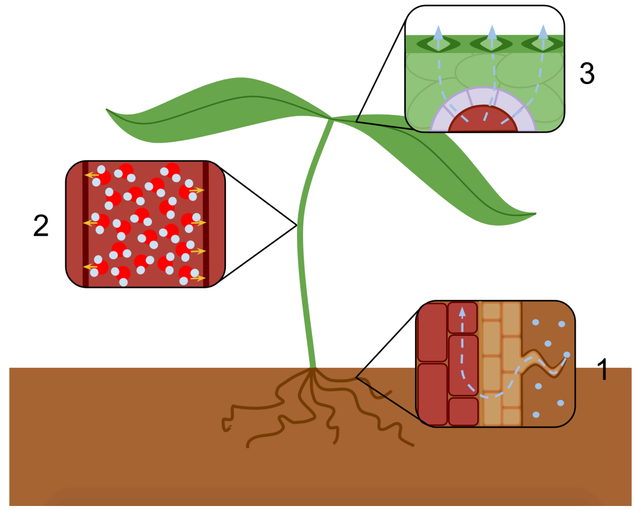


Figure 1.10

Temperature and wind are primary factors that drive evapotranspiration, the loss of surface and ground water to the atmosphere directly from the surface of the Earth (evaporation) and from plant leaves (transpiration). Recall that plants are key components of the water cycle, as adhesion and cohesion move water from the soil through the roots to the xylem and then throughout the plant, and some of that water is lost as vapor to the atmosphere through stomata on leaves. Evapotranspiration greatly influences water storage and availability in deserts, shrubland, and woodland systems. In these arid and semiarid systems, however, many plant species are adapted to mitigate transpiration. (We will discuss some of these species and their adaptations in chapter 2.)

Growing Degree-Days and the Likelihood of Frost

Each plant species has a specific mean minimum temperature required for growth and development. Growing degree-days are the number of days on which the temperature is at or above a mean minimum temperature. In assessing an ecosystem, close attention is paid to when temperatures facilitate plant growth and development, but equal attention is paid in hot desert systems to periods when freezing temperatures persist for more than twenty-four hours, as a high degree of plant mortality can occur.

Drought

Lack of precipitation and high evapotranspiration causes drought, which can be a persistent issue in these arid and semiarid systems. Drought is the condition in which growing season precipitation falls below 75 percent of the normal annual level. The US Drought Monitor watches precipitation levels very closely and generates daily maps of current and predicted drought.

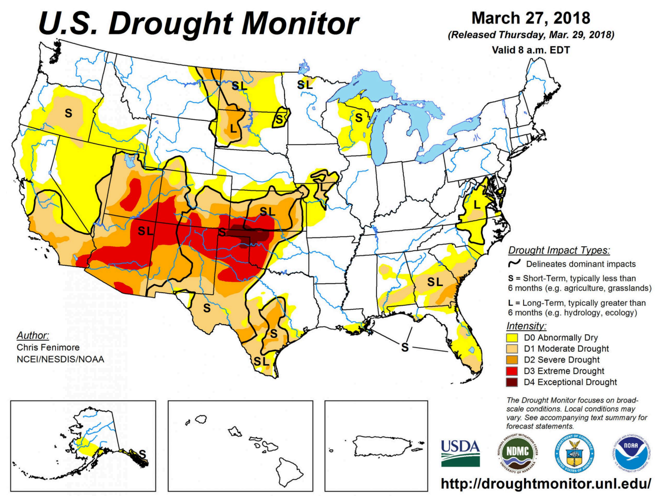


Figure 1.11

Understanding the water balance of a system is another lens through which to view drought. If you think about a bank checking account, it has a balance, deposits, and withdrawals. The aim is to cover all the withdrawals and maintain a balance. If we apply this to water in a system it may look like the graph to the right. This type of climate graph is also known as a Walter Climate Graph.

A number of plants in arid and semiarid systems are what are referred to as "drought tolerant"—they compensate for the shortage of water deposits by adjusting their withdrawals. One such adjustment, the ability to reduce transpiration, or evapotranspiration, was noted above. (We will discuss drought-tolerant species in chapter 2.)

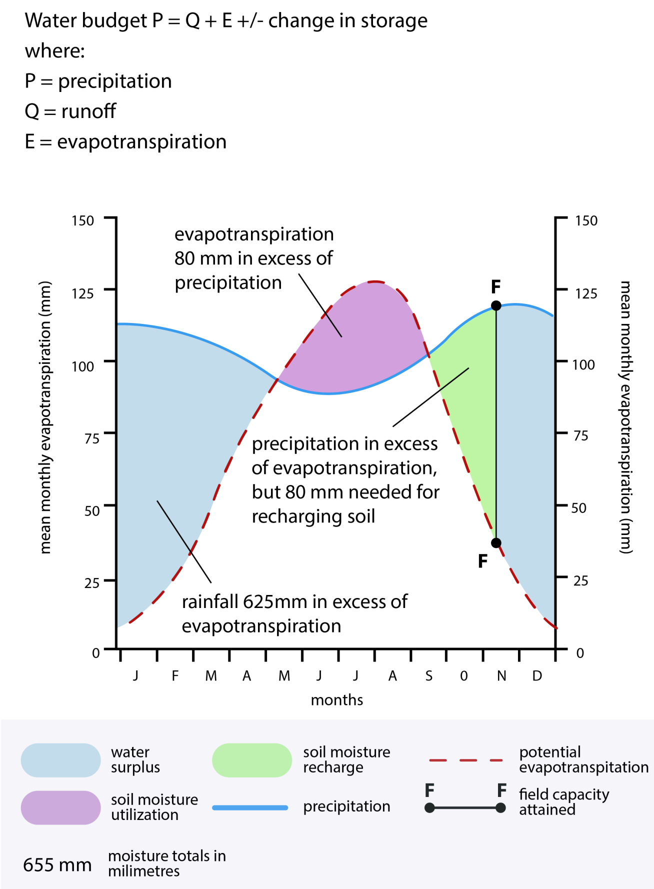


Figure 1.12

Section 3: Topography

Topography influences the two other factors that underlie biogeography: climate and geology. As elevation increases, temperature decreases. As noted in section 2.2.1 above, temperature influences rates of evaporation, growing degree-days, and period of frost, all of which influence the type, species, and abundance of plants in a given area.

Topographic features can also strongly influence the biogeography of the semiarid and arid biomes that are the focus of this text:

1. Orographic effect
2. Basins and playas
3. Alluvial fans and bajadas

Orographic Effect

Looking at a map of precipitation distribution across the United States, we see a narrow strip of high precipitation in the Pacific Northwest while the rest of the western United States has low annual precipitation. This distribution is the result of the orographic effect.

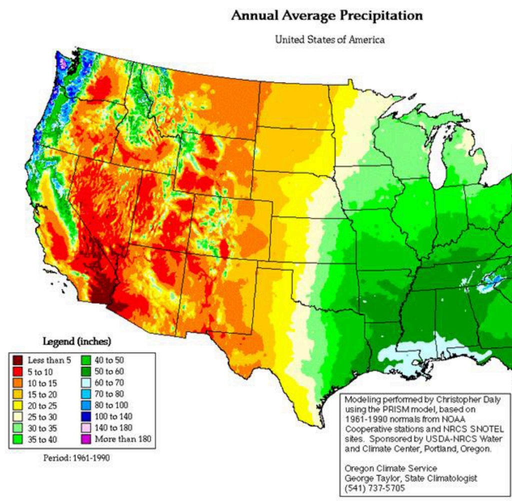


Figure 1.13

The orographic effect describes what happens when warm air masses flow inland off the ocean and come up against a mountain. As the warm air rises, it cools, and moisture condenses into rain; by the time the air mass goes over the mountain, the water it contained is essentially wrung out. On the other side of the mountain—that is, on its leeward side—the air mass is dry, and precipitation is reduced.

Applying the orographic effect to Oregon—water evaporates off the Pacific Ocean. These water-laden air masses move over land, hit the Oregon Coast Range, and rise, leading to rain over the mountains. The Coast Range isn't high enough to "wring out" all the water, however, so the air masses continue to rain over the Willamette Valley. As they move through the valley, the water cycles from the air to the land surface and back to the atmosphere until the masses reach the Cascade Range.

As air masses move up the Cascades, it rains or snows, depending on the season. Because the Cascade Range is much higher in elevation than the Coast Range, much of the moisture is wrung out as the air masses move up the mountains; by the time they have ascended and passed over the mountain, very little moisture remains, and the land east of the Cascades—lying in what is referred to as the "rain shadow"—receives considerably less precipitation than the western side of the mountains.

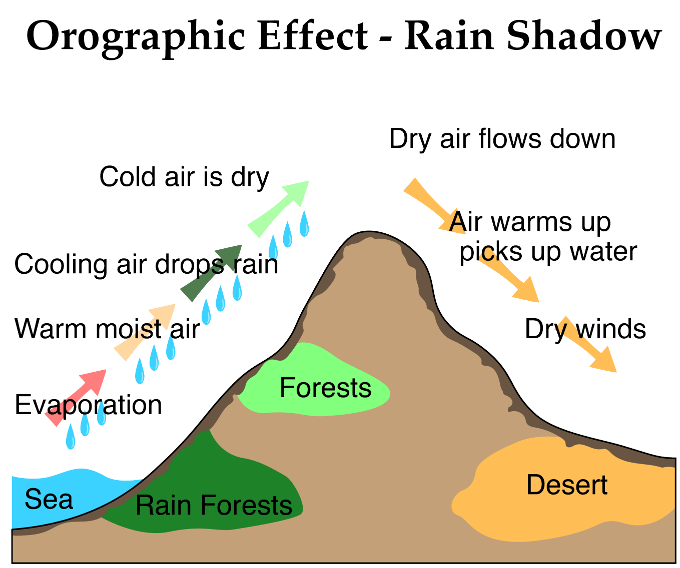


Figure 1.14

Driving up and over the Cascades makes the relationship between vegetation and precipitation clear. The western base of the mountain exhibits a lush growth of grasses, forbs, and hardwood trees. As you begin to traverse up the mountain, hardwoods covered in moss slowly transition to fir trees covered in moss, to just fir trees, to fir and pine trees and shrubs with much less dense grasses and forbs… to just pine trees and shrubs… to shrubs, grass and forb systems around Bend and across central Oregon.

The orographic effect is the primary reason most of the intermountain region of the western United States is semiarid and arid.

Basins and Playas

Large areas of the western United States are basins, lower elevation areas flanked by parallel mountain ranges. The Great Basin is flanked by the Cascade and Sierra Nevada Mountains to the west and the Wasatch Range of the Rocky Mountains to the east. This topographic phenomenon is the product of tectonic movement and expansion. A common feature of basins is playas, ephemeral lakes that are formed in land depressions throughout a basin that collect snowmelt and precipitation run-off from surrounding mountains. When the water in the playas evaporates, it leaves deposits high in salt and calcium. The Saltbush Desert of western Nevada and eastern Utah is a product of playas and geologic history.

Figure 1.15

Alluvial Fans and Bajadas

Common in more arid areas, alluvial fans consist of water-transported sediment that eroded en masse from breaks in a slope and formed a fan-shaped area of deposition in a valley. Areas susceptible to forming alluvial fans are generally denuded of vegetation or have very low vegetation density. The surface layer of soil is usually a very coarse material. A point at which multiple alluvial fans merge is called a bajada. Alluvial fans and bajadas, particularly in upper areas, may have diverse communities of shrubs and grasses, particularly in areas where rills form and channel water.

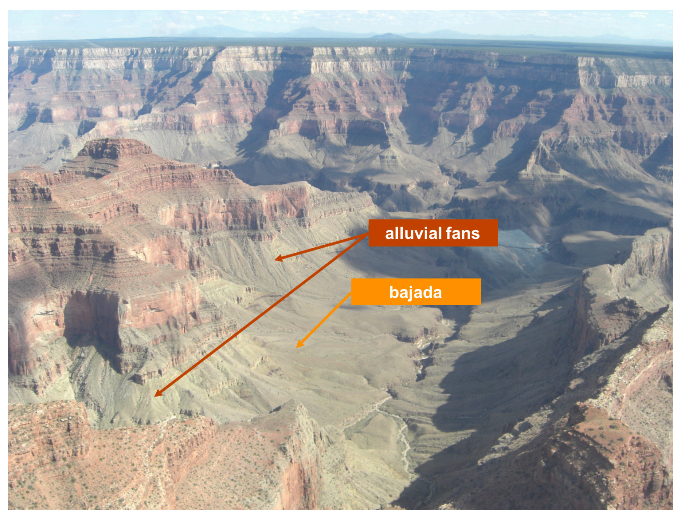


Figure 1.16

Section 4: Soil

While precipitation is the primary determinant of vegetation production, soil is the primary determinant of the type of plant species present in a given area. For example, most desert soils are Aridisols or Entisols that are low in organic matter and high in mineral content and support plants adapted to drought, salinity, or high levels of calcium carbonate. The influence of soil is determined by the following:

1. Parent material
2. Soil organic matter (SOM)
3. Texture and structure
4. Salinity and pH
5. Physical and biological crusts

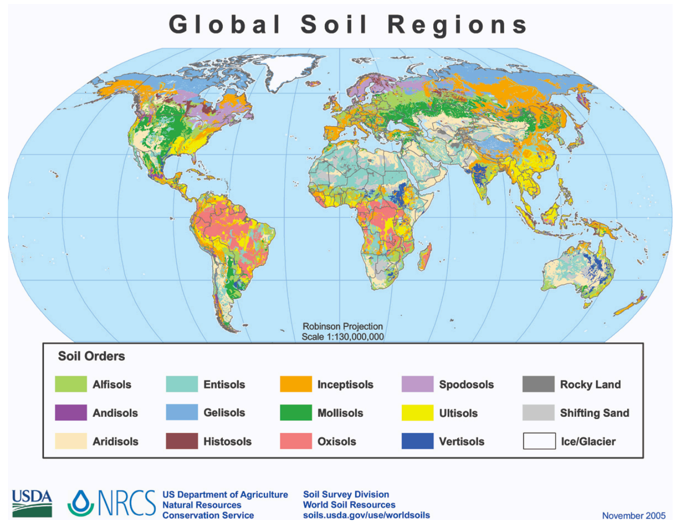


Figure 1.17

Parent Material

Recall primary succession and the soil formation process. Parent material (sedimentary, igneous, and metamorphic rock) weathered over extended periods of geologic time; then, as plant communities developed and succession continued, soil horizons formed as organic matter mixed with parent material. In many systems with relatively shallow "B" and "C" horizons, bedrock (i.e., parent material) is still a substantial influence on soil characteristics.

Organic Matter (SOM) Parent Material

The fertility of a system is reflected in the amount of soil organic matter (SOM) it contains, a mixture of decomposing roots, microbial residue, plants, and animals that is rich in carbon and varying concentrations of nutrients. The amount of SOM influences the degree of nutrient cycling and carbon sequestration, soil structure and plant rooting, water infiltration and holding capacity, and available habitat for microbes.

SOM comprises light and heavy fraction components. Light fraction is recently dead material in the early stages of decomposition; it provides nutrients for plants and food for soil microbes. Heavy fraction has two types—physically protected and chemically stable—both of which contribute to soil structure and stability, water-holding capacity, and nutrient sequestration.

The amount and rate of SOM in a system depend on the amount of productivity, which in turn depends on rain and temperature. Hot deserts therefore generally have very little organic matter, while shrublands and woodland savannas have varying levels of organic matter, ranging from little in sandy saltbush desert to moderate in the sagebrush steppe and woodland areas of the Colorado plateau and California.

Texture and Structure

Soil texture is determined by the percentage of sand, silt, and clay in the soil composition. Sand particles are composed of silica and are generally large. Soil that is predominantly sand has large pore sizes and thus does not hold water or nutrients. Because silt particles are smaller than sand particles, silt has a much higher water-holding capacity (WHC) than sand. Silt particles are composed of minerals that weather quickly and release nutrients. Clay particles, the smallest of the three, have a great capacity to absorb and hold water in the soil profile, making much of that water unavailable to plants. Most soil combines two or all three types of soil particles and therefore has varying WHC and nutrient availability.

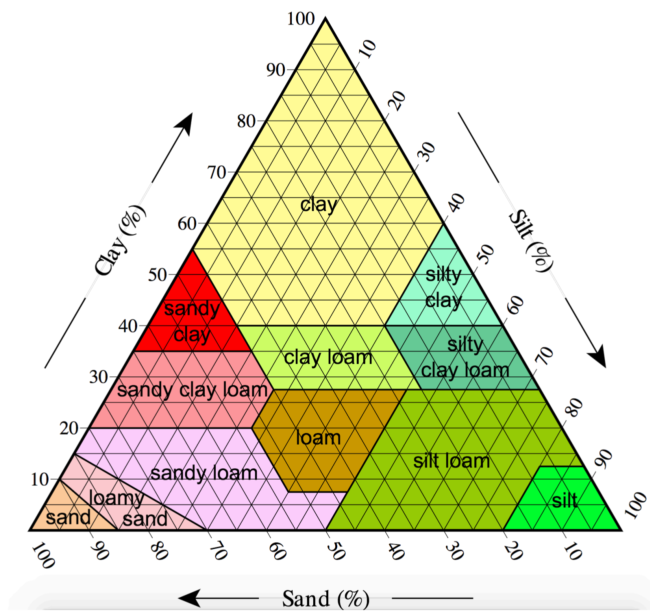


Figure 1.18

The term soil aggregate refers to the arrangement of soil particle units. Units have one of four shapes: spheroidal, platy, prism-like, and blocklike. Aggregate stability refers to the ability of an aggregate to resist degradation. Aggregate stability is determined by the soil texture and the amount of SOM present in the aggregate. The stability of aggregates may differ when wet or dry, and aggregates are susceptible to degradation by wind, water, and other physical disturbances, such as pressure from human activities. Aggregate stability is a key to erosion resistance, water infiltration, nutrient availability, and ease of root growth.

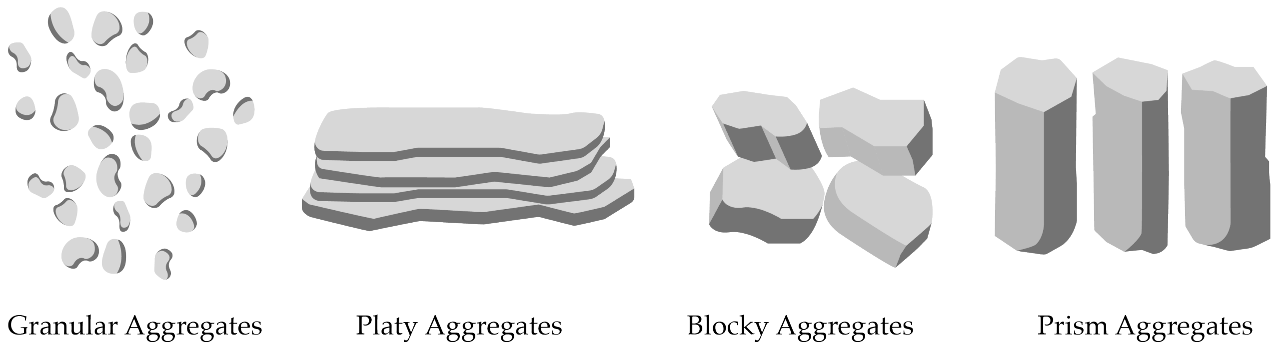


Figure 1.19

In systems such as sandy deserts where the small, spheroidal aggregates break apart easily, the risk of soil erosion is high. Systems with platy aggregates also have a high risk of edge erosion. Systems with prism-like or blocky aggregates, however, have reduced risk of soil erosion.

Soil Crusts

Arid and semiarid ecosystems often develop physical, biological, or chemical crusts. A physical crust is a thin, nonliving layer of mostly mineral content with low porosity. These crusts have low aggregate stability and are generally the result of a high degree of aridity and soils subject to erosion. Physical crusts limit water infiltration, thus reducing the water available to plants and impeding seedling emergence.

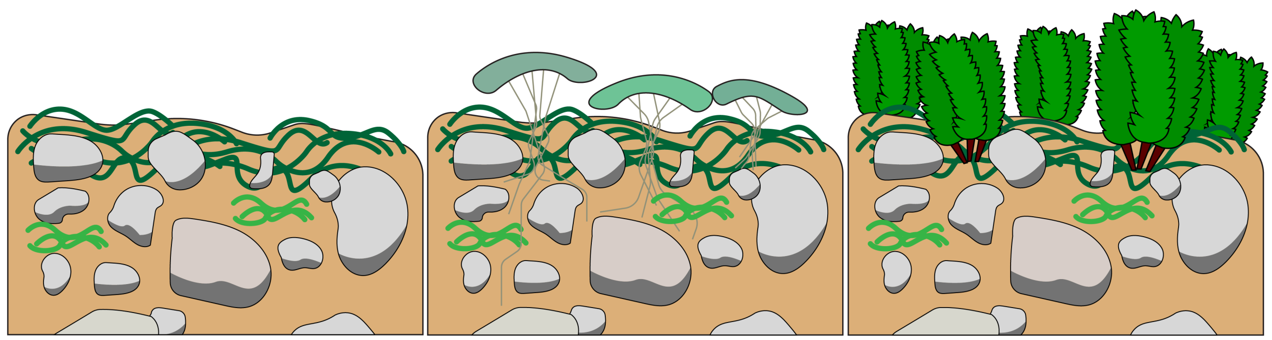


Figure 1.20

Biological crusts are living crusts comprised of interwoven communities of cyanobacteria, lichens, and moss. These crusts facilitate water infiltration, nutrient cycling, and soil-surface stability. Biological crusts generally form in arid ecosystems, or in systems spanning the border between arid and semiarid conditions, where soils are calcareous (possessing high concentrations of calcium carbonate) or gypsiferous (with high gypsum concentrations), as both these types of soils tend to limit plant growth.

The composition of organisms that form the biological crust is influenced by climate, soil texture, and disturbance history.

Chemical crusts are thin layers of salt residue left after evaporation. This type of crust is found in the Great Salt Desert in the western United States. Conditions are very arid, and the soils are highly saline.

Figure 1.21

Conclusion

Biogeography is the study of the geographic distribution of life on Earth. It provides a framework for understanding why certain species occupy specific geographic ranges. The biogeographic framework encompasses climate (solar radiation, air and water circulation patterns, precipitation, temperature) and geology (soils, landforms, and topography). In the next few chapters, we will add an understanding of autecology and synecology to understand the biological and ecological structure and function of deserts, shrublands, and woodlands.

Species Biology

Species biology is reflected in the species' life strategies: how it allocates energy and materials to compete for survival and reproduction. Life strategies evolve via natural selection and reflect the trade-offs among growth, survival, and reproduction. A species' life strategies are a sum of its morphology; physiology; environmental responses; resource requirements; energy acquisition, storage, and allocation; reproduction strategy; and life cycle. In this textbook, we focus on the specific aspects of species biology that relate to the environmental stresses of aridity and heat.

Section 1: Plants

Photosynthesis

Photosynthesis is the foundational process of the food chain. Through photosynthesis, plants are powered by solar radiation to convert water and carbon dioxide (CO_2) into carbohydrates that provide energy for the plant and for organisms throughout the food chain. This textbook assumes you are familiar with the general process of photosynthesis, so we will focus here on the three photosynthetic pathways—C3, C4, and CAM—and how they relate to plant species' ability to survive and thrive in arid environments.

C3 Plants

The photosynthetic product of C3 plants is a 3-carbonic acid (hence the name). C3 plants have a one-step carbon fixation process in which rubisco fixes CO_2 directly in chloroplasts. Although with adequate moisture and high concentrations of CO_2 these plants can maximize growth efficiency, the C3 pathway can be inhibited by oxygen, which reduces efficiency.

C3 plants are referred to as cool-season plants because the optimum ambient and soil temperature range for function and growth is 65–75°F and 40–45°F, respectively. As the ambient temperature increases beyond the optimum range, the plant becomes less efficient. The annual growth cycle of C3 plants, therefore, is generally most efficient in fall and spring, and C3 plants experience reduced production capacity in warm, dry climates.

C4 Plants

The photosynthetic product of C4 plants is a 4-carbonic acid, giving it its name. C4 plants have the advantage of flexibility within the photosynthetic process. Depending on the oxygen and carbon dioxide concentration in the palisade mesophyll, C4 plants can perform either the one-step photosynthetic process of C3 plants or a two-step photosynthetic process that is not inhibited by oxygen. The two-step photosynthetic process is not as energy efficient, however, as it requires a molecule of ATP. The video linked here from BOGO Biology explains clearly the differences in photosynthetic pathways.

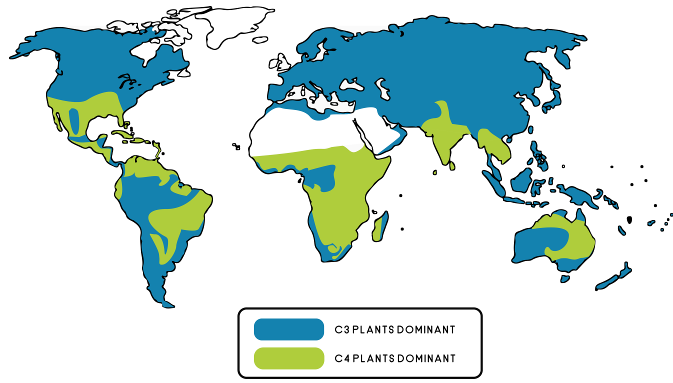


Figure 2.1

C4 plants are referred to as warm-season plants because their optimum ambient and soil temperature range for function and growth is 90–95°F and 60–65°F, respectively. These plants are generally affected by ambient temperature increases beyond their optimum range, and they require less water for biomass production; C4 plants' geographic distribution is thus generally within the lower latitudes that encompass tropical and desert areas.

CAM Plants

CAM (crassulacean acid metabolism) is a diurnal photosynthetic process adapted to conserve water in hot and arid environments where evapotranspiration is high. During the nighttime process, the stomata open and CO_2 can enter the plant. Since there is no solar radiation during this nighttime process, however, CAM plants begin the photosynthetic process just like C4 plants do, using PEP (phosphoenolpyruvate) and CO_2 to produce malate. Then, during the daytime process when solar radiation is available and the stomata are closed, the photosynthetic process continues very much as it does in the bundle sheaths of C4 plants.

Plant Adaptations to Drought and Heat

Plants in arid environments have mechanisms to avoid, tolerate, or resist the environmental stress (low precipitation, high temperatures, heavy winds, and high salinity) of arid and semiarid environments.

Avoidance

A basic avoidance strategy for some plants, particularly annuals, is to simply not grow until there is sufficient water (~25 mm of rainfall) available for growth and reproduction. These plant species are generally small and shallow-rooted. These types of species require not only precipitation but also specific thresholds of temperatures (25–30°C for summer annuals; 15–18°C for winter annuals) coincide with the precipitation. When these plants do germinate and grow, they generally have large leaves for maximum photosynthesis so growth and reproduction can take place quickly over a short period of time.

Tolerance

Plants that are tolerant of heat and drought evade or endure ill effects by leveraging one or more strategies: (1) they demonstrate leaf polymorphism or leaf features that reduce transpiration and photosynthesis; (2) they use stem photosynthesis; and/or (3) they are phreatophytes.

Figure 2.2

Leaf polymorphism allows a plant to develop a set of large leaves to maximize photosynthesis in early spring but then to drop those leaves and develop a second, smaller set at the onset of the dry period. Brittlebush (*Encelia farinosa*) is an example of a plant that leverages leaf polymorphism. Some plants, such as creosote bush (*Larrea tridentata*), not only use leaf polymorphism but also develop a resin that helps reduce transpiration and photosynthesis. Other plants, such as bursage (*Ambrosia dumosa*), employ leaf polymorphism and pubescence (small hairs) to reduce photosynthetic rates, transpiration rates, and surface heating.

Stem photosynthesis greatly reduces transpiration rates because the stem is vertical rather than horizontal like leaves, and so it receives less surface heat. In addition, stems generally have thicker epidermis and/or waxy coatings. In conditions of high aridity and water stress, these plants are able to both maintain photosynthesis and conserve water. Some plants, such as white burrobrush (*Hymenoclea salsola*), trade off leaf photosynthesis for stem photosynthesis when under water stress, while other plants, such as Mormon tea (*Ephedra viridis*), are leafless and rely solely on stem photosynthesis.

Phreatophytes, which include plants such as mesquite (*Prosopis glandulosa*), have root systems that can reach the water table several meters down. They may also have lateral surface root systems that can take advantage of water from passing precipitation events before it infiltrates what are usually sandy-clayey soils.

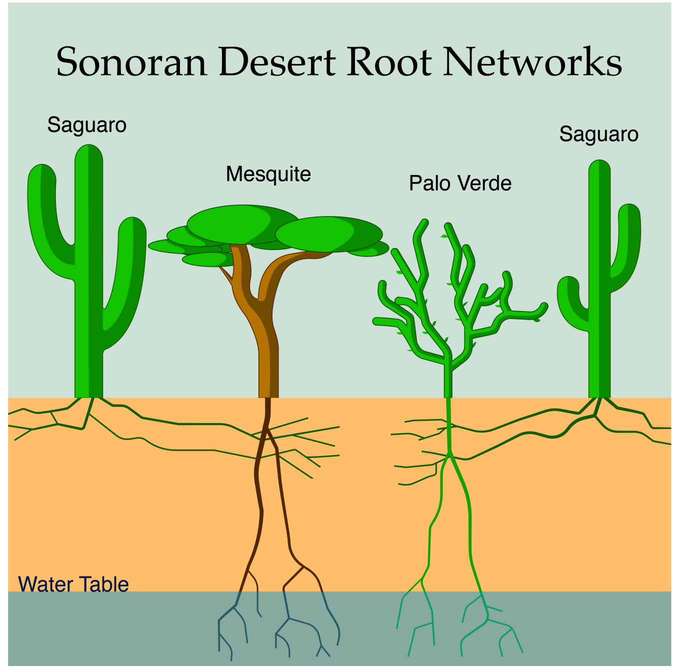


Figure 2.3

Resistance

Succulents have evolved to resist and thrive in aridity and drought. Like some phreatophytes, succulents are shallow rooted to take advantage of precipitation events. Waxy coatings on their thick, fleshy leaves or stems help reduce transpiration, allowing the plants to withstand high temperatures that would wilt nonsucculents.

Many succulent species are also CAM plants, which close stomata during daylight hours when temperatures are highest to reduce water loss and conserve energy. The trade-off for succulents' ability to resist and thrive in aridity and drought is reduced photosynthesis and concomitantly reduced growth rates.

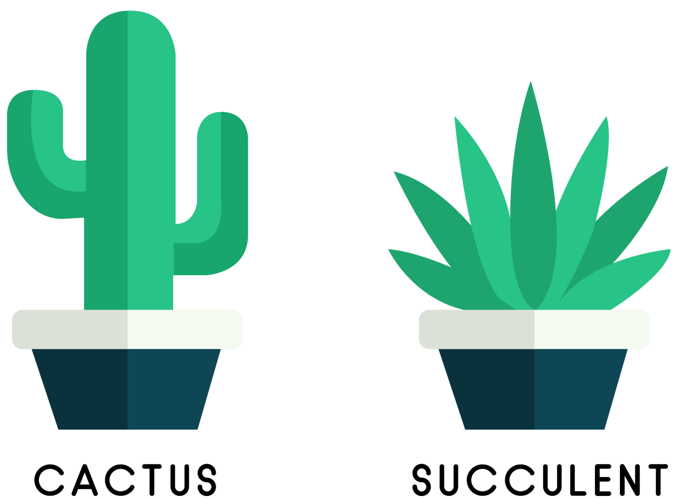


Figure 2.4

Cacti are a category of succulent with additional adaptations to heat and aridity—spines rather than leaves. Compared to most plants' flat, broad leaves, spines have a considerably higher surface-to-volume ratio and hence dissipate heat at a much faster and higher rate. Spines also shade areas below them, reducing the plant's heat stress.

Seeds in Wildland

Figure 2.5

Before plants can employ survival strategies, their seeds must be available in a seedbed appropriate for germination. As a protein-packed food source, many seeds are lost to small mammal predation. Wind can drive seeds across open spaces until they accumulate in areas where they are protected from further wind dispersal, such as at the base of a larger plant. These factors, which can either reduce species densities or foster development of cluster plant communities, are part of the reason plant species are not more uniformly distributed across a landscape.

Soil Biotic Crusts

Figure 2.6

In many arid and semiarid areas, soil biotic crusts form clusters of bacterial, algae, moss, and lichen growth in the top few millimeters of soil. These crusts thrive under the stresses of arid and semiarid climates as they are generally resistant to heat, require low amounts of water, and have the capacity to fixate their own nitrogen. Soil biotic crusts serve many functions, including soil stability and erosion mitigation, facilitation of water infiltration and nitrogen fixation, and provision of nutrients and safe sites for seed germination. Have you ever been hiking in the Southwest and seen signs reading, “Stay on the Trail”? These signs usually indicate an effort to protect soil biotic crusts, which are highly vulnerable to disturbance and slow to recover.

Section 2: Animals

Behavioral Adaptations to Drought and Heat

Figure 2.7

The primary strategy used by birds and mammals living in dry, hot environments is simply avoidance. Many animals in arid and semiarid environments are nocturnal (active only at night), such as the javelina (*Tayassu tajacu*), or crepuscular (active only at dawn and dusk), such as the coyote (*Canis latrans*). During the heat of the day, many species seek the cooler microclimates of burrows, crevices between rocks, north-facing areas, or plant shadows. Larger mammals have the advantage of thermal inertia (a larger body size takes longer to heat up); however, at midday, they too take shelter in cooler microclimates. Some species, such as the desert woodrat (*Neotoma lepida*), aptly called the "pack rat," create their own elaborate tunneled microclimate by building a den from plant litter.

Morphological and Physiological Adaptations to Drought and Heat

In addition to avoidance, some species have morphological and physiological adaptations to aridity and drought. These adaptations fall into three categories: heat dissipation; evaporative cooling; and alternate water acquisition.

Heat Dissipation

Likely the most commonly known adaptation to heat is seasonal shedding of fur or hair to reduce insulation and allow the body to dissipate heat more readily. Species such as the jackrabbit (*Lepus californicus*) have long, tall ears containing dilating blood vessels that facilitate the dissipation of body heat into the air.

Figure 2.8

Evaporative Cooling

Water evaporating from the surface of an animal has a cooling effect—that's why dogs pant. As saliva in the mouth evaporates, it cools the surfaces of the mouth and throat and the blood vessels just below these surfaces, circulating cooled blood throughout the body. Evaporative cooling in the nasal passages works in a similar way, providing cooling to the brain. Vultures (*Cathartes aura*) take evaporative cooling to another level by urinating on their leg. The urine evaporates into the air, drawing heat from the bird's body along with it.

Alternate Water Acquisition

Water is vital for life. In arid and semiarid environments, species need a physiological system to balance internal water availability and water use, particularly when faced with limited free water. Species may obtain water through the food they eat. Pronghorn (*Antilocapra Americana*) are well known for obtaining nutrients and water from cholla fruits. Pronghorn, like other large mammals, correlate their ranges to free water sources, while some species, such as the kangaroo rat (*Dipodomys deserti*), employ multiple methods to obtain and use water efficiently. Kangaroo rats obtain oxidized water from metabolized seeds, particularly those stored in high-humidity burrows; they also produce concentrated urea and very dry feces, both of which allow the animal to retain more water in the body.

Conclusion

Species biology reflects a species' life strategies—the niche they occupy and how they survive and thrive. Plants and animals in the arid and semiarid environments of deserts, shrublands, and woodland savannas have an array of adaptations that allow them to avoid, tolerate, or resist heat and drought. The next chapter will further our understanding of species in relation to their environment by developing an understanding of the growth and distribution of populations of species.

Population Ecology

Population ecology provides scientists and managers with information on populations of species that can indicate that population's sustainability over time and the degree to which the species utilizes the available habitat.

Section 1: Demography

A population is the total of the individuals of a given species living in a given area. Examples are the population of sage grouse in one hundred acres of sagebrush steppe or all the individuals of the Gunnison sage grouse throughout the western United States. The study of how a population of a given species changes over time is referred to as demography. Changes studied can include population size, population density, species distribution, sex ratios, births, deaths, or any characteristic that describes the entire population under study or management.

Population Size and Density

Population size is the number of individuals of a species in a given area. Population density is the number of individuals per unit area. For plant species and many animal species, these numbers are estimates obtained using sampling methods. For example, if we want to know the *population density* of big basin sagebrush (*Artemisia tridentata*) we might lay out a quadrat (an area of a given size, such as a meter or an acre) and count all the individuals of the species within that quadrat. This sampling method is conducted randomly throughout the study area, then statistics are used to estimate the population. If we want to know the population size of pronghorn, we might use visual observation counts from random sites or from the same site over a period of time (days to weeks) and then use statistical analysis to estimate the *population size*. Another common method in wildlife population counts is mark and recapture.

Population and density size tell us several things about the species and the ecosystem such as the following:

1. *The population's degree of stability.* Larger populations tend to be more stable as they can absorb a certain threshold of increase or decrease in population size. Larger populations also have a greater degree of phenotypic plasticity and a greater ability to adapt to environmental shifts.
2. *Habitat availability in some instances can be <u>one</u> indicator of the ecosystem function and structure in a*

given area.

3. *Population size is directly dependent on the carrying capacity of a given area.*
4. Among wildlife and with livestock, population size informs *dietary overlap.*
5. In general, humans are most interested in species' population size *in relation to humans or human activity*, such as conservation efforts, hunting, endangered species survival, and so on.

Species Distribution

Species distribution is how individuals of a population are distributed across a given area and reflects species dispersal methods and population interactions. There are three general distribution types:

Figure 3.1

In uniform distribution, individuals are spaced uniformly across a given area. It is fairly easy to recognize a population of creosote bushes (*Larrea tridentata*) from a distance, as shown in figure 3.1, for example, because of their allelopathic effect (fibrous roots just below the soil surface spread out and release a toxin that inhibits the growth of other plants).

Individuals in random distribution are spaced across a given area without any predictable pattern, as shown in figure 3.2. The least frequently seen type of distribution, random distribution is not much influenced by ecosystem dynamics. Typical species with this type of distribution are plant species with wind-driven seed dispersal, such as a dandelion.

Figure 3.2

Figure 3.3

In clustered distribution, the most common distribution type, individuals clump in groups across a given area, as shown in figure 3.3. Clustered distribution is driven by species biology and ecosystem dynamics. Plants, such as aspen trees, that reproduce vegetatively expand outward from the cluster. Herd animals, such as pronghorn, are distributed in clusters in the proximity of available habitat. Pack animals, such as wolves, distribute in clusters in defined territories with the carrying capacity to support their density.

Species Birth and Death Rates, Age-Sex Structure, and Survivorship Curves

Life tables, age-sex structures, and survivorship curves can indicate the likelihood of whether a population will grow or contract in the near future.

Life tables are comprised of birth and death data. These tables convey reproduction rates and death rates, as well as age of death, thus indicating the age at which individuals of a species are at highest risk of death. This information can guide conservation planning and underlies survivorship curves.

Survivorship curves, tied to life tables, use three types of curves to represent a population's general duration of life and age of mortality. Knowing the survivorship curve of a species can contribute to predicting its population growth.

Age-sex structure graphs, as shown in figure 3.5, represent age and sex distribution across a population, which indicates a population's potential to grow or shrink. Age-sex structure combined with life tables can predict the rate at which a population may grow or contract in the future.

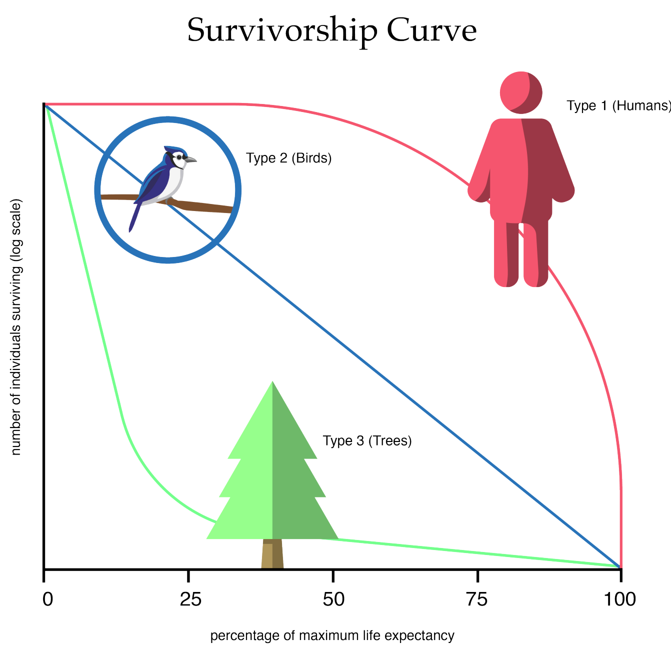


Figure 3.4

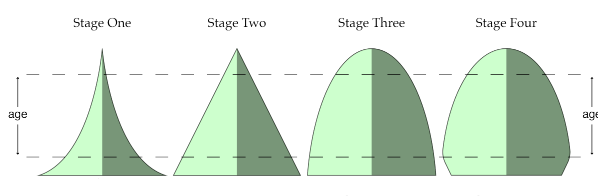


Figure 3.5

Section 2: Population Growth and Control

In the previous section, we noted that populations grow and contract and that monitoring growth and contractions can guide management efforts. Managing populations, however, requires understanding the multitude of factors underlying population growth and contraction. The many factors that can influence fluctuations in population size and density are generally divided into two categories: density dependent and density independent.

Density Dependence

If resources are unlimited, populations will grow at an unlimited geometric rate (if reproduction is periodic, with the population going through the reproduction cycle annually; deer are an example) or at an unlimited exponential rate (if reproduction is continuous, with individuals in a population reproducing at any time; rabbits, for example). In reality, resources are not unlimited, and at some point carrying capacity (the maximum number of individuals a system's resources can support) is reached, and population growth slows or declines. When carrying capacity is reached, sustained birth and death rates must be balanced to limit population growth unless more resources become available either through migration of individuals out of the population or through expansion of the population habitat. Thus density dependence indicates regulation of population size based on population size related to carrying capacity.

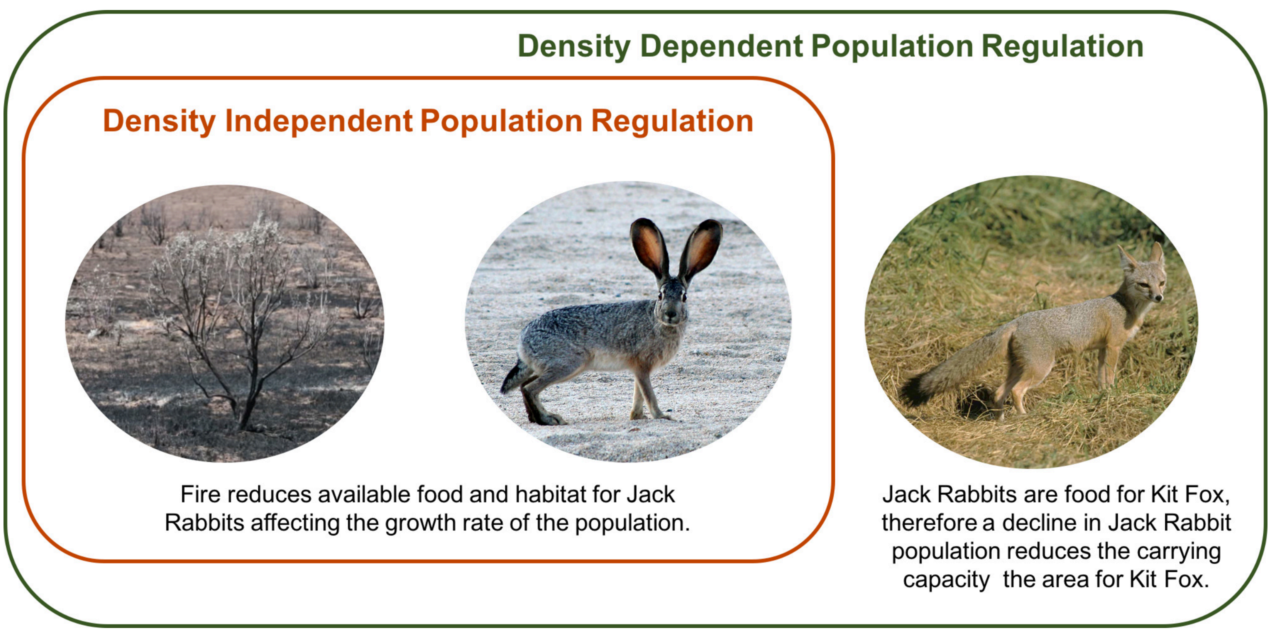


Figure 3.6

Density Independence

Density-independent population regulation may be driven by environmental factors, such as drought or wildfire, or by community dynamics, such as predation or allelopathy.

Factors favoring density dependence and density independence can interplay, resulting in fluctuations in population growth and contraction.

Section 3: Influences on Population Dynamics and Distribution

A multitude of abiotic, biotic, and disturbance factors can influence population dynamics, and this section examines a few of the dominant and most concerning ones.

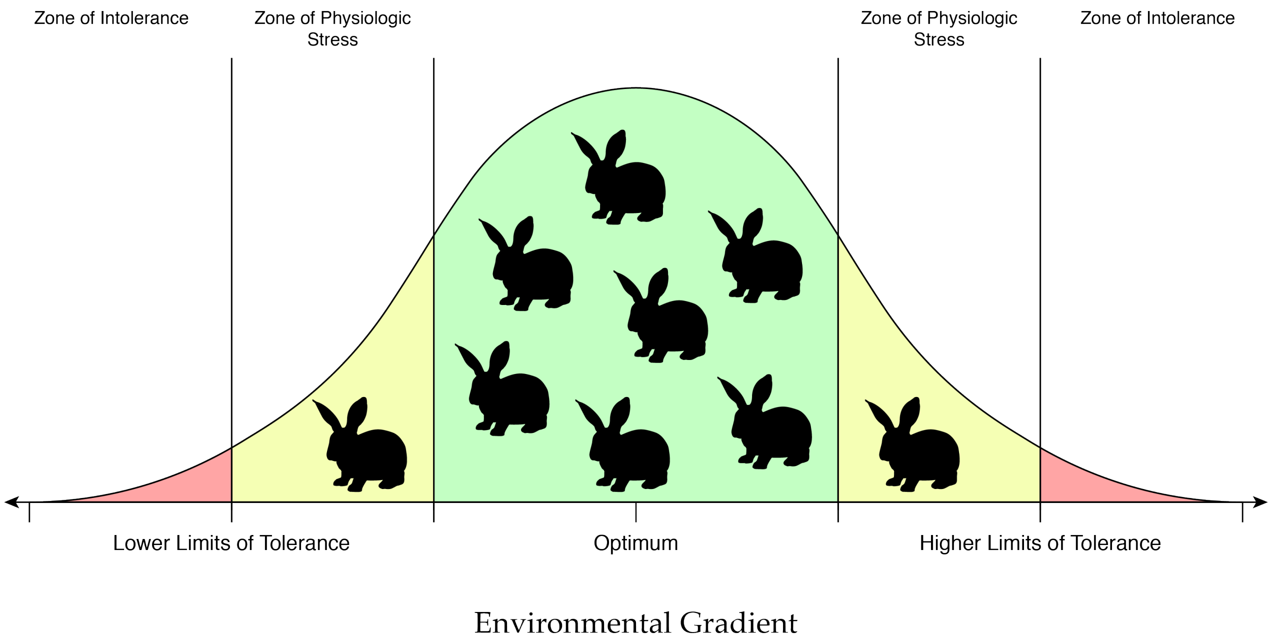


Figure 3.7

Abiotic Factors

Two primary abiotic factors influence population dynamics and distribution: physical geography and climate. A third factor, specific to plants, is soil. Physical geography includes physical barriers, such as mountain ranges and bodies of water, that influence establishment, dispersal, and distribution. If a species cannot physically move over or around a mountain, wide-open space, or body of water, its range is bounded. Species may also be temporarily constrained by disturbances, such as a fire or flood. Fire, for example, may temporarily remove vegetative cover needed as shelter or protection or alter soil chemistry and water infiltration, diminishing a food source or soil accessibility for burrowing animals.

Physical barriers also create climatic conditions and environmental gradients. Environmental gradients of temperature, precipitation, soil texture, water, or chemistry can all create physical barriers that confine a population. As discussed in chapter 2, species have a niche that includes the range of environmental conditions they can tolerate. Species generally inhabit a range of optimal conditions and exist at decreasing population levels under the stresses toward the edges of that range.

Disturbance often constrains a species' range by shifting the temperature, precipitation, soil texture, and nutrient cycling gradients.

Biotic Factors: Species Interactions

Species distribution can also or additionally be constrained by species interaction factors, such as allelopathy, predation, competition, and mutualism. These will be briefly covered here and in more depth in chapter 4: Ecological Systems Thinking.

Allelopathy

Plants using allelopathy excrete a chemical substance that inhibits the growth of other plants. Driving through the Mojave and Chihuahuan Deserts the distribution pattern of a certain shrub, the creosote bush (*Larrea tridentata*), seen in figure 3.8, becomes noticeable. The creosote bush diminishes competition through allelopathy.

Figure 3.8

Predation

The abundance of predators may encourage prey to constrain their movements, while a low population of prey may encourage a predator to expand its niche within its range. For example, in eastern Oregon use of radio collars has documented that if wolves (*Canis lupus*) are present, black-tail deer (*Odocoileus hemionus*) as well as cattle restrict their movement across a landscape (Clark et al. 2017a).

Competition

Competition occurs among many species, both plants and animals. A frequently noted competition is the dietary overlap between cattle and other grazing ungulates. It has been documented that black-tail deer (*Odocoileus hemionus*) and elk (*Cervus canadensis*) will not graze or browse in an area occupied by cattle.

Invasive species compete for resources with native plants, and as an invasive species becomes dominant it constrains the local range of native species. Cheatgrass (*Bromus tectorum*) has restricted the distribution of native bunchgrasses, such as Idaho fescue (*Festuca idahoensis*) and bluebunch wheatgrass (*Pseudoroegneria spicata*), throughout the Columbia Basin.

Competition is not always based solely on dietary overlap; it may also involve food for one species and habitat for another. For example, the threatened sage grouse (*Centrocercus urophasianus*) does not directly compete with cattle for food; rather, it competes for the vegetation structure it requires for mating and nesting.

Mutualism

The phrase "pollinators in peril" reflects the mutualistic relationship between plants and pollinators and the increasing concern that species reproduction and dispersal are being diminished by a reduction in pollinator populations. Reduced reproduction and dispersal capacity can constrain a species within its range.

Disturbance: Invasive Plants

Disturbances, particularly invasive plant proliferation, have greatly influenced native plant and animal populations throughout the western United States. On landscapes disturbed by land uses such as grazing, urbanization, conversion to agriculture, and recreation, and environmental events such as drought and fire, invasive plants are able to establish themselves in resource-limited niches and then outcompete native species, proliferating to the point of dominating a system and thus degrading its biotic integrity; in many cases, soil stability and hydrologic function are degraded as well. Degradation creates ripple effects not only in vegetation composition but also in microbial, insect, and wildlife habitat, with concomitant population decline.

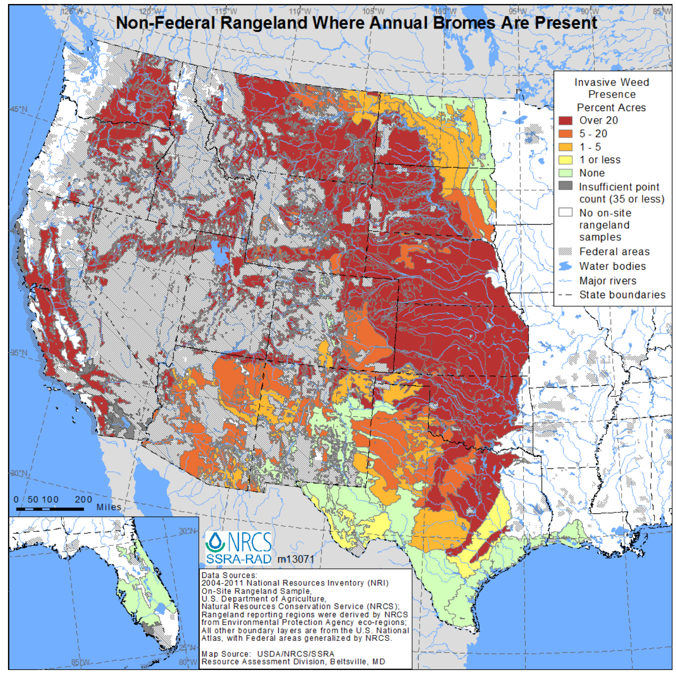


Figure 3.9

One of the most widespread and impactful groups of invasive species is annual bromes. Figure 3.9 maps the intensity of annual brome distribution on nonfederal land throughout the West. The dominant red shading indicates that for each acre, over 20 percent of the vegetation population is annual brome species. A map of federal lands would reflect a similar extent and intensity of annual brome populations. The dominance of annual bromes throughout the West contributes to reduced populations of wildlife species (e.g., sage grouse); increased fire risk; reduced hydrologic function; reduced grazing capacity; and reduced capacity of many other ecosystem goods and services. Other invasive species, such as thistles, knapweeds, and spurges, have similar impacts on vegetation and wildlife communities. Chapters 6 and 8 of this text will discuss ecological, economic, and social impacts of invasive species in more detail.

Influence of Climate Change

Climate change is the shifting in variation, intensity, and global distribution of climatic factors such as precipitation, temperature, wind, pressure fronts that create storm systems, and others. For example, an area that in recent history experienced summer maximum temperatures in the 80°F range may currently be experiencing summer maximum temperatures in the 90°F range (IPCC 2007). Areas that received on average two feet of snowfall from December through March now receive less than a foot of snowfall, while areas that generally do not receive snowfall are recording multiple winter storm events averaging four to six inches of snowfall (IPCC 2007). These are pronounced events and shifts. In addition, subtle shifts occur at different geographic scales from a few square miles to large geographic regions (IPCC 2007).

These types of shifts can greatly influence the distribution and density of plants and animals. Since biogeography is based on climate and geology, shifts in climate will result in biogeographic shifts for some species over time. One of the most evident shifts in the rangeland systems that are the focus of this text is occurring in C3 and C4 species. Recall that C3 species are cool-season species (growth cycle starts in fall and ends in summer), and C4 species are warm-season species (growth cycle starts in spring and ends in fall). The strategic difference between C3 and C4 species is based in photosynthesis and optimal growth conditions. C3 plants begin growing when soil temperature is 40–45°F, and their optimum temperature range for growth is 65–75°F, after which plant production becomes less efficient and diminishes (IPCC 2007). The soil temperature range for growth initiation of C4 plants is twenty degrees higher (60–65°F), and the optimum temperature for growth is twenty to thirty degrees higher (90–95°F). Additionally, C4 plants also require less water for plant physiological processes. Therefore, the range for C4 plants is expanding as atmospheric carbon and temperatures increase.

Chapter 4 will explore the complex interrelationships among biotic and abiotic system components in the context of the influences of climate change on populations. We will examine how a shift in C3 and C4 species influences shifts in populations of other species and community interaction dynamics.

Conclusion

In chapter 2 we focused on specific adaptations of plants and animals for survival under the environmental stress of heat and aridity. In this chapter, we focused on factors that influence species survival, growth, and distribution. The concepts we learned in these two chapters will underlie our understanding of community ecology—how populations of species interact and influence one another—which is the focus of chapter 4.

Synecology

Ecological Systems Thinking

To understand systems thinking, we should first align on what a system is. A system is a set of interrelated, interactive, and interdependent cofpomponents. For example, an area of sagebrush steppe is a system of plants, soil, animals, water, solar radiation, and so on (figure 4.1), all of which interact with one another in one or more ways.

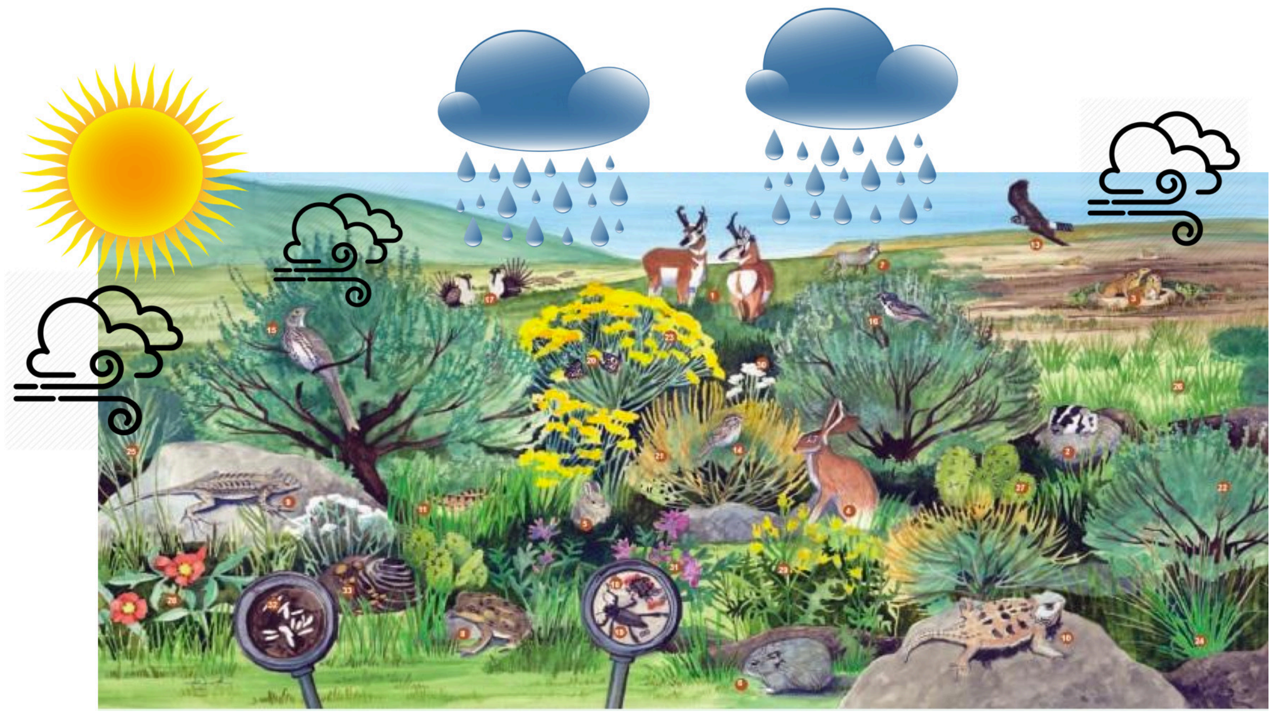


Figure 4.1 Ecological System

Systems comprise various components, interactions, and controls. *Systems have purpose*. A good way to think about the purpose of an ecological system is to describe it as an ecosystem providing goods and services. Understanding the fundamental purposes (note plural—more than one purpose) of ecological systems is critical for land use and management.

For a system to function optimally, all components must be present and functional. This characteristic of a system relates to biodiversity and redundancy. When a component, interaction, or control is missing from a system, a ripple effect may be put in motion. For example, when wolves (*Canis lupus*) were removed from Yellowstone, predation pressure on elk (*Cervus canadensis*) dropped dramatically, and elk populations increased. Elk prefer to browse on woody species, and as a result of the increased elk population, birch species in riparian areas were overbrowsed; riparian areas, stream channels, and ecosystems degraded. The reintroduction of wolves to the

Yellowstone system illustrates the last characteristic of a system: *through interactions, controls, and feedback, a system is capable of maintaining stability.*

Systems thinking considers the cohesive whole: how all the components relate to and influence one another. Systems thinking reveals how changes in one component, control, or interaction impact other components, controls, or interactions. Understanding these dynamics gives us multidimensional insight into a system. For example, figure 4.2 illustrates many basic connections along the banks of the Green River outside of Moab, Utah.

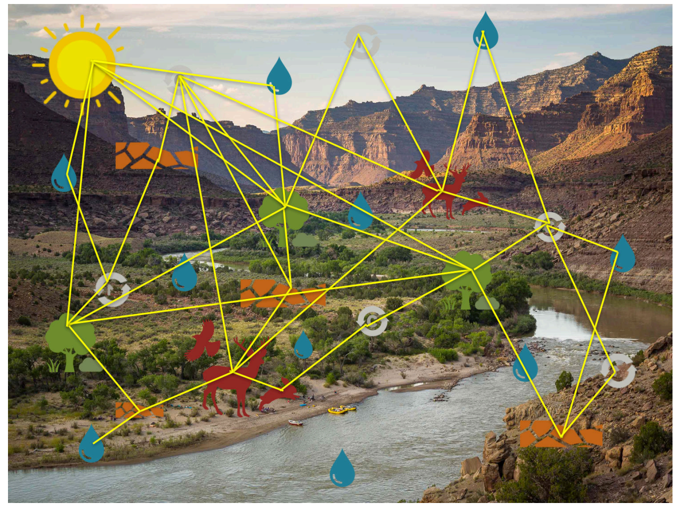


Figure 4.2 A few of the basic connections among water, solar radiation, plants, animals, soil, nitrogen, and carbon in an ecological system

It is important to remember that ecological systems are highly dynamic and ever-changing. Thinking in systems enables one to better understand system dynamisms and thus to anticipate trajectories of change due to land use, management, or disturbance. What we most readily notice about systems are events, such as a fire disturbance, grazing, or the surface of a landscape view, and these events generally drive our management decisions. What we need to see and understand to make better, holistic, management decisions are the patterns and the system structure that underlie those events.

Section 1: System Components

Components in a system are things that interact, such as plants, animals, water, microbes, nitrogen, and so on. Components may be categorized as abiotic or biotic; components may also be controls. Components each have their own structure function and purpose in the system, all of which must be understood to comprehend the system's processes, functions, and purposes.

Abiotic Components

Abiotic components are the nonliving elements in the system. They may be single discrete units, such as nitrogen, or an aggregation of many components, such as soil. Looking at figure 4.1, how many abiotic components can you identify? Several are wind, solar radiation, precipitation water, soil, carbon, various forms of nitrogen in the atmosphere and soil, carbon and nitrogen in plants and animals, rocks, and minerals in rocks.

Biotic Components

Biotic components are the system's living elements. They may be single discrete units, such as a plant, or an aggregation of many components, such as a community of animals. Looking at figure 4.1, how many biotic components can you identify? Several are pronghorn (*Antilocapra Americana*), sage grouse (*Centrocercus urophasianus*), Wyoming big sagebrush (*Artemisia tridentata wyomingensis*), rabbitbrush (*Ericameria nauseosa*), soil microbes, Great Basin spadefoot toad (*Spea intermontana*), western wheatgrass (*Pascopyrum smithii*), bluebunch wheatgrass (*Pseudoroegneria spicata*), and many more.

Section 2: Interactions

Interactions in a system include any events involving two or more components. For example, the interaction among solar radiation, water, and carbon dioxide is the interaction of photosynthesis. The interaction between a jack rabbit (*Lepus californicus*) and a coyote (*Canis latrans*) is one of prey and predator. Thousands of interactions occur in any given ecological system (some will be covered in chapter 5). Each interaction involves its own chain of events, functions, and purposes, all of which must be understood to fully comprehend the processes, functions, and purposes of the system.

Section 3: Controls

Controls in a system are any component that influences an interaction between other components. Controls can be thought of as inputs. For example, solar radiation is an abiotic component in a system, but it is also a control or input of photosynthesis. Water is another example of an abiotic component that is a control or input in many processes within an ecological community.

Components may be controls or inputs removed two to three degrees or more from the primary interaction output of interest. For example, say we are interested in the distribution and population density of coyotes and foxes. The components of water and solar radiation can be viewed as controls because they control plant growth. Jack rabbits eat grasses and forbs as well as nest in and use sagebrush for cover. Jack rabbits are a food source for coyotes and foxes. In this chain of linkages, water and solar radiation are one control of coyote and fox distribution and population density, since without adequate growth of plants for jack rabbit food and cover, the carrying capacity of jack rabbits is reduced; having fewer jack rabbits reduces the carrying capacity of coyote and foxes or shifts their predation targets to other species. Often components as controls are complex interaction and feedback chains.

Section 4: Feedbacks

Feedbacks in a system are outputs that are then routed back into the system to cause an amplifying (positive) or stabilizing (negative) effect.

Positive Feedbacks

Positive feedbacks in a system cause an amplifying effect, that is, they cause the system to continue to change in the same direction. For example, the more fossil fuels burned, the more atmospheric buildup of CO2 and the greater the greenhouse effect; the greater the greenhouse effect, the warmer the atmosphere; the warmer the atmosphere, the greater the level of evaporation, which further warms the atmosphere, amplifying the ongoing change. (See figure 4.3.)

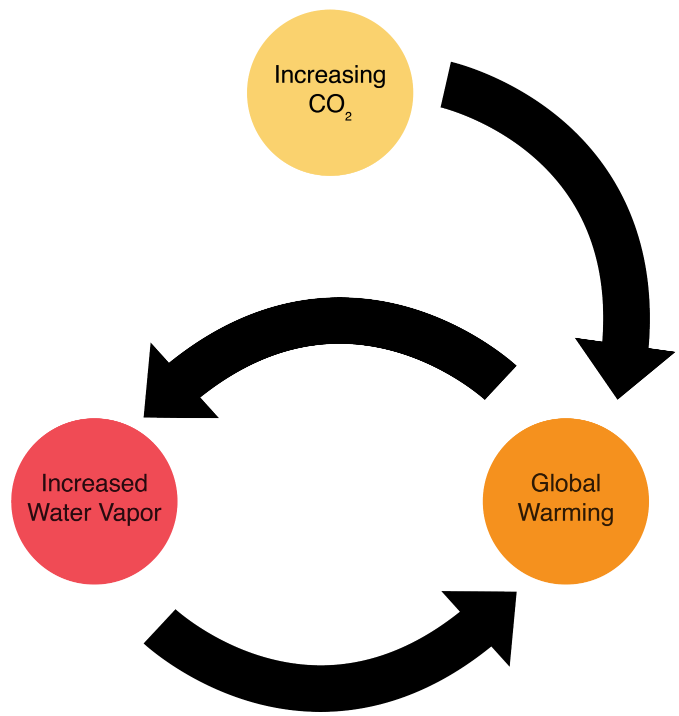


Figure 4.3

Negative Feedbacks

Negative feedbacks in a system cause a stabilizing effect; the input and outputs of the system work toward equilibrium or balance. For example, an abundant hare population can support an abundant lynx population, but as the lynx predate on the hare, reducing the hare population, the lynx population subsequently declines. With a reduced predation threat, the hare population increases, and the cycle starts all over again.

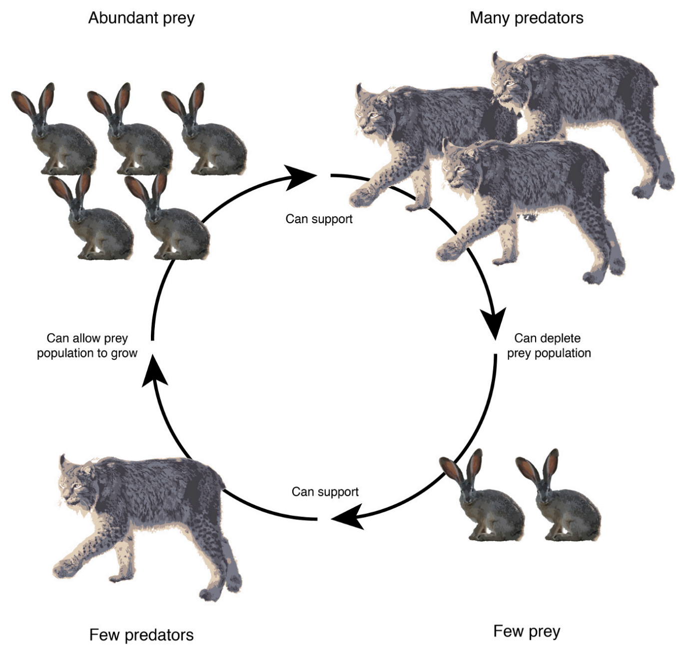


Figure 4.4

It is important to recognize that feedbacks may have short or longtime frames and that positive feedbacks often lead to degradation. A common positive feedback example involves undisturbed plant biomass production, which leads to more soil organic matter. Sounds like a good thing, right? Consider an undisturbed grassland prairie—lush fields of grass grow year after year, providing habitat for a range of ground-nesting birds and small mammals. As time passes, biomass production and soil fertility increase, but the thatch layer builds up, shading out germinating plants, and high plant density increases competition. Species able to germinate early and grow fast begin to dominate, reducing biodiversity in the system and establishing an incipient monoculture or opening niches for invasive species. So what originally sounded like a good positive feedback over time may not be. All natural systems seek balance.

Section 5: System Patterns and Structure

Patterns and structure, the last characteristics of systems covered in this chapter, can illuminate the broader functions and processes in a system. Understanding interactions generally requires focusing on one or even several components, but understanding patterns and structure requires looking across the system as a whole.

System Patterns

System patterns are the trends, the recurring events. For example, in a system dominated by C4 plants, we can expect late spring germination with a growth season climax in mid- to late summer. In a mountain system adjacent to lower valley or mesa areas, we can expect elk to descend from the mountains after the first heavy snow to graze and browse where vegetation is still accessible. If wildfire burns through a sagebrush system, regrowth is likely to follow a predictable successional trajectory.

System Structure

System structure is the way the components are arranged. In ecological systems, the structure might include the composition, density, and distribution of vegetation communities and the density and distribution of wildlife niches. It could also involve the below-to-above-ground vertical structure of a specific area. Systems structure can mean a trophic cascade, the food web, or any recurring interactions and feedback loops in a system.

We haven't accounted here for the roles of economics, culture, and society in systems thinking. These aspects are covered in other courses. Layering in these categories of components (e.g., people), interactions (e.g., land use), and controls (e.g., money and values) illuminate even greater and more powerful details of the system. Systems thinking is at the foundation of understanding community ecology and the effective and sustainable management of any ecosystem.

Community Ecology

Community ecology is the interactions between and among populations of species over time and space within a specified area. Species interactions underlie ecosystem functions such as nutrient cycling and influence ecosystem structure. Understanding the community ecology of an area can guide management of species as well as land management of a given area.

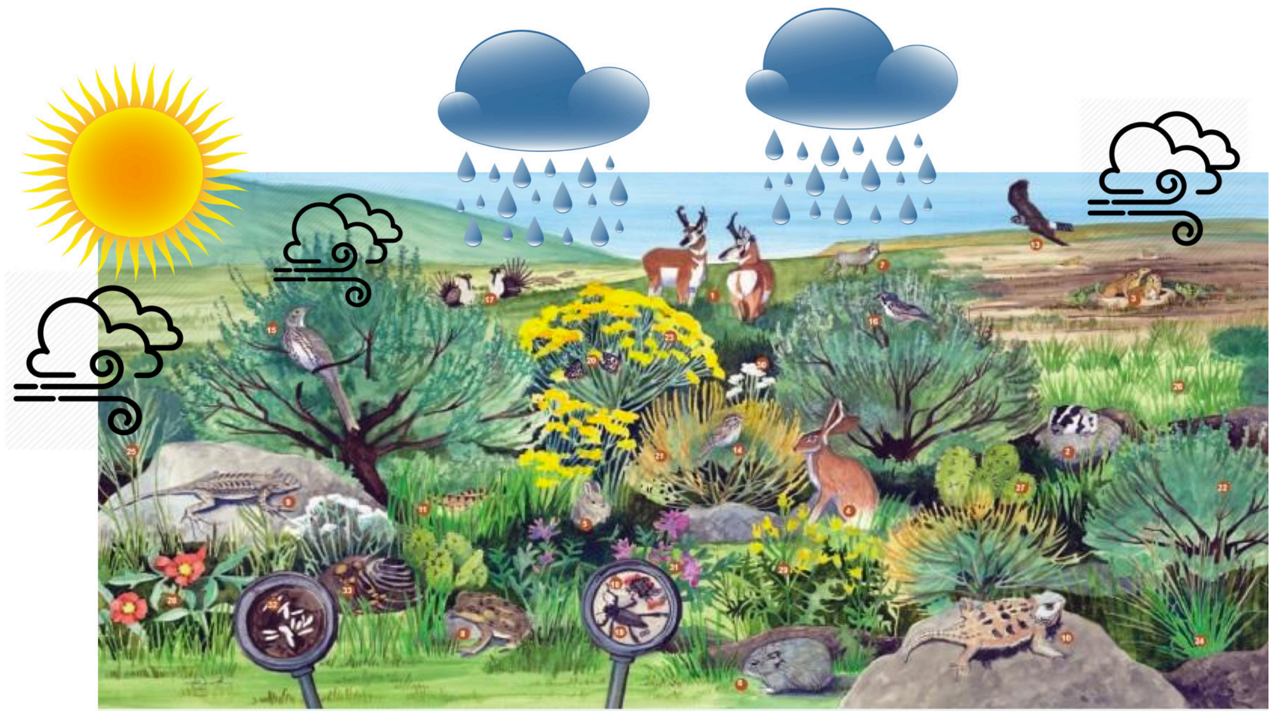


Figure 5.1 Sagebrush system/community

Recall the diagram (figure 4.1) from the previous chapter on "systems"? An ecological community is generally defined as interacting populations of species. Although this text won't dive into the nuances of delineating an ecological community, it may be helpful to quickly list the key delineating approaches:

- *Physical boundaries*, based on ecological site(s), differences of land uses (e.g., natural forest vs. cropland), physical land features (e.g., valley bounded by mountain range), ecotones (e.g., woodland to grassland), management units (e.g., ranch), or geopolitical area (e.g., Bureau of Land Management [BLM] land).
- *Habitat boundaries*, based on habitat characteristics of one or more key species (e.g., habitat of elk—mountains and valley)
- *Interaction boundaries*, based on areas of interaction between key species (e.g., eagle and small

mammal—forest edge and valley)
- *Ecosystem-type boundaries*, based on ecosystem (e.g., forest or wetland).

Section 1: Properties of Ecological Communities

Ecological communities have three key properties: richness, diversity, and community structure.

Community Richness

Species richness is the count of species in a given area. It is a simple indicator of biodiversity. Its application is limited in that it is simply a count with no weight given to any specific type or class of species, such as endemic, or functional groups (e.g., nitrogen fixers or mesopredators). A community may have a high count of small mammal species, but what does that mean for the structure and function of that community and ecosystem?

Community Diversity

Species diversity is the count of different species (richness) and the relative abundance of those species (evenness). In figure 5.2 the communities have the same number of species (five), but Community A is essentially a monoculture of cheatgrass (*Bromus tectorum*), while community B presents a more even balance and distribution among species.

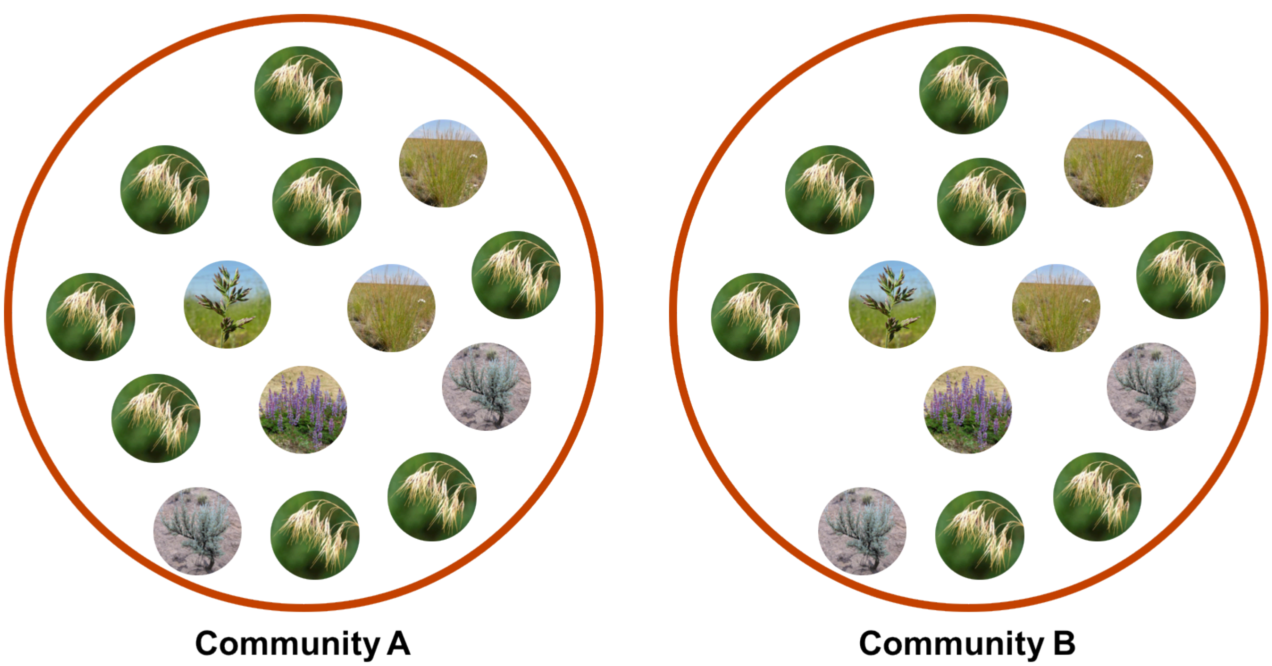


Figure 5.2

Community Structure

Community structure is species richness and diversity as well as the spatial and temporal distribution of species in the community. Community structure is determined by climate, geography, disturbances, and the interactions in section 2 and their influences covered in sections 3 and 4 below.

Section 2: Species Interactions

The study of community ecology focuses on interspecific interactions: competition, predation, and symbiosis.

Competition Interactions

Competition occurs between individuals of two (or more) species or populations of species utilizing the same resource in a given area. For example, elk (*Cervus canadensis*) and black-tail deer (*Odocoileus hemionus*) both forage and browse on greater than 50 percent of the same vegetation species in many areas of Colorado (Sandoval et al. 2005). Another general common example is the competition for water and nutrient resources between invasive plant species and native plant species. Competition interactions can be divided into three different categories: interference, exploitative, and apparent.

Interference Interactions

Interference interactions occur when an individual or population of a species directly prevents or influences the ability of an individual or population of another species to obtain a resource. For example, cattle grazing on and around lek sites during sage grouse (*Centrocercus urophasianus*) mating season directly prevents sage grouse from using the area for mating rituals and may influence the sage grouse to find another lek and nesting site.

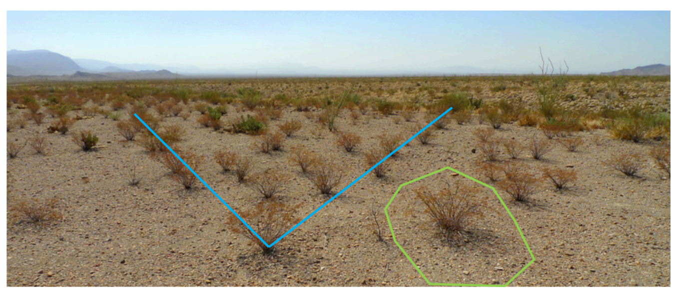


Figure 5.3 Creosote bush (*Larrea tridentate*) allelopathy

Allelopathy, the chemical inhibition by one organism of another, is an interference interaction. Allelopathic plants exude chemicals from the roots that inhibit the growth of other plants. In figure 5.3 you see that each creosote bush (*Larrea tridentata*) is surrounded by a bare area (outlined in green); this reflects the extent of its roots, which exude chemicals that prevent the growth of other plant species. Looking across a landscape dominated by creosote bush, one can see a pattern of plant distribution (blue lines).

Exploitative Interactions

Exploitative interactions occur when an individual or population of one species indirectly reduces access of an individual or population of another species to a resource in a given area. For example, black-tail deer tend to utilize valley areas year-round, thus reducing the fall and winter forage and browse available for elk in valley areas. Exploitative interactions for food resources are also called dietary overlap, a term most often associated with describing forage and browse competition between livestock and wildlife.

Apparent Interactions

Apparent interactions are not true competition, but a favorable outcome for resources occurs when the population of one species is targeted by a predator, thus giving an advantage to the other species population to obtain a resource. For example, when a predator species such as an owl favors predating on mouse species A more than on mouse species B, the result is reduced competition for food resources for mouse species B.

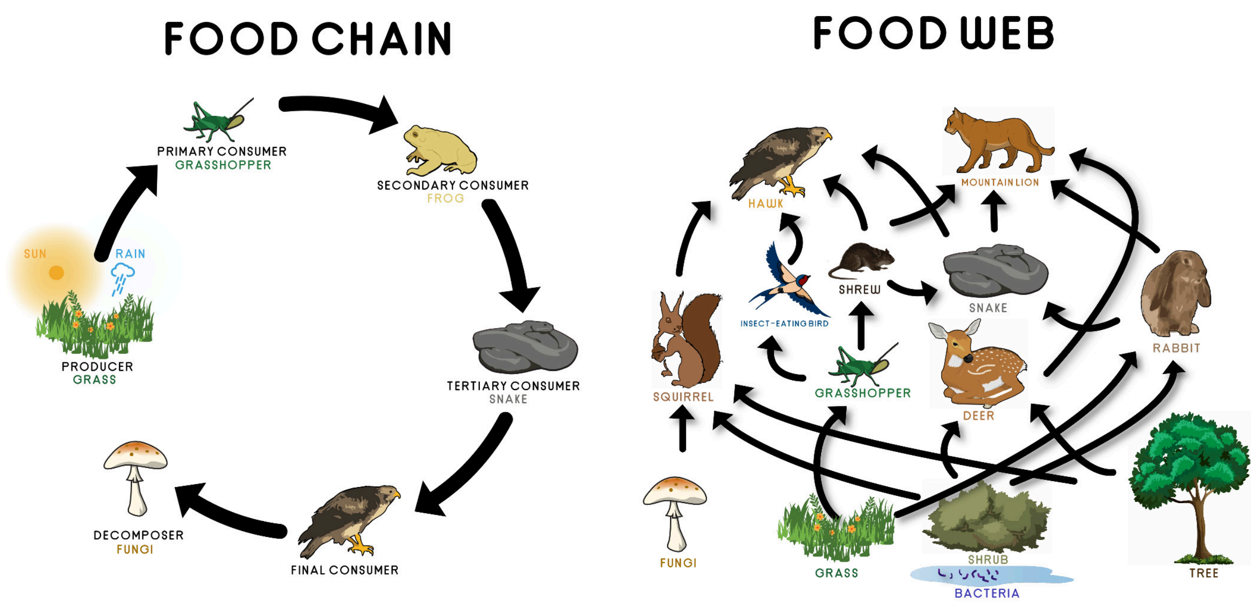


Figure 5.4

There are three general outcomes of competition: (1) one species excludes the other and the species that is excluded disperses; (2) sharing of resources with population density and carrying capacity facilitating division of the resources; and (3) coexistence through resource partitioning (each species adjusts its habitat selection within the area).

Predation Interactions

Predation is one species killing and eating another species. Included in predation is herbivory, in which an animal or insect species eats a plant species, either temporarily reducing its capacity for survival and growth or killing it. Predation interactions are the basis of the food chain (figure 5.4), which is the basis of the food web (figure 5.4).

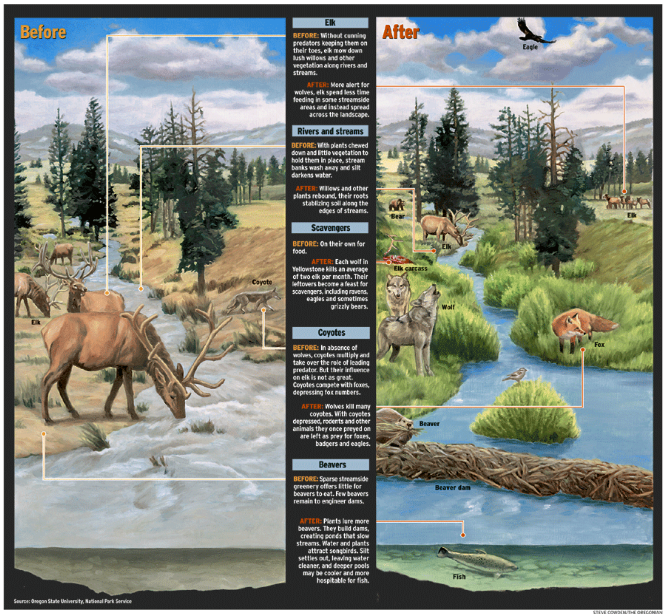


Figure 5.5 Before and after wolf reintroduction. Created by Oregon State University and National Park Service

Note that the food chain is organized by tropic levels—primary producers, primary consumers, secondary consumers, tertiary consumers, and quaternary consumers. This trophic structure is vital to ecosystem stability and resiliency; therefore, when a trophic level is suppressed or removed from a system, thus opening or widening a niche for another trophic level, trophic cascade occurs, and the ecosystem progressively becomes increasingly imbalanced. A prime example was the removal of the quaternary consumer wolves (*Canis lupus*) from the Greater Yellowstone ecosystem, which reduced predation pressure on elk populations. The increasing elk populations heavily browsed and grazed riparian areas resulting in highly altered riparian ecosystems. Figure 5.5 illustrates the impacts of trophic cascade as a result of wolf removal. For more details about this trophic cascade example, see Beschta, "Trophic Cascades from Wolves to Grizzly Bears in Yellowstone," in the *Journal of Animal Ecology* (2003).

Keystone Species and Ecological Engineers

Keystone species are those species that have a specific and unique niche or function in an ecosystem that gives the species a disproportionate impact on the ecosystem relative to its abundance. This role is also reflected in the trophic cascade example above. The removal of wolves, a keystone species, from the ecosystem impacted the structure and diversity of riparian areas in the Greater Yellowstone Ecosystem (GYE).

Also reflected in this GYE example above is the role of ecosystem engineers, those species that create, modify, or alter habitat in a manner and to a degree that it impacts the structure and diversity of the ecosystem. Without beavers building dams in the river, riparian and aquatic habitat was reduced and degraded.

Symbiotic Interactions

Symbiotic interactions are those in which two or more species directly and purposefully interact for the gain of either one or both. There are many types of symbiotic interactions, but they fall into one of three categories: mutualism, parasitism, and commensalism.

Mutualistic Interactions

Mutualistic interactions are those in which all species benefit. For example, the nectar of flowers is the food source for a number of insects (e.g., bees) or birds (e.g., hummingbird), while the insects and birds feeding on nectar and moving from flower to flower facilitate pollination. Neither insect nor flower could exist without the other, making this mutualistic interaction obligate.

Facultative Mutualistic Relationships

Facultative mutualistic relationships are beneficial, but not required for either species. For example, nitrogen-fixing plants such as alfalfa (*Medicago sativa*) have a mutualistic relationship with rhizobia bacteria in nodules on the plants' roots. This bacteria fixes nitrogen for the plant and inputs it into the soil for uptake by other plants and microbes. Alfalfa often obtains the nitrogen it needs from this relationship with rhizobia bacteria, but it is not dependent on this source of nitrogen to survive.

Parasitic Interactions

Parasitic interactions are those in which one species (the parasite) benefits from living with another species (the host), but the host is harmed. A common example is a deer tick (*Ixodes scapularis*), which feeds off the blood of animals and humans and in the process transmits diseases to the host that can weaken or sicken the host. In some instances, a parasite will weaken a host to make it more accessible to a predator or reduce competition between the host species and another species; in this context, parasitic interactions can be beneficial by helping to maintain ecosystem stability and diversity.

Commensal Interactions

Commensal interactions are those in which one species benefits and there is no apparent effect on the other species. A bird riding on the back of a large mammal is a commonly cited example. Commensal interactions are often overlooked in ecosystems, but they may be important, if not critical, interactions for broader ecosystem stability and resiliency.

The role of *nurse plants* falls under commensal interactions. Nurse plants provide microhabitats to facilitate the growth and development of seedlings. Nurse plants provide protection from shade, fire, herbivory, wind, and so on, and provide advantages (such as collecting needed resources, moderating soil temperatures, etc.). For example, barrel cactus (*Ferocactus spp.*) seedlings utilize the loose and wide canopy cover of bursage (*Ambrosia deltoidea*) for protection from predation (figure 5.6). Saguaro (*Carnegiea gigantitea*) in the Sonoran Desert require the shade of mature plants at the seedling stage. In sagebrush steppe systems, sagebrush species (*Artemisia tridentata spp.*) provide cover and resources for native grass seedlings. Nurse plants can be a critical component of seeding success in restoration efforts.

Figure 5.6 Barrel cactus (*Ferocactus spp.*) in bursage (*Ambrosia deltoidea*) nurse plant

Section 3: Influences on Interactions

To fully understand interactions between and among populations of species one must understand the key factors influencing these interactions: season, habitat selection, succession, disturbance, and retrogression.

Seasonal Influences

In discussing exploitative competition interaction (see above), we noted that deer use the valley area year-round, while elk use it in winter. Although these two species may both be in the valley seasonally, deer use in spring, summer, and fall may impact resources available for elk use in the winter. The secondary influence in this scenario is climate. If precipitation timing and amount supported a high degree of biomass production, then the competition interaction may be reduced; while the inverse may be the case if precipitation timing and amount limited biomass production.

Season of use may also be germination and growing season of plant species. C3 species generally grow and mature in the spring, while C4 species generally grow and mature over summer into early fall. Periods of most resource use occur during elongation, floral initiation, and reproduction; during these periods, plants focus on resource acquisition and distribution of physiological processes and are generally more susceptible to adverse effects of herbivory and disturbance. This can be important to know when guiding land use and in wildlife management.

When considering interactions, it is also important to understand season of use, as it may affect guide management before and after use season. One way to understand what species are using what resources when is to map it out or create a chart, both of which will illuminate periods of use sequence and overlap.

Habitat Selection Influences

Habitat selection is the free movement of animals through areas of suitable habitat and their choice of where to get food and water, mate, nest, and so on, much of which is driven by the potential of negative, positive, or mutual interactions. For example, sage grouse (*Centrocercus urophasianus*) distribution depends largely on the availability of a mosaic with open areas to serve as a lek and nearby sagebrush to serve as nesting cover (figure 5.7). Jack rabbits may also look to sagebrush for nesting and cover, but they are also well aware of predation threats.

Figure 5.7 Sage grouse habitat, Montana

A number of songbirds nest in juniper trees (*Juniperus occidentalis*), often multiple birds in a single tree. This is possible due to resource partitioning, an influential factor in habitat selection.

Succession, Disturbance, and Retrogression Influences

Succession, disturbance, and retrogression change in vegetation communities and concomitant changes in wildlife, insect, and microbial composition and population dynamics have a substantial influence on community interactions. Chapter 6 will cover this influence in depth.

The best method for identifying and understanding species interactions and what influences them is by understanding each species' biology and population dynamics. As stated at the beginning of this chapter, species interactions underlie ecosystem functions, such as nutrient cycling, and influence ecosystem structure. Understanding the community ecology of an area can guide management of species as well as land management of a given area. Therefore, it is imperative to identify and understand the nature, drivers, and influences of these interactions, which are the key value of ecological systems thinking.

Section 4: Plant Community Ecology

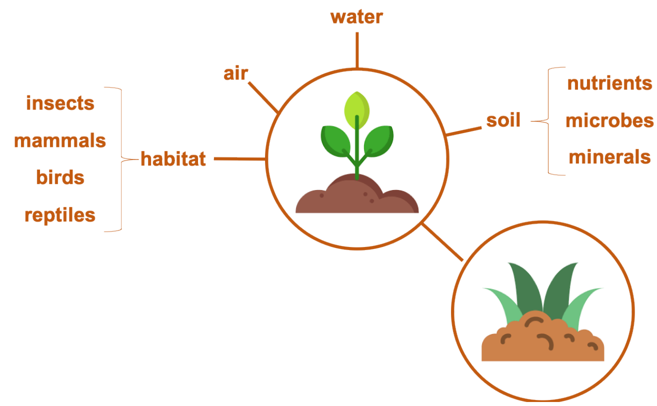


Figure 5.8 Basic important relations of plants within an ecosystem

The discipline of rangeland science places a focus on plants and plant communities. A substantial driver underlying this focus is rooted in the grazing management legacy of rangeland science. Although grazing is still a cornerstone, the discipline has evolved to center on sustainable land stewardship with emphasis on ecosystem goods and services delivery, regeneration and resiliency, and social-ecological systems. Plant community composition and production play a critical role in the structure and function of all ecosystems and their ability to deliver ecosystem goods and services. Figure 5.8 hints at the most basic important relationships of plants within an ecosystem; if you think back to introductory ecology you should be able to explain in moderate detail the nature and function of these relationships and how they contribute to ecosystem goods and services delivery. As such we will round out this chapter with a brief focus on plant community ecology, specifically plant functional groups.

Plant Functional Groups

A number of organizing characteristics and attributes can be used to divide plants into functional groups, all of which individually and taken together have value when inventorying and assessing an ecosystem. In this section, we take in a bird's-eye view of two categories of functional groups: biology and ecosystem function.

Biological Function Groups

Biological function groups to focus on in relation to arid and semiarid environments include but are not limited to (1) life-form (grass, forb, shrub, tree); (2) life cycle (summer annual, winter annual, biennial, perennial); and (3) rooting structure and depth (shallow fibrous; shallow tap root; deep tap root, both fibrous and tap root).

Knowing the relative abundance of grasses, forbs, shrubs, and trees can tell you a lot about the site's soil stability, hydrologic function, biotic integrity, and resiliency. An arid or semiarid site on which shrubs or trees dominate tells you there is moderate to no understory and that the soil stability, hydrologic function, and biotic integrity of the site are low. A site dominated by grasses and forbs could indicate the opposite, at least in terms of soil stability and hydrologic function. Depending on the degree of invasive species, the biotic integrity may be low.

Often species data gathered focuses on gauging biodiversity, degree of invasion of an invasive species, or abundance of a specific species. These are all vital uses of species-specific data; however, not often is species data used to group and map out the life cycles of vegetation on a site. Knowing the life cycles of the species and their reproductive strategies can guide grazing management, invasive species mitigation, restoration efforts, and so on.

One of the most biologically functional groups in arid and semiarid environments comprises rooting structures and depths—in other words, who is getting the water and when. Knowing this can illuminate competitive interactions among plant species; inform when and where habitat may be available for wildlife and microorganisms; and guide grazing management, restoration efforts, and understanding the hydrology of the site.

Ecosystem Function Groups

Ecosystem function groups to focus on in relation to arid and semiarid environments include but are not limited to (1) nitrogen fixers, (2) habitat, and (3) intra- and interspecific interactions.

Nitrogen is a critical nutrient for plant function and growth. The nitrogen cycle is at work in all ecosystems through denitrification, nitrification, and fixation. Knowing the source and abundance of fixation provides some indication of the nitrogen availability in the system. Knowing the distribution of those sources also gives some indication of where nitrogen may be a limiting factor. This information can be useful for invasive species mitigation, seeding and restoration efforts, grazing management, and so on.

Often when we look at a plant community, we also see wildlife habitat; however, our vision can be somewhat simplistic. Across a site or ecosystem, only specific components are directly related to the habitat available for a specific wildlife species. For example, figure 5.9 shows a sagebrush system, but only specific components and characteristics of the system are sage grouse habitat.

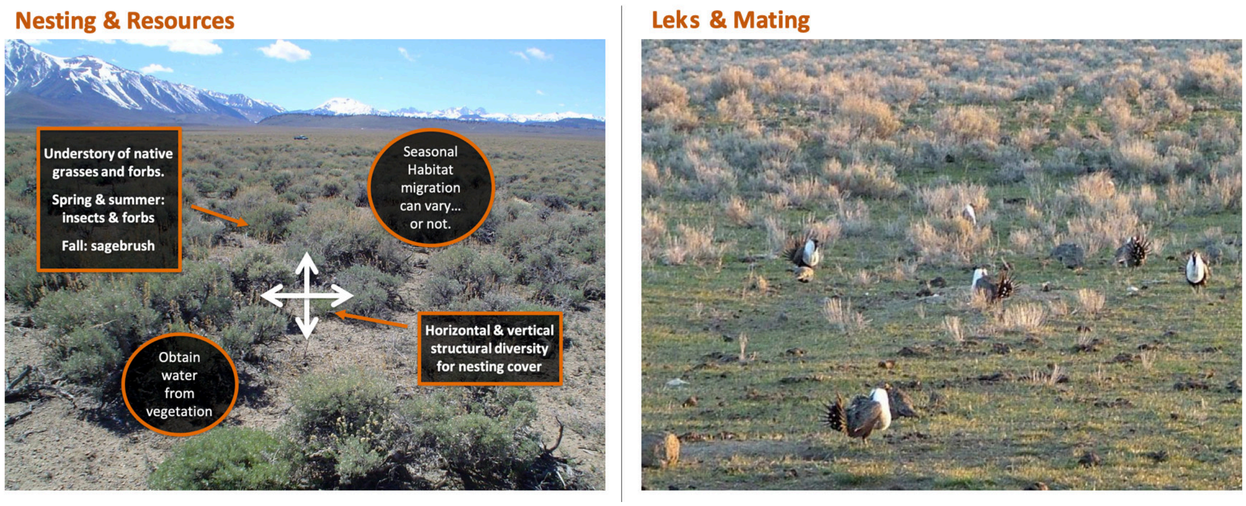


Figure 5.9

Looking at a plant community through a habit lens across all or target species can guide restoration efforts, grazing management, or any type of land management (e.g., where to construct a road or path, where to place infrastructure such as a water pipeline, etc.).

To be truly strategic in land management efforts, particularly restoration, one would be well served by examining the intra- and interspecific interactions within plant communities and among plant species or plant communities and the broader ecosystem. Taking this approach could identify structural and functional gaps in the system and its degree of biodiversity and resiliency. In upcoming chapters on specific ecosystems, we will engage in thought exercises exploring how elements of these ecosystems are interconnected and what would happen if a system's plant components were reduced, increased, or completely removed.

Ecosystem Disturbance

The previous chapters provided a baseline of concepts and dynamics for a community on a linear successional path. Succession is community change over time toward a climax community. Successional communities are based in equilibrium: a balancing of populations and community dynamics based on competition, predation, and other species interactions. This chapter will focus on a dominant ecological driver in rangelands throughout the world—disturbance and retrogression.

Section 1: Ecosystem Disturbance

Ecosystem disturbance is an event or series of events altering the ecosystem structure and function, to be more specific: the removal of biomass and therefore ecosystem process. Disturbance affects plant composition, soil structure and function, hydrology, and nutrient cycling as well as intra- and interspecies interactions. In a nutshell, disturbance disrupts and alters the current successional trajectory.

Disturbance Types

Figure 6.1 Pine beetle infestation, Colorado

There are dozens of types of disturbance, but they can be divided up into two primary categories—physical and biological—which can each then be broken down into natural occurrences or human-induced events.

Physical disturbances are disturbance events that alter the physical structure and arrangement of the landscape.

Physical disturbances usually occur swiftly in a short period of time; examples include a wildfire, flood, landslide, or volcanic eruption. Physical disturbances can also be human-induced events, such as plowing a field or clear-cutting a forest.

Figure 6.2 Cheatgrass monoculture, Utah

Biological disturbances are disturbance events that impact a species and community structure and function within an ecosystem.

They often occur through death—such as the effect of the mountain pine beetle (*Dendroctonus ponderosae*) on intermountain pine forests (figure 6.1)—or through dominance—such as the expanses of cheatgrass (Bromus tectorum) throughout the western United States (figure 6.2).

Characteristics of Disturbance Regimes

Disturbances vary across a number of characteristics that influence the degree of their impacts on ecosystem structure and function: frequency, spatial scale, timing, predictability, and synergism.

Understanding the frequency of the disturbance regime indicates the degree to which an ecosystem has time to recover or not. Disturbance frequency can be a one-time or rare event, such as a volcanic eruption or land conversion from a natural ecosystem to agriculture, establishing a road or well-pad site, or some other human use. Disturbances such as fires and floods recur at intervals, allowing periods of recovery, while hiking or off-road vehicle trail use or continuous year-round grazing are persistent disturbances that accelerate and exacerbate degradation because there is no period of recovery.

The spatial scale is the physical extent of the impacts of the disturbance on the landscape. It can vary from a couple of acres to thousands of acres. The spatial scale relates directly to the magnitude and severity of the disturbance, as well as to the management options to mitigate impacts or undertake restoration efforts. For example, ten acres used as a holding area for cattle twice a year could become infested with invasive species. Once established, invasive species could aggressively spread, particularly if facilitated by wind or drought. The impacts of this invasive species infestation would increase slowly over time. On the other hand, a fire that burned thousands of acres has an immediate impact on the ecosystem structure and function.

The timing or season of a disturbance is the point in the area's climatic regime, plant season of growth, or wildlife reproduction cycle at which the disturbance occurs or is most intense. For example, a fire in the middle of a hot dry windy summer is different than a late fall fire just prior to a period of cooler temperatures and increased precipitation. Plowing a field in spring or early summer prior to invasive plant seed production will minimize seed disbursement, whereas plowing in midsummer or fall will facilitate seed disbursement. Cutting a road through sagebrush, specifically a lek site, to a well-pad site during sage grouse mating season will reduce the reproductive rate for that year.

Disturbances tend to be viewed through a lens of uncertainty, but in reality, disturbances can have a degree of predictability. A grass valley several years into a drought will have more fine fuels, and as such is more likely to catch fire and burn intensely than if previous and current years' precipitation is average and the valley is managed through grazing or mowing to reduce fuel load buildup. Understanding disturbance ecology, invasive species biology, and fire science underlie disturbance predictability and management actions to prevent, control, and mitigate.

With each disturbance, all the aforementioned characteristics combined determine the extent, magnitude, and severity of the disturbance. These characteristics, combined with interconnected impacts (some of which are discussed below), create a synergy that amplifies positive feedback loops and ripple effects within an ecosystem. A common example is the invasion of juniper and increasing degradation of soil stability, hydrologic function, and biotic integrity. Not only is the invaded juniper area impacted, but the surrounding shrubland and grassland areas in terms of hydrology, plant and wildlife composition, and nutrient cycling are as well.

Disturbance Impacts on Ecosystem Structure and Function

There are a multitude of impacts on ecosystems post-disturbance, all of which depend on the type of system, the disturbance, and the system's degree of resiliency (covered in chapter 7). This section will highlight impacts on several key ecosystem functions and ecosystem biodiversity.

Disturbance has varying effects on nutrient cycles. Fire can initially accelerate and amplify the carbon and nitrogen cycles through the accelerated decomposition of above- and belowground biomass, depending on the intensity of the fire. Drought, which reduces biomass production and in some systems maintains many species in a semidormant state, can inhibit and decrease carbon and nitrogen cycles. Invasive species can also greatly affect these cycles, particularly nitrogen, as in nitrogen-saturated or -limited environments, as many invasive species have the ability to acquire soil nitrogen quickly and use it efficiently, thus giving the invasive species an advantage over native species. One of the reasons invasive species tend to dominate post-cultivation is due to the low nutrient levels, as cropped systems over time deplete soil nutrients and microbial communities.

Hydrologic function, in which water is captured, stored, and released safely in a system, requires biotic integrity and soil stability. The vegetative structure of an ecosystem plays a critical role in the capture of water. Infiltration of water from a precipitation event is greatly reduced and runoff greatly increased in a system with minimal vegetative canopy. Belowground, a system dominated by shallow-rooted species also reduces the capture and storage of water. Soil structure and stability are often degraded post-disturbance, exacerbating soil erosion and loss of soil organic matter and minerals.

Biodiversity is often the most evident impact of a disturbance. Depending on the type, timing, and spatial scale of the disturbance the influence on biotic integrity can be locally focused and gradually increase (e.g., invasive species establishment and proliferation) or widespread and swift (e.g., fire or flood). The end result of either path is often shifts and/or reductions in biodiversity throughout the ecosystem. Not only the vegetation composition but also the structure of the vegetation influencing the habitat of small mammals and ground-nesting birds and the density of foraging ungulates may change. Soil structure (density and ped stability) may change, altering hydrology; soil organic matter, nutrient cycling, and soil microbial community composition and productivity may be altered or reduced, all of which can further impact biotic integrity and diversity.

Disturbance is fairly ubiquitous, so much so that we have management methods and models that focus on disturbance, such as state and transition models (see the example at the end of this chapter). Before we move on to understanding retrogression and modeling impacts of disturbance, we will look at intermediate disturbance hypothesis (IDH), which suggests that, under a disturbance regime (frequency of disturbance), species diversity is highest with a moderate disturbance regime (figure 6.3). What defines moderate depends on the ecosystem, the type of disturbance, and its characteristics.

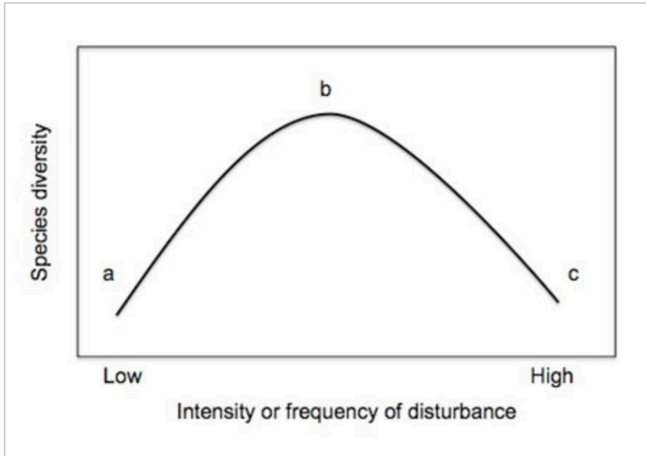


Figure 1: The intermediate disturbance hypothesis (IDH)
(A) Species diversity is low at low disturbance frequency because of competitive exclusion. (B) Species diversity is higher at intermediate disturbance frequency due to a mix of good colonizer and good competitor species. (C) Species diversity is low at high disturbance frequency because only good colonizers or highly tolerant species can persist.

Figure 6.3 From Hughes, A. 2010. "Disturbance and Diversity: An Ecological Chicken and Egg Problem." *Nature Education Knowledge* 3 (10): 48

Why is it that moderate disturbance can result in a higher level of biodiversity? Moderate disturbance serves to facilitate a retrogression-successional cycle in an ecosystem. This retrogression-successional cycle maintains balance among species densities. For example, we often hear how fire suppression results in woody species encroachment and that brush management through prescribed fire or mechanical means opens up niches for an increase in grasses and forbs.

Frequent high-intensity disturbance maintains an ecosystem in an early successional state. In the arid West, where water and nutrients can be limited, maintaining a system in an early successional state often facilitates invasive species establishment and proliferation. A synergy can develop between a frequent high-intensity disturbance such as fire and the invasive species; this not only maintains the system in an early successional state but also exacerbates spiraling degradation of the system. The fire–cheatgrass (*Bromus tectorum*) cycle is a class example of this dynamic.

Infrequent low-intensity disturbance tends not to facilitate an adequate degree of shifting of vegetation composition and structure, soil processes, and animal communities to achieve rebalancing. Under low intensity or infrequent disturbances, open niches are few to none, and competitive exclusion remains the status quo. The aforementioned woody species encroachment serves as an example of how infrequent low-intensity disturbance maintains competitive exclusion for species such as juniper (*Juniperus occidentalis*) and sagebrush (*Artemisia tridentata*).

Figure 6.4 From Hanna, S., and K. Fulgham. 2015. "Post-fire Vegetation Dynamics of a Sagebrush Steppe Community Change Significantly Over Time." *California Agriculture* 69 (1): 36–42

Moderate intensity or frequency disturbance results in the highest level of biodiversity because an adequate degree of structure and processes are altered, increasing available resources and opening niches. In systems with moderate disturbance, niches open for colonization, while established species with tolerances and competitive advantages remain. As we can see from figure 6.5 a dense sagebrush system was "reset" to rebalance to a mix of shrubs, forbs, and perennial grasses. The graph in figure 6.3 conveys how the system rebalanced over the twenty-seven-year period following the fire.

Figure 6.4 shows how this ecosystem was able to rebalance to a vegetation composition dominated by perennial grasses (green curve) as shown on the graph (figure 6.5) rather than a system dominated by annual grasses. The answer lies in the concept of resiliency, the focus of chapter 7.

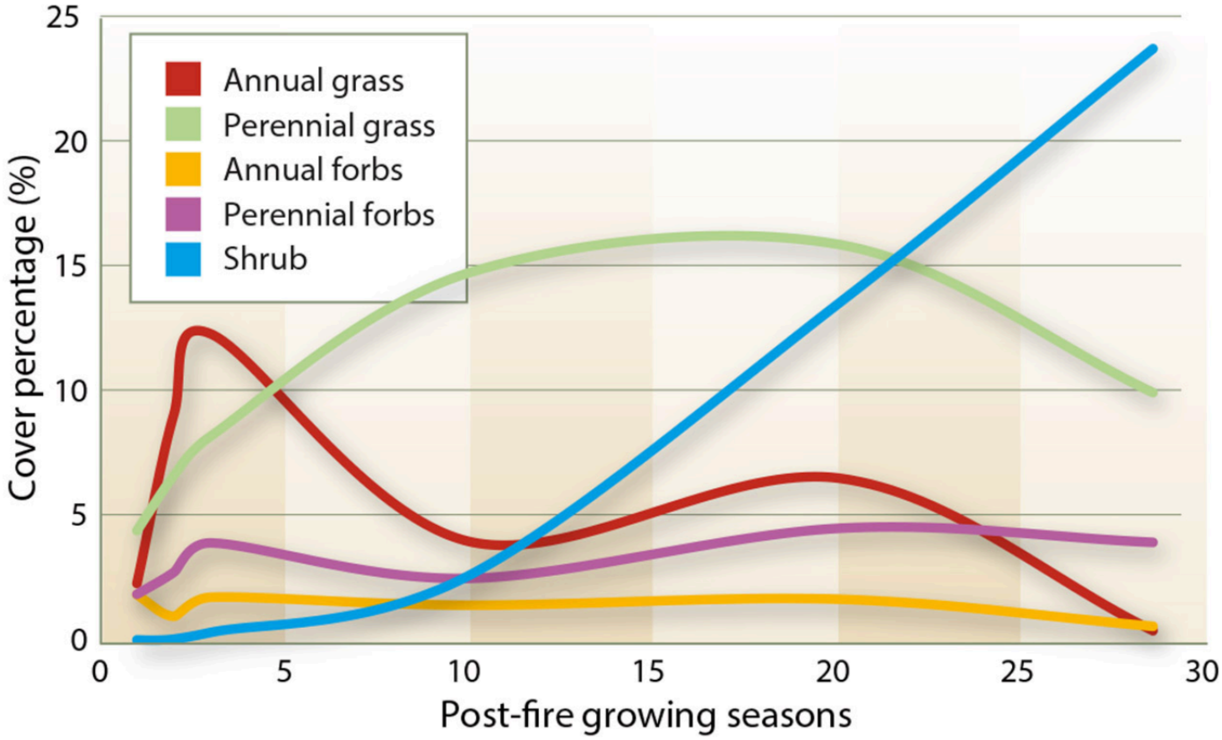


Figure 6.5 From Hanna, S., and K. Fulgham. 2015. “Post-fire Vegetation Dynamics of a Sagebrush Steppe Community Change Significantly Over Time.” *California Agriculture* 69 (1): 36–42

Nonequilibrium Ecology and Ecosystem Resiliency

The model for understanding ecosystems has long been based in equilibrium theory and linear succession. In recent decades, it has been recognized that climatic succession may be a concept well suited to some ecosystems that remain largely undisturbed, such as the nonlogged mesic forests of the Pacific Northwest. Most ecosystems throughout the world do not remain undisturbed, however, and therefore have perturbations (i.e., disturbances) that shift the ecosystem to alternate states. Nonequilibrium theory emerged as a way to think about ecosystems under the influence of disturbance and increased competition (Folke 2006). Nonequilibrium theory is now coupled with resiliency theory and resiliency thinking to recognize that ecosystems are not only under the influence of disturbance shifting; they are also subject to the influence of humans in and on ecosystems.

Section 1: Nonequilibrium Ecology

Nonequilibrium ecology asserts that ecosystems under disturbance pressure have a limited capacity for autogenic balancing and reach thresholds at which the system shifts to an altered state. An altered state likely includes a change in plant species composition and dominance and concomitant shifts in animal composition and ecosystem processes.

Equilibrium Systems vs. Nonequilibrium Systems

To better understand nonequilibrium ecology, let's compare an equilibrium system to a nonequilibrium system. Briske et al. (2017) in *Rangeland Systems: Processes, Management and Challenges* provide us with a concise table comparison.

Table 7.1 Proposed characteristics of equilibrium and nonequilibrium systems (from Briske et al. 2017)

Type	Equilibrium systems	Nonequilibrium systems
Abiotic patterns	Relatively constant	Stochastic/variable
Plant-herbivore interactions	Tight coupling	Weak coupling
	Biotic regulation	Abiotic drivers
Population Patterns	Density dependence	Density Independence
	Populations track carrying capacity	Dynamic carrying capacity limits population tracking
Community/ecosystem characteristics	Competitive structuring of communities	Competition not expressed
	Internal regulation	External drivers

If we were to apply these characteristics to a real-life scenario such as an overgrazed and cheatgrass-invaded (disturbance) sagebrush perennial bunchgrass system, shifts in soil stability and hydrology (abiotic patterns) would be evident, limiting resources for the native community and opening up niches to which cheatgrass is well adapted. The vegetation community composition, through the external drivers of overgrazing and invasive species establishment and facilitated through feedback loops, crosses a threshold to shift from a native perennial bunchgrass community to a new state dominated by cheatgrass. This scenario is fairly well-known. What may not be as well-known, however, is that the process of transition from sagebrush perennial bunchgrass system to a cheatgrass-dominated system is nonequilibrium, but the altered state of cheatgrass dominance is a new state working toward equilibrium until another disturbance restarts the transition process.

So rather than thinking equilibrium versus nonequilibrium system, think about how stable systems are under the stress of disturbance shift; altered systems will reach a point of stability until another disturbance driver pushes them back to the previous system or to a new altered state. This is where resiliency theory comes in.

Section 2: Resiliency Theory

Resiliency is a system's ability to autogenically either return to a high degree of predisturbance structure and function or move to a new stable, alternative state with similar function and structure. The driving objective of human land use and management is to maintain ecosystem integrity to deliver maximum ecosystem goods and services, which requires a high degree of continuity in system structure and function. This section will further explain resiliency theory, while the next section will provide a brief overview of resiliency thinking.

"Ball and Cup"

The diagram in figure 7.1, adapted from Briske et al. (2017), *Rangeland Systems: Processes, Management and Challenges,* illustrates the concept of resiliency.

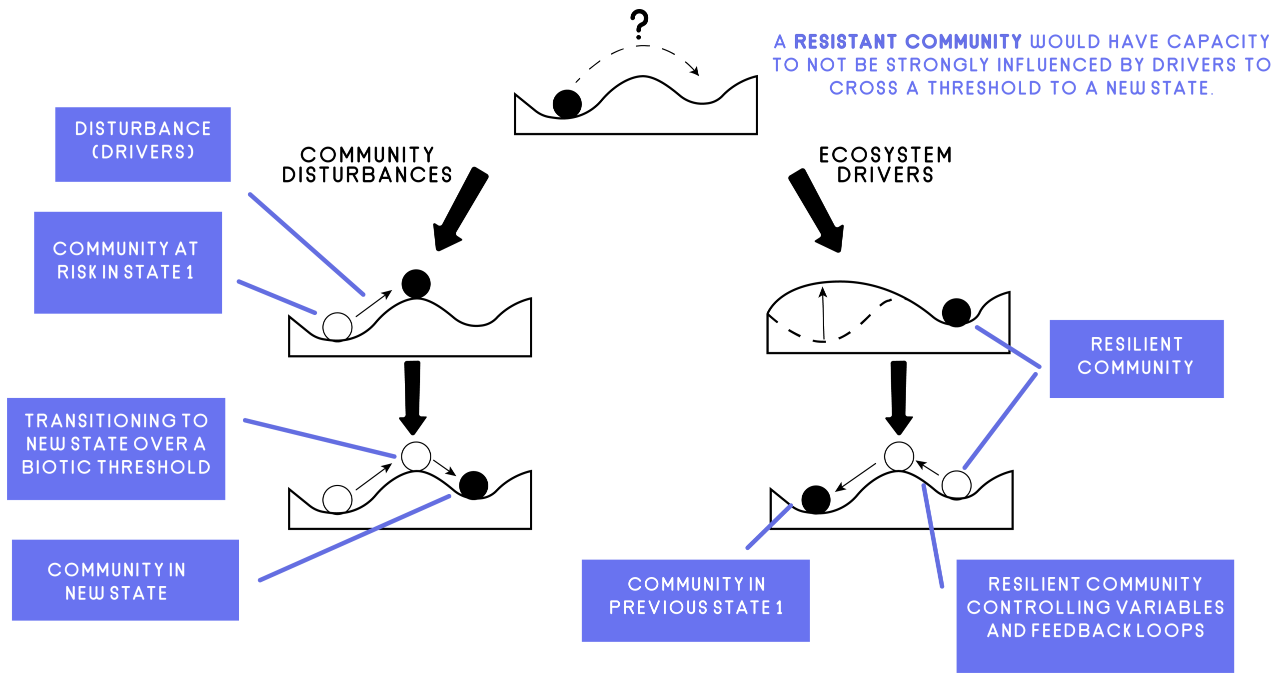


Figure 7.1

To solidify our understanding, let's apply this model to a simplistic real-life scenario. A perennial bunchgrass-shrub community under heavy grazing and drought conditions (disturbance/drivers) crosses a biotic threshold to a new state with a shrub-dominated community. The perennial bunchgrass-shrub community had a high degree of ecological structure and function, as does the shrub-dominated community. After either a fire or the mowing of the shrubs, the system, because of its ecological integrity, reverts back to a perennial bunchgrass community.

In contrast, western juniper (*Juniperus occidentalis*) encroaches in a perennial bunchgrass community, which is also experiencing drought conditions (disturbance/drivers). As western juniper increases in density, the hydrology of the system changes, and the grass and forb community decreases, thus reducing soil quality and stability. This degraded system has a low level of resiliency and therefore crosses an abiotic threshold to a new state dominated by western juniper. After a fire or the felling of the western juniper, the ecological integrity of the system has been degraded to the point that it does not have the capacity to revert to any semblance of perennial bunchgrass community.

Key Elements of the "Ball-and-Cup" Model

To garner an understanding of how to make management decisions framed by the "Ball-and-Cup" model, one must have a grasp of elements: drivers, variables, and feedback loops.

Drivers are disturbances, both naturally occurring and anthropogenic in origin. Drivers disrupt the ecosystem's structure and processes and are not integrated into the system's organic feedback loops. Now fire may be an exception to this. Fire is a naturally occurring process that at low to moderate intensity and recurrence frequency can benefit a system. High-intensity fires or frequent fire occurrences, however, can be a disturbance driver that results in an altered nonresilient state.

Variables are ecosystem components, interactions, and processes. There are two types of variables: fast and slow. Fast variables reflect short-term cycles and immediate response to drivers. Examples include annual plant growth, seasonal soil hydrology, organism population fluctuations, and so on. Slow variables are the controlling variables in a system and are the greatest determinants of a system's resiliency, as they influence fast variables and feedback loops. Slow variables are ecosystem attributes (see the outline in section 2.2).

Feedback loops are ecosystem processes that influence variable rates of change. There are two types of feedback loops—positive (amplifying and accelerating effect) and negative (stabilizing effect). Ecosystems with a high degree of resiliency are dominated by negative feedback loops, while ecosystems with a low degree of resiliency are dominated by positive feedback loops.

Attributes of and Influences on Ecosystem Resiliency

What are the attributes and influences that make an ecosystem resilient and that foster ecological integrity of structure and function? There are three categories of attributes and functions that indicate degree of resiliency: biotic integrity, soil stability, and hydrologic function.

Biotic Integrity

Biotic integrity is reflected by the degree of diversity in the system in terms of species composition, structure, function, and adaptations; genetic diversity, habitat diversity, and so on. *Functional diversity* (redundancy of species or groups of species functions in an ecosystem) is particularly important for resiliency, as it increases the system's capacity to maintain balance and carry out ecosystem functions.

Soil Stability

Soil stability is reflected in maintained integrity of soil aggregate structure, bulk density, and belowground biomass and biotic functions. Soil type also influences ecosystem resiliency. The greater degree of soil development, and concomitant soil organic matter and available minerals, the greater the resiliency capacity.

Hydrologic Function

Hydrologic function is reflected in the system's ability to capture, store, and safely release water. This ability is highly dependent on biotic integrity and soil stability.

Additional influences include climate and disturbance history.

Climate

Climate greatly influences a system's ability to leverage its biotic integrity, soil stability, and hydrologic function. Hot, dry years can reduce plant production, which can reduce a system's carrying capacity. Reduced plant production can reduce canopy cover and water interceptions and infiltration during precipitation events. Plant and soil evapotranspiration can increase, leaving soils with a fragile crust susceptible to erosion and reduced water infiltration. Reduced belowground plant rooting and microbial functions reduce nutrient cycling and increase bulk density.

Disturbance History, Frequency, Intensity, and Type

Disturbance history, frequency, intensity, and type (covered in chapter 6) also influence a system's resiliency. An accumulation effect can build if the disturbance regime is frequent or if there is synergy among disturbance events.

Section 3: Resiliency Thinking and Social-Ecological Systems (SES)

Resiliency thinking is the integration of human understanding of nonequilibrium ecology, resiliency theory, and desire to maximize ecosystem goods and service delivery. It is a framework for humans in nature and a way of thinking that can help guide management, either by guiding change or by bolstering a system's ability to recover post-disturbance. It is comprised of two approaches: (1) adaptive management and (2) social learning. These are elements in the overarching concept of social resilience.

Adaptive Management

Adaptive management is learning through doing. It is an approach that allows action to be taken in the face of uncertainty and to be adjusted based on progress, impacts, or outcome trajectories. Adaptive management provides flexibility to expand and contract the scope of management. This is of particular value, as interconnections previously not considered are illuminated and social and economic factors can be progressively included.

Social Learning

Social learning allows multiple stakeholders to contribute varying perspectives so that management decisions represent the ecological, social, and economic complexity of an ecosystem. The spirit of this approach aims not only to give all stakeholders a voice but also to learn from one another's perspectives and interpretations to achieve the greatest degree of resiliency possible.

Social Resilience

Social resilience is a concept that emphasizes the integration of the social and economic into the focus on ecological resiliency. Social resilience is supported by the idea that socioeconomic systems that are resilient support communities or populations of people that have the capacity to thrive will in turn reduce anthropogenic pressures on natural resources and systems. It acknowledges that ecological, social, and economic factors are intricately tied together and of equal importance.

The ubiquity of human impacts and our dependence on the delivery of ecosystem requires resiliency thinking and a social-ecological framework. To achieve this, managers and decision makers representing multiple perspectives must work collaboratively to understand as completely as possible the autecology and synecology of ecosystems; the disturbance dynamics and resilient capacity of ecosystems; and the social-economic-economic connections of ecosystems.

Shrubland and Desert Ecosystems

Sagebrush Ecosystems

Sagebrush ecosystems are located throughout the Great Basin, but they are considered by many to be an endangered ecosystem due to invasive species proliferation (particularly cheatgrass [*Bromus tectorum*]), alternations of fire regimes, and land conversion and uses (e.g., urbanization, dryland farming, overgrazing). The peril face by the sagebrush ecosystem has been brought to light by its namesake species—sage grouse (*Centrocercus urophasianus*), whose populations have declined to the point of being considered a threatened species because of loss of habitat.

Section 1: Geographic Distribution

Geographic Location

Sagebrush steppe is located throughout the regions of the Intermountain West, the Columbia and Colorado Plateaus, and the Great Basin in the states of Washington, Oregon, California, Idaho, Nevada, Wyoming, Utah, Colorado, Arizona, and New Mexico (figure 8.1).

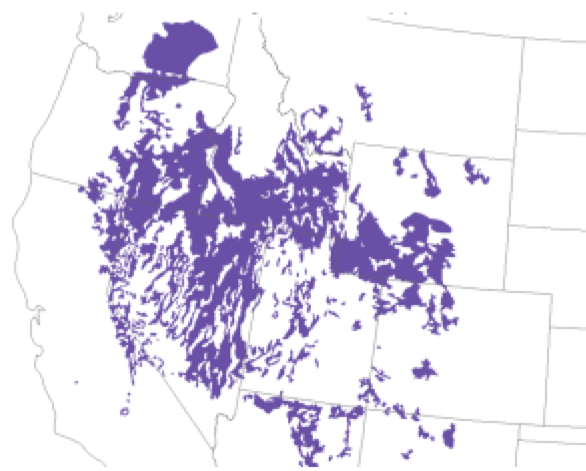


Figure 8.1 Distribution of sagebrush steppe

Section 2: Major Land Resource Areas of Sagebrush Ecosystems

Sagebrush ecosystems are present in varying extents and densities throughout the following Major Land Resource Areas (MLRAs):

- Region B-7 Columbia Basin
- Region B-8 Columbia Plateau
- Region B-10 Central Rocky and Blue Mountain Foothills
- Region B-11 Snake River Plains

Sagebrush is present in Regions B-12 Lost River Valleys and Mountains and B-13 Eastern Idaho Plateaus, but these areas are dominated by bunchgrass, grass, and forb species.

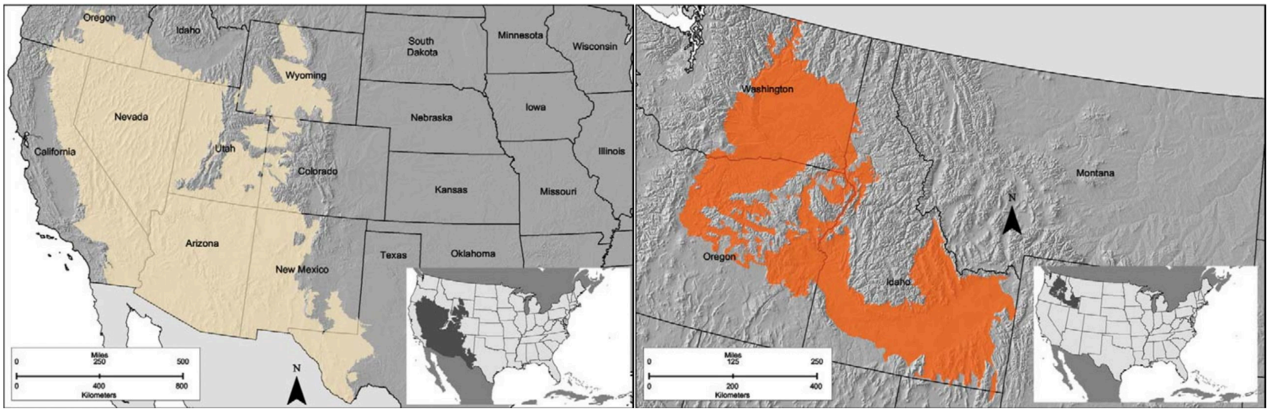


Figure 8.2 MRLA region D & B maps

- Region D-23 Malheur High Plateau
- Region D-24 Humboldt Area
- Region D-25 Owyhee High Plateau
- Region D-26 Carson Basin and Mountains
- Region D-32 Northern Intermountain Desertic Basins
- Region D-34A Cool Central Desertic Basin and Plateaus (higher precipitation)
- Region D-35 Colorado Plateau (sagebrush and pinyon-juniper)
- Region D-36 Southwestern Plateaus, Mesas, and Foothills (sagebrush and pinyon-juniper)

Each MLRA has reflective physiography, geology, climate, water, soil and biological resources, and associated land uses. There is a great degree of variation across the MLRAs of sagebrush ecosystems in terms of climate, topography, soil, plant species composition, hydrology, and community dynamics. This text will look at each system through an MLRA lens. To find out more information about specific MLRAs, the US Department of Agriculture Handbook 296, Land Resource Regions and Major Land Resource Areas of the United States, the Caribbean, and the Pacific Basin, is available online, as well as interactive MLRA maps.

B-Region MLRAs

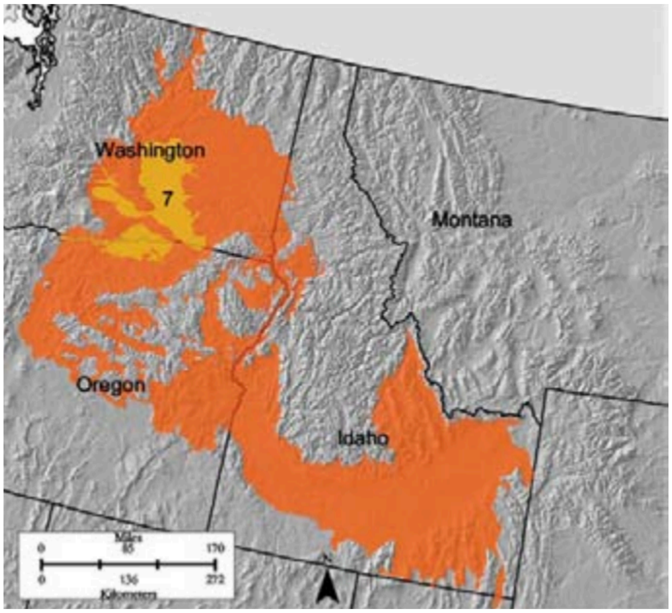


Figure 8.3

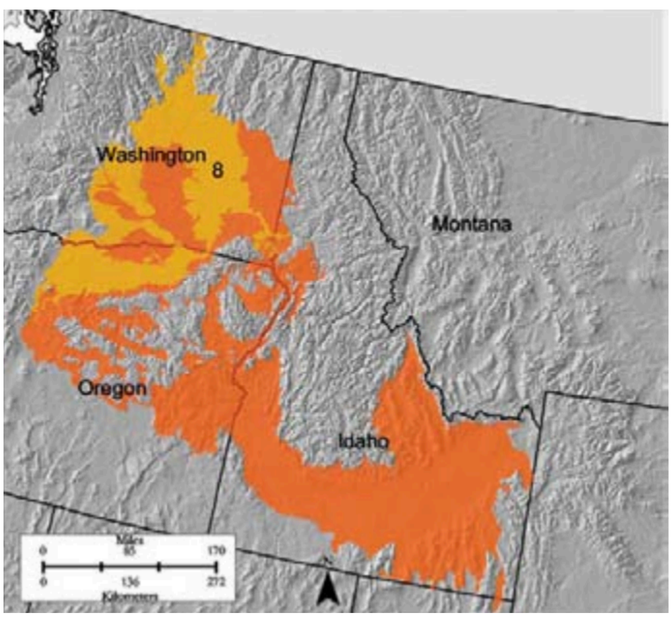


Figure 8.4

This region comprises plains and plateaus across 81,225 square miles of Idaho, Washington, Oregon, and a small area of Utah, on the leeward side of the Cascade Mountains (figure 8.2). The topography of the region ranges from smooth, rolling plain dissected by rivers and streams to steep slopes, and young incised valleys. Alluvial fans of glacial washout are prevalent in some northern areas. The formation of the area's topography and soils were heavily influenced by Missoulian floods. Soils across the region are dominantly and moderately deep to very deep well-drained Aridisols and Entisols.

Precipitation occurs mostly in fall, winter (snow), and spring as a result of low-intensity storms in the form of rain or snow. Summers are generally dry. Out of all the land resource regions, this region uses the largest amount of water (91 percent of it for irrigation). Although the region is underlain with basalt aquifers, most of the water use is from surface waters of the Snake and Columbia River systems. Mollisols, Aridisols, and Entisols are the dominant soil orders of the region.

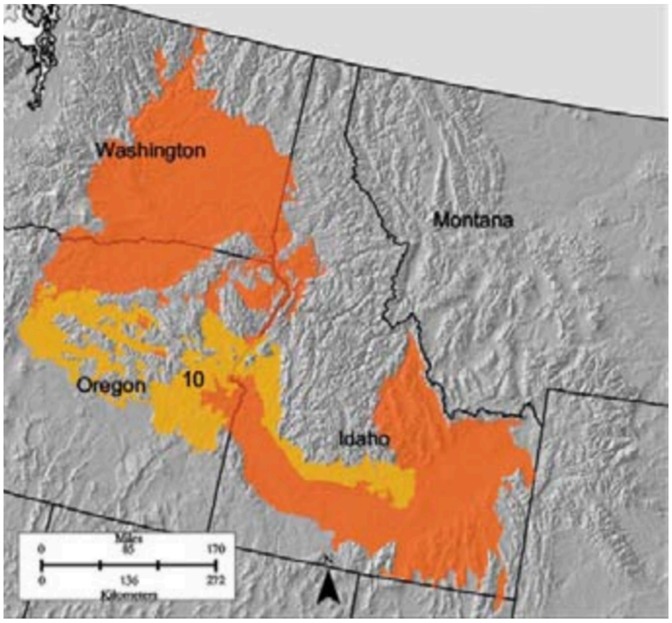


Figure 8.5

B-7 Columbian Basin vegetation communities are shrub-grass associations comprised of big basin sagebrush (*Artemisia tridentata*) and Wyoming big sagebrush (*Artemisia tridentata wyomingensis*). Understory grass is dominated by bluebunch wheatgrass (*Pseudoroegneria spicata*). In sandier soil areas, needle-and-thread grass (*Hesperostipa comata*) and bitterbrush (*Purshia tridentata*) are dominant. In inland riparian areas, saltgrass (*Distichlis spicata*), basin wildrye (*Leymus cinereus*), and greasewood (*Sarcobatus vermiculatus*) are dominant.

B-8 Columbia Plateau vegetation communities are similar to those in the B-7 Columbia Basin region; however, Idaho fescue (*Festuca idahoensis*) are dominant among sagebrush on north-facing slopes. In warmer areas, there are stands of ponderosa pine (*Pinus ponderosa*) with a Snowberry (*Gaultheria spp.*) shrub understory, and in warmer and more mesic areas there are oak species (*Quercus spp.*) and dwarf hardwoods.

Blue Mountain Foothills *vegetation* communities are similar to those in the Columbia Basin Region with the addition of antelope bitterbrush (*Purshia tridentata*) in more mesic areas, and western juniper (*Juniperus occidentalis*) on rocky outcrops. Due to a history of fire suppression and a reduction in the shrub understory, western juniper has expanded into shrub-grass communities to the extent that the species is becoming increasingly dominant. The Columbia Basin and Plateau regions are upland salmon and trout stream and spawning habitat.

Landownership and management in B7 and B8 are largely private, while in B-10 about half of the region is federally managed by the Bureau of Land Management (BLM). The regions are generally used for livestock grazing, with hay, small grains, and some herbs and vegetables grown in areas in close proximity to surface water. Overgrazing, riparian area degradation, woody species encroachment, and reductions in native grass species are primary concerns across all three regions. Much of the region is challenged by soil erosion, invasive species, and soil compaction. Conservation practices include: brush management, prescribed burning, native plant seeding, and riparian area restoration.

D-Region MLRAs

Figure 8.6

Figure 8.7

Region D is the largest of the land resource regions. It consists of desert or semidesert plateaus, plains, basins, and isolated mountain ranges across 549,725 square miles of California, Nevada, Oregon, Utah, Arizona, western New Mexico, Colorado, and central portions of Wyoming (figure 8.2). It is a region comprised of plains, basins, valleys, and moderately steep plateaus. North-south fault-block mountain ranges separate basins in some areas. Elevation ranges from 3,900 to 6,900 feet, with some mountain peaks upward of 9,000 feet.

Precipitation ranges from six inches in the lower-lying areas to forty-two inches in the mountains. Warm-season monsoonal precipitation dominants in the southern portions, while cool-season winter storms are the source of precipitation in the northern areas of the region. Annual average temperatures range from 40°F to 60°F along a gradient increasing in temperature from North to South, which is reflected in the spectrum of frost-free days: 105 in the north to 260 in the south. Given the aridity of the area, it is worth noting that daily water draws across the region average more than thirty billion gallons a day.

Figure 8.8

Surface water is the primary source for use, although streams are intermittent, as they are driven by snow melt runoff. Due to high evaporation rates, salt accumulation is high, which reduces the quality of water when precipitation events occur and water pools in basin areas. Although there is a large supply of groundwater, it is trapped beneath alluvial-fan-driven gravel and sand-filled basins and valleys.

Land uses are primarily cropping, grazing, and recreation; however, cropping is a very minor land use for the regions included in this text. Sixty percent of the region is federally managed and largely used for grazing. Much of the region is challenged by a history of overgrazing, woody species encroachment, soil erosion, invasive species, and increasing pressures from outdoor recreation. Conservation practices include brush management, prescribed burning, native plant seeding, and riparian area restoration.

Figure 8.9

The D-23 Malheur High Plateau is a 22,895-square-mile area across Oregon, Nevada, and California; it includes no major cities and has one major highway crossing a small section of its southern portion. Alluvial fans, playas, and large areas with ash particles and glassy minerals are characteristic of the region. Dominant soils are Aridisols and Mollisols.

Vegetation communities are similar to those of MLRA Region B, with the addition of silver sage (*Artemisia cana*) in wetter areas along la playa edges and halophyte species such as saltbush (*Atriplex canescens*). Aspen groves and Douglas fir stands occur at higher elevations.

Figure 8.10

Figure 8.11

In the D-24 Humboldt Area, 93 percent of which is in Nevada, this region of 12,680 square miles is a series of North-South fault mountains interspersed with wide alluvium and lacustrine valleys (elevation ranges from 3,000 to 5,900 feet), most of which drain to the Humboldt River. Soils are generally well drained, a deep and loamy mosaic of Aridisols, Entisols, Inceptisols, and Mollisols.

Figure 8.12

In areas with precipitation greater than eight inches, big basin sagebrush is the characteristic plant. On drier sites, shadescale (*Atriplex confertifolia*) and bud sagebrush (*Picrothamnus desertorum*) are dominant. Grass species in the region include Thurber's needlegrass (*Achnatherum thurberianum*), bluebunch wheatgrass (*Pseudoroegneria spicata*; wetter sites), and Sandberg bluegrass (*Poa secunda*).

The area of the D-25 Owyhee High Plateau is adjacent to the Humboldt Area MLRA and covers 28,930 square miles into the southeast corner of Oregon, southern Idaho, and a very small area of northwestern Utah. It has similar characteristics to the Humboldt Area; however, its topography and soils are the product of volcanic activity and resulting basalt flows. Like other D and B regions, vegetation is dominated by big and low sagebrush with an understory of bluebunch wheatgrass with the addition of western wheatgrass (*Pascopyrum spp.*) and a variety of other grasses and forbs. Woody species, such as juniper, curly leaf mountain mahogany (*Cercocarpus ledifolius*), snowberry, and ceanothus species, are found on high plateaus. At higher elevations vegetation shifts to conifers.

The D-32 Northern Intermountain Desertic Basin is 8,910 square miles of basin areas among mountains largely in Wyoming. The Aridisols and Entisol soils of the area are the product of mountain drainage. Prevalent are big sagebrush species, black sage (*Artemisia nova*), and Gardner's saltbush (*Atriplex gardneri*), with an understory of wheatgrasses, Indian ricegrass (*Oryzopsis hymenoides*), and other grasses.

The D-34A Cool Central Desertic Basins and Plateaus region, just below the Northern Intermountain Desertic Basin, is 33,005 square miles, also largely in Wyoming with small reaches into Utah and Colorado, and bounded by mountains. The area's geology is similar to the Northern Intermountain Desertic Basin region; however, it encompasses three distinct vegetation zones delineated by precipitation:

- The Salt Desert Zone receives less than eight inches of precipitation and is dominated by shrub species, such as four-wing saltbush (*Atriplex canescens*), greasewood (*Adenostoma fasciculatum*), shadescale (*Atriplex confertifolia*), bud sagebrush (*Picrothamnus desertorum*), and winterfat (*Krascheninnikovia lanata*).

- The Grass-shrub Zone, receiving eight to sixteen inches of precipitation, is a typical sagebrush steppe region that may be dotted by Utah juniper (*Juniperus osteosperma*). Cottonwoods and willow species line riparian areas.
- The Foothill-Mountain Zone receives more than sixteen inches of precipitation to support a pine system with an understory of big sagebrush, Saskatoon serviceberry (*Amelanchier alnifolia*), antelope bitterbrush, and bunchgrasses.

The D-35 Colorado Plateau encompasses some of the most beautiful landscapes in the Southwest, at least by your author's standards. This region is 71,735 square miles largely in Arizona, but with reaches into southern Utah and northwest New Mexico, and a small corner of southwest Colorado. This region is home to the heavily used Canyonlands, the Grand Canyon, Grand Staircase–Escalante, and the Navajo Nation. It is a mix of deep canyons, plateaus, basins, and isolated mountains as a result of uplift and rivers. Whereas surface water was the primary source in most regions discussed, groundwater is the source in this region. Vegetation shifts to sagebrush mixed with a pinyon-juniper system; the grama grasses (*Bouteloua eriopoda* and *Bouteloua gracilis*) form the understory, among other grass and shrub species. Soil salinity becomes an increasing issue in areas of this region.

D-36 Southwestern Plateaus, Mesas, and Foothills, in which the author of this text lives along with a number of Native American tribes, is 23,885 square miles across southwest Colorado, north-central New Mexico, and a small area in southeastern Utah. Distinctive on the landscape are horizontal layers of sedimentary rock from the Jurassic, Cretaceous, and Tertiary periods that have eroded into plateaus, mesas, hills, and canyons. While the Colorado Plateau relied on groundwater, this region relies on the surface waters of the Dolores, Animas, and San Juan Rivers. Vegetation is similar to the Colorado Plateau region with the addition of firs and pines at higher elevations and Gambel oak (*Quercus gambelii*) among the pinyon-juniper system. Prairie dogs, bears, and coyotes are particularly challenging in this region, as is extensive recreation.

Section 3: Sagebrush Species

Common to all the MLRAs above is sagebrush species (*Artemisia spp.*). Knowing the general soil conditions (moisture and temperature) and plant associations in which each sagebrush species generally occurs can give a head start in gathering knowledge of a specific site.

Big and Low Sagebrush

The first categorization of sagebrush species is big and low sagebrush species.

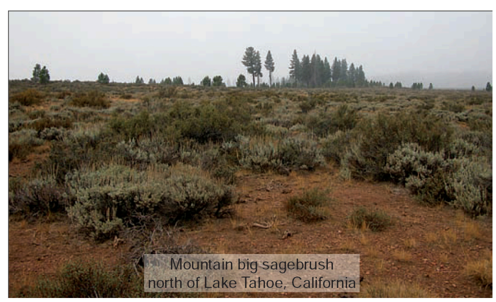
Big Sagebrush Species

Big sagebrush species (*Artemisia tridentata*) are divided into four subspecies:

<table>
<tr>
<td>Big Basin Sagebrush

Artemisia tridentata tridentata</td>
<td>
Figure 8.13</td>
</tr>
<tr>
<td>Wyoming Big Sagebrush

Artemisia tridentata wyomingensis</td>
<td>
Figure 8.14</td>
</tr>
<tr>
<td>Mountain Big Sagebrush

Artemisia tridentata vaseyana</td>
<td>
Figure 8.15</td>
</tr>
<tr>
<td>Scabland Big Sagebrush

Artemisia rigida</td>
<td>
Figure 8.16</td>
</tr>
</table>

The dominance of Artemisia species is due to two primary factors:

- *Dimorphic leaves*. The species has large ephemeral leaves that develop in late spring to maximize photosynthetic capacity and growth. The large leaves remain until moisture stress develops in summer, then they drop and give way to smaller leaves that reduce moisture loss through transpiration. These remain until the following spring.
- *Phreatophytic rooting system*. The species has both fibrous lateral surface roots that can draw water and nutrients near the surface and a taproot that can obtain water and nutrients from deep in the soil profile.

One may logically conclude that if sagebrush is removed, soil moisture increases. This is true, but only at a certain rooting depth. Also of note, big sagebrush species are not tolerant of flood conditions for more than two or three days.

Low Sagebrush Species

Low sagebrush species include the following:

Low Sagebrush *Artemisia arbuscula*	Low-growing evergreen shrubs usually less than two feet tall with multiple stems that appear to rise from the ground, often lacking an apparent trunk. Plants are usually found on shallow clay or rocky soil “islands” amid large stands of big sagebrush.	 Figure 8.17
Bigelow Sagebrush *Artemisia bigelovii*	Bigelow sagebrush is distinctive for its small, round (not bell-shaped) flowering heads, wand-like stems, and leaves with pointed lobes. Even so, this lovely silvery-leaved shrub is often overlooked because it can blend in with other gray-colored sagebrush. It grows primarily in sandy or rocky soils of warm deserts. It is sometimes called “plateau sagebrush” for its occurrence in slick rock habitats of the Colorado Plateau region of Arizona and Utah. Bigelow sagebrush also occurs in the short-grass shrubland of west Texas and New Mexico, the Mohave Desert of Arizona, California, and southern Nevada, and it extends north into the frigid clay soils of the Uinta Basin of Utah.	 Figure 8.18

Silver Sagebrush *Artemisia cana*	Silver sagebrush has long, mostly entire leaves, and it freely resprouts after disturbance. Its deciduous habit and tendency to grow in sites that are wet or seasonally waterlogged distinguishes it clearly from the evergreen big sagebrush. Great Plains weather influences its distribution. *A. cana* resprouts from fire and other disturbances. There are three subspecies of silver sagebrush that are geographically distinct: (1) Bolander sagebrush (subsp. *bolanderi*) occurs from the Sierras of California to Oregon, usually on poorly drained clay soils or in standing water. It is highly variable in morphology, ranging from short to tall plants with narrow or broad leaves. (2) Mountain silver sagebrush (subsp. *viscidula*) is the most abundant of the three subspecies of silver sagebrush and is distinguished by its somewhat sticky (viscid) yellow-green or gray leaves. It is found in mountain meadows, along streams, or in depressions with late-lying snows. (3) Plains silver sagebrush (subsp. *cana*) is taller and bushier than the other two subspecies and is found in areas with summer rain, primarily east of the Continental Divide in deep, loamy soils.	 Figure 8.19
Fringed Sagebrush *Artemisia frigida*	Fringed sage forms distinctive mounds, and it is the most widely distributed of all the species of *Artemisia*. It is found throughout the northern hemisphere from boreal regions near the Arctic Circle to the cool-season grasslands of Asia and North America. It is found in shallow soils that are regularly disturbed by either natural forces (e.g., wind) or mechanical disturbance. Widely distributed and highly variable, this species has recently been marketed in the horticultural trade. Fringed sage is the only species included in this guide that has a hairy receptacle.	 Figure 8.20

Black Sagebrush *Artemisia nova*	Black sagebrush has leaves that are darker green than other species of sagebrush. The dark green glands exposed on the sparsely hairy surface are often used as a way to identify the species. The glossy flower bracts and reddish-brown persistent flowering stalks also help to identify this species. Black sagebrush is highly drought-tolerant and often found on dry microsites such as west- or south-facing slopes, usually in shallow, rocky, calcareous soils.	 Figure 8.21
Bud sagebrush *Picrothamnus desertorum*	Bud sagebrush is distinctive in a number of ways: it has spine-tipped branches (for which the species is named), flowers in the spring, and has large-headed yellow flower stalks tucked within the vegetative portion. The spiny stems, short flower stalks, and multilobed leaves make it unlike anything else in the sagebrush complex. It is extremely drought tolerant, often growing with saltbush, and is remarkably palatable to domestic livestock. It provides good forage during winter months, but it is potentially poisonous to young livestock if consumed in great quantities. It grows primarily in valleys, often in saltbush or greasewood communities.	 Figure 8.22

Low sagebrush species generally occur where soil erosion in former big sagebrush communities has exposed the clay-textured and/or calcified horizons in the subsoil. These species are also more water tolerant and tolerant of monsoonal events that occur in the southern portions of the MLRA B and D regions.

General Characteristics of Sagebrush Species

Regardless of their classification as big or small, sagebrush species share a number of characteristics. They all belong to the sunflower family, or Asteraceae, even though they do not have the showy flowers that are common to most members of that family.

Many volatile compounds in sagebrush give it its characteristic odor. Many are produced in the glands on the leaves, which is why sagebrush smells so strong when you crush the leaves in your hand. Some of these compounds confer protection by deterring insects and other predators, and some of the compounds actually attract grazing animals. Water-soluble coumarins and other compounds fluoresce under ultraviolet light, and the presence of these compounds correlates with increased palatability. Determining the presence of coumarins can thus be used as a measure of a plant's relative importance to wildlife. The volatile compounds as well as other secondary compounds also have antibacterial properties that have led to numerous medicinal uses of sagebrush as well as ritualistic cleansing.

All Artemisia species are fairly prolific seeders following flowering in late summer or fall. Rather than depending on insect pollination under cold desert conditions, sagebrush depends on wind for pollination. Seeds germinate in late winter or early spring, and once past the seedling stage, they are generally long-lived. Sagebrush does not resprout, which is why when burned or mechanically removed retrogression to substantially earlier successional state results.

Section 4: Succession and Retrogression in Sagebrush Ecosystems

Sagebrush ecosystems have a high degree of disturbance, whether from overgrazing, land conversion, fire suppression and resulting woody species encroachment, invasive species establishment and proliferation, or other land uses such as recreation. Although we cannot cover all variations of succession and retrogression across all ecological sites of the MLRAs covered in this text we can review a few examples that reflect generalized ecosystem change across sagebrush ecosystems.

Historic Nonnative Crested Wheatgrass Seeding

Many areas of the "B" MLRAs were subject to land conversion due to homesteading activities in the mid to late 1800s. In the early 1900s, due to economic downturn and the Great Depression era, many of these homesteaded areas were abandoned and subsequently returned to federal ownership. To "rehabilitate" these areas to make them once again "productive," in the 1950s they were seeded with nonnative species, largely crested wheatgrass (*Agropyron cristatum*), a palatable forage for cattle. These areas were then subject to grazing pressure. The state and transition model below reflects the

Keystone Ranch, about 1890.

Keystone Ranch, 1989.

Figure 8.23

impacts on sagebrush systems throughout Oregon, Idaho, Wyoming, and northern Nevada from overgrazing, crested wheatgrass seeding, and cheatgrass invasion.

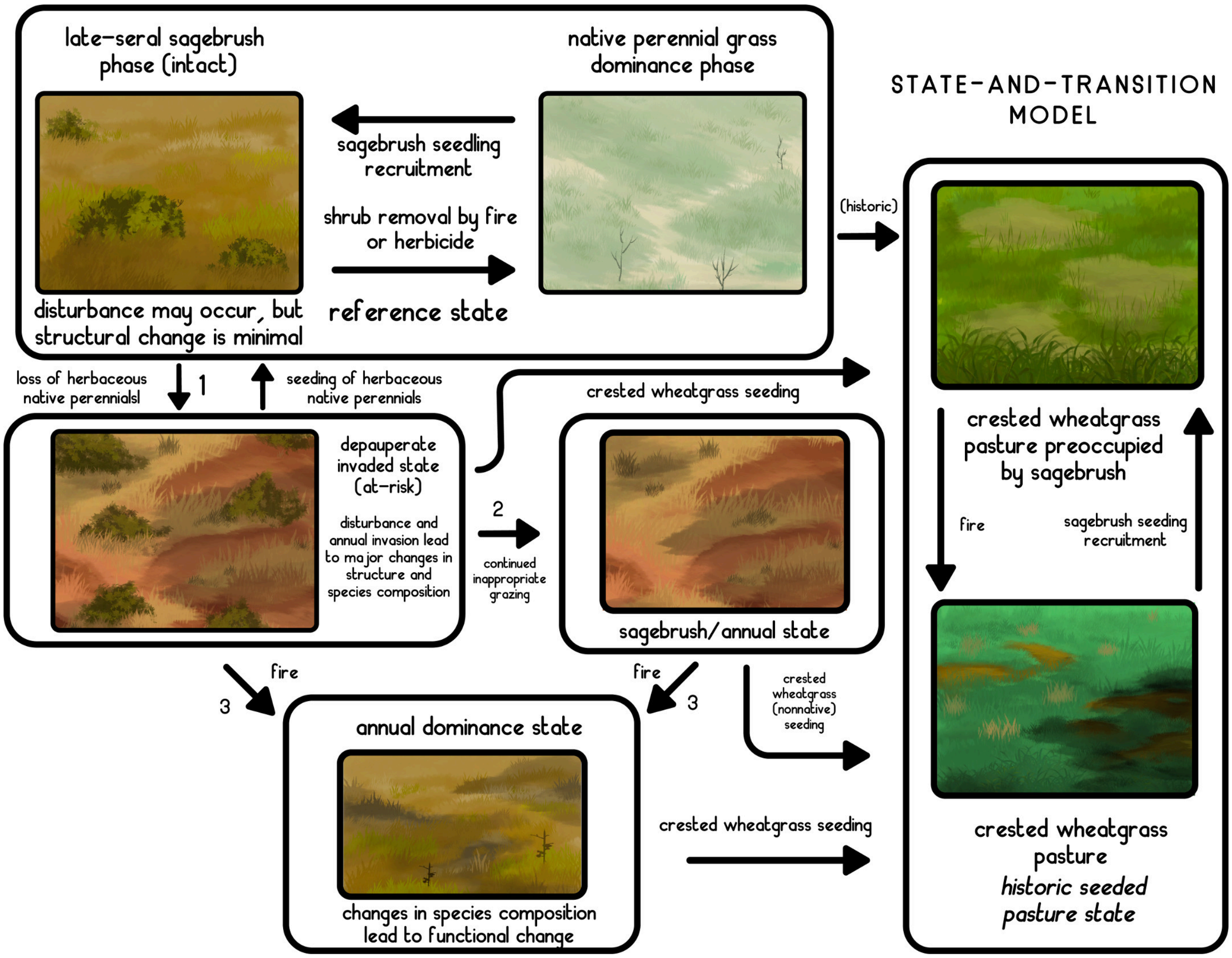


Figure 8.24

Juniper-Invaded Sagebrush System

The image in figure 8.25 depicts a common occurrence across many of the MLRAs of sagebrush systems. Historically, juniper species are found on rocky hillsides, but as a result of overgrazing and fire suppression, juniper species have continuously proliferated down hillsides and into lower-lying areas of sagebrush sites. North of Utah or lower Idaho the encroachment is limited to juniper species, but from northern Utah south, the encroachment is either juniper species only or a mix of juniper and pinyon pine.

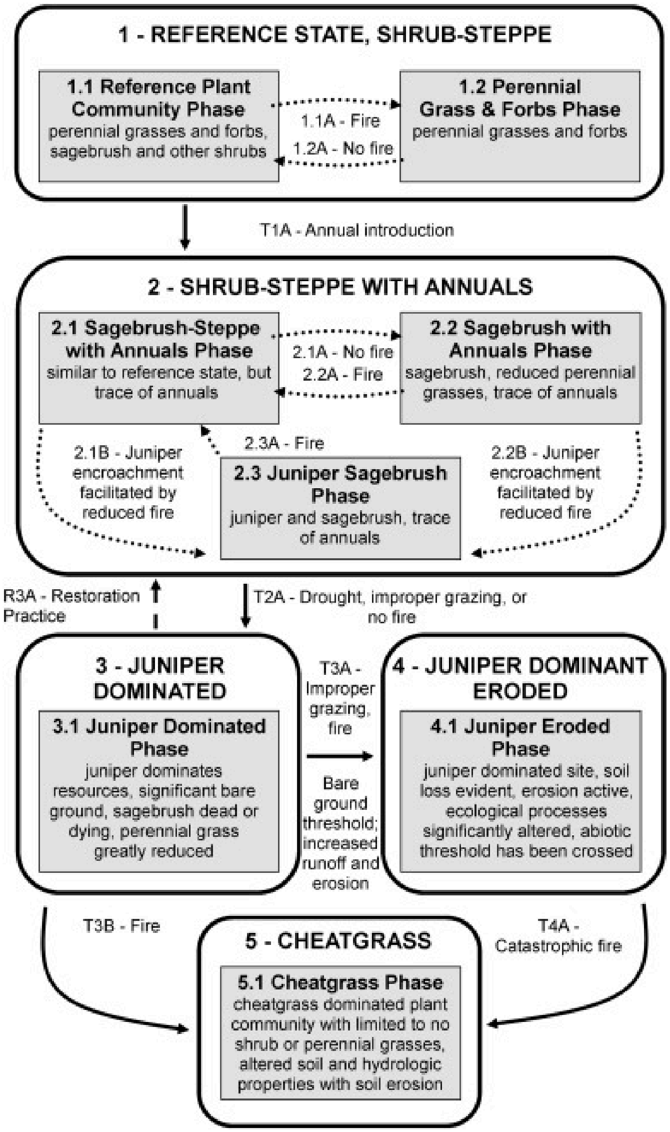
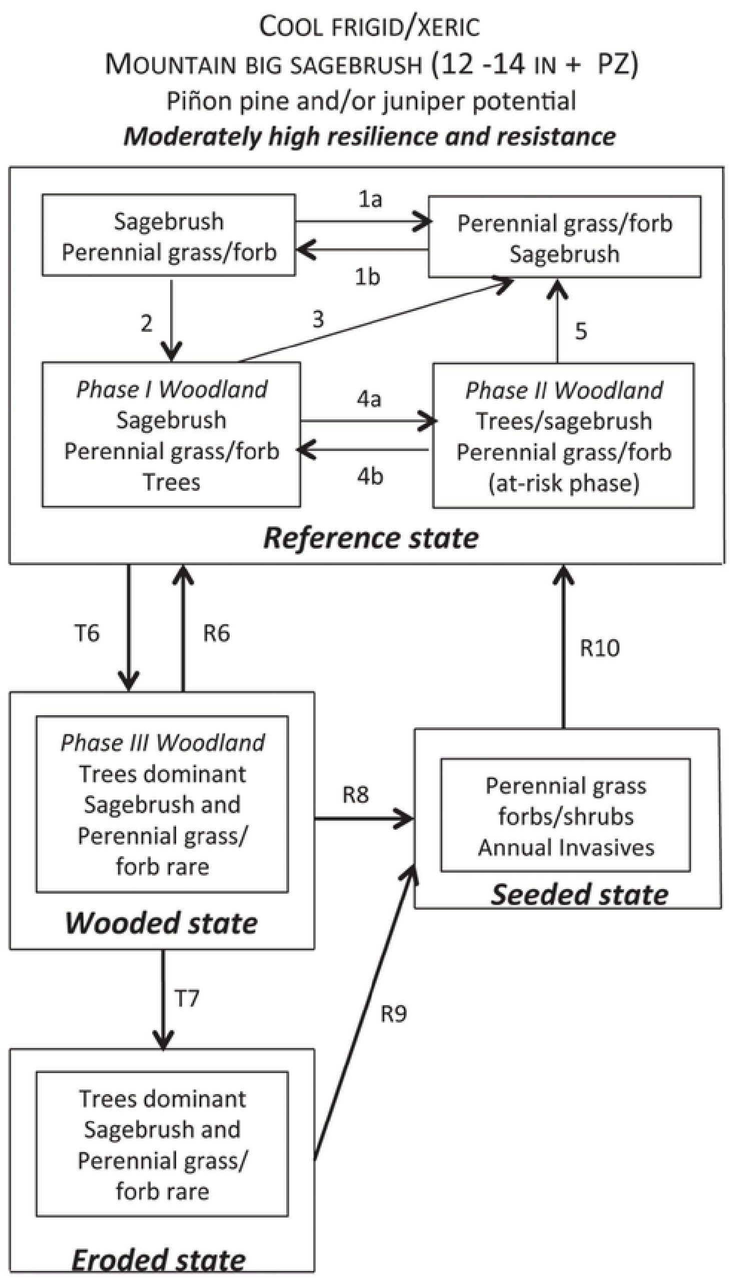


Figure 8.25

Following the state-and-transition model (STM) (figure 8.25) we see that the process of juniper encroachment begins with fire suppression and establishment of annual invasive grasses; the process is then exacerbated by continued fire suppression, overgrazing, and drought condition. As the grass and forb community in the juniper-invaded site is reduced, soil stability decreases and soil erosion increases, creating a positive feedback loop that accelerates woody species and annual invasive grass proliferation.

Figure 8.26 presents another STM example of the progression from a sagebrush system to a tree-dominated (here pinyon-juniper) system. This site is more southern and at a higher elevation; however, the same drivers (fire suppression and invasive annuals) of system change apply. STMs across sagebrush systems largely tell the same story.



(1a) Disturbances such as wildfire, insects, disease, and pathogens result in less sagebrush and more perennial grass/forb.

(1b) Sagebrush increases with time .

(2) Time combined with seed sources for piñon and/or juniper trigger a Phase I Woodland.

(3 and 5) Fire and or fire surrogates (herbicides and/or mechanical treatments) that remove trees may restore perennial grass/forb and sagebrush dominance.

(4a) Increasing tree abundance results in a Phase II woodland with depleted perennial grass/forb and shrubs and an at-risk phase.

(4b) Fire surrogates (herbicides and/or mechanical treatments) that remove trees may restore perennial grass/forb and sagebrush dominance.

(T6) Infilling of trees and/or improper grazing can result in a biotic threshold crossing to a wooded state with increased risk of high severity crown fires .

(R6) Fire, herbicides and/or mechanical treatments that remove trees may restore perennial grass/forb and sagebrush dominance.

(T7) An irreversible abiotic threshold crossing to an eroded state can occur depending on soils, slope, and understory species.

(R8 and R9) Seeding after fire may be required on sites with depleted perennial grass/forb, but seeding with aggressive introduced species can decrease native perennial grass/forb. Annual invasives are typically rare. Seeded eroded states may have lower productivity.

(R10) Depending on seed mix and grazing, return to the reference state may be possible if an irreversible threshold has not been crossed.

Figure 8.26

Pinyon-Juniper Woodland Ecosystems

Pinyon-juniper (PJ) systems create a mosaic with sagebrush, pine, and montane ecosystems covering millions of acres. They are not well-studied systems, and they are often seen as barren "wasteland." However, they most certainly are not: they are a dominant ecosystem in some of the West's more beautiful landscapes and recreation areas. PJ systems are woodlands that have at least one *Pinus* species mixed with juniper (*Juniperus spp.*). Due to temperature tolerances, pinyon is generally not found beyond the reaches of northern Utah and southern portions of Wyoming and Idaho. PJ systems generally sit at mid-elevations on the landscape, with shrubland and grasslands at lower elevations and ponderosa pine, and montane PJ systems at higher elevations. Like most ecosystems in the West, PJ systems are stressed by a history of overgrazing, invasive species, and heavy recreational use. PJ systems are also under pressure from intensive natural gas extraction in southern Colorado and New Mexico.

Section 1: Geographic Distribution

Pinyon-juniper woodlands are in regions subject to temperature extremes and limited precipitation throughout Nevada, Utah, Colorado, and New Mexico (figure 9.1). Geologic records indicate that around thirteen thousand years ago PJ systems moved north to areas of higher elevation as a result of climate conditions that were becoming drier and warmer.

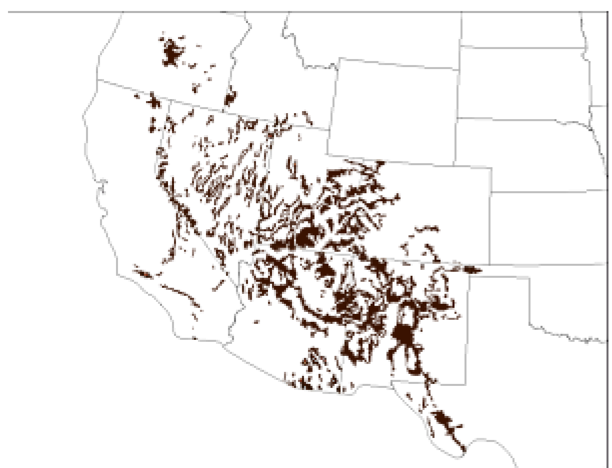


Figure 9.1 Geographic distribution or pinyon-juniper ecosystems in the western United States

Today PJ systems occur between 4,500 and 7,500 feet elevation and in areas with precipitation regimes that range from seven to twenty-five inches.

This chapter will also include systems in which PJ is present, but not dominant. These systems are mosaic gradients across elevations and include grasslands, shrublands, woodlands, and pine and alpine systems in transition zones between the Colorado Plateau province and the Basin and Range province (the area around the bold black line in Arizona and New Mexico in figure 9.2).

Section 2: Major Land Resource Areas (MLRAs) of Pinyon-Juniper Ecosystems

Figure 9.2 Map of the physiographic provinces in the western United States

PJ systems are interspersed throughout sagebrush ecosystems in Land Resource Areas D and two regions of Land Resource Area E.

- Region D-35
- Region D-36
- Region D-38
- Region D-39
- Region E-49
- Region E-51

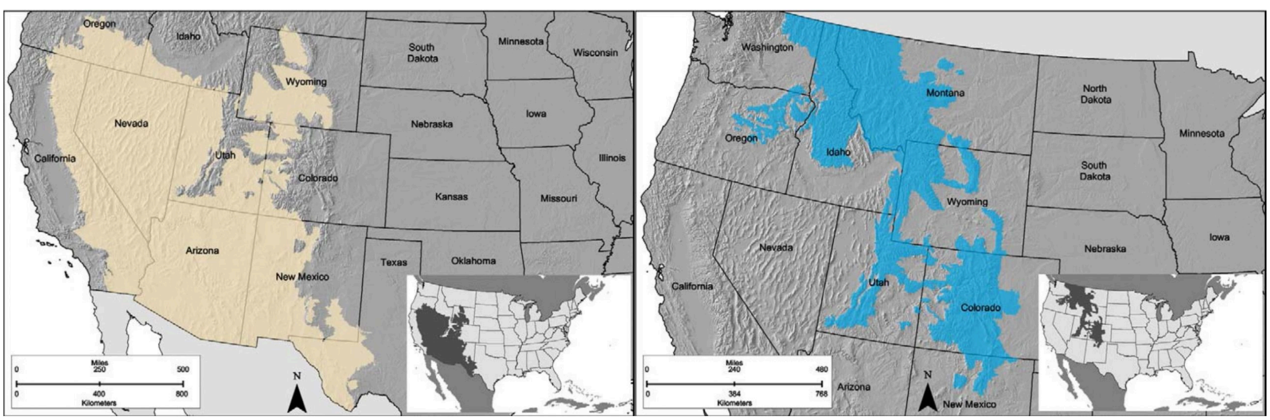


Figure 9.3

D-Region MLRAs

A general description of the D Land Resource Area is covered in chapter 8 on sagebrush systems.

Figure 9.4

D-35 Colorado Plateau is located across the only location in the United States where a boundary of four states (UT, CO, AZ, NM) meet at a single point—Four Corners National Monument. This MLRA also encompasses multiple national parks and monuments, including the Grand Canyon, Canyonlands, Arches, and Grand Staircase–Escalante. Reservations of numerous Native American tribes are in this region, including Navajo, Hopi, Zuni, Hualapai, and Southern Utes. This region experiences a high volume of use as a tourist destination with many recreational and cultural opportunities. Vegetation across the region is a mosaic of sagebrush and PJ systems with understories of galleta (*Hilaria rigida*), blue grama (*Bouteloua gracilis*), black grama (*Bouteloua eriopoda*), and western wheatgrass. In lower elevation areas with alkaline soils vegetation includes alkali sacaton (*Sporobolus airoides*), Indian ricegrass (*Oryzopsis hymenoides*), needled grasses (*Stipa spp.*), four-wing saltbush (*Atriplex canescens*), and winterfat (*Krascheninnikovia lanata*). In areas with more saline soils, greasewood (*Adenostoma fasciculatum*) and shadescale (*Atriplex confertifolia*) are present among the sage, pinyon, juniper, and grasses.

D-36 Southwestern Plateaus, Mesas, and *Foothills* is home to the author of this text as well as to the reservations of many tribes (Southern Ute, Jemez, Jicarilla Apache, Navajo, Santa Domingo, Zia, and others). This MLRA borders the Southern Rockies to the north. Vegetation is a mosaic across the elevation gradient (figure 9.6). Interspersed throughout the systems at lower elevations are Gambel Oak (*Quercus gambelii*), mountain muhly (*Muhlenbergia montana*), and snowberry (*Symphoricarpos spp.*).

Figure 9.5

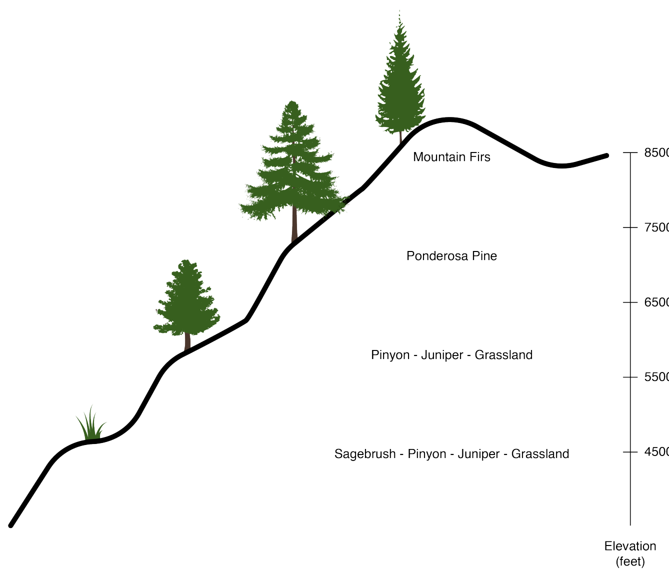


Figure 9.6 Vegetation gradient that encompasses PJ systems

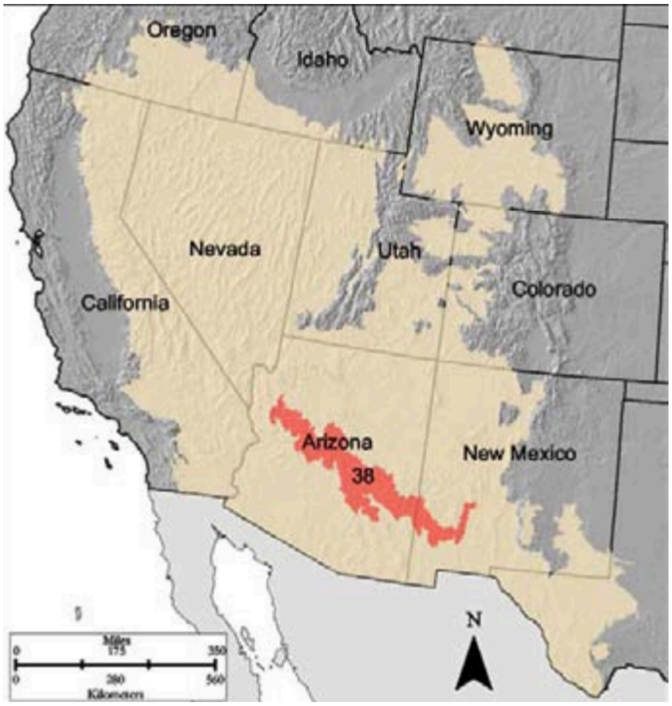


Figure 9.7

D-38 Mogollon Transition is a boundary diagonal strip of rugged low mountains interspersed with canyons, including the Salt River Canyon, across Central Arizona into the Gila National Forest area of southwest New Mexico between the Colorado Plateau and the southern portion of the Basin and Range province. Deep alluvium washed from surrounding mountains covers much of the lower elevation areas. A volcanic history with extensive basalt flows dominates the area. Higher elevations have granite peaks that are dated at over one billion years old.

Like MLRA D-36, D-38 has a mosaic gradient of shrubs to woodland to pine to fir systems. The pinyon in the PJ woodlands is largely Mexican pinyon pine (*Pinus cembroides*). Included in the PJ woodland system are Mexican blue oak (*Quercus oblongifolia*), New Mexico locust (*Robinia neomexicana*), buckbrush (*Ceanothus cuneatus*), and manzanita (*Arctostaphylos spp.*). Understory includes grama, needlegrasses, and jojoba, among a diversity of other grass and forb species. Given the MLRA's location adjacent to the Sonoran Desert, diversity of plant, animal, bird, reptile, and insect species increases greatly over northern MLRAs of the D Land Resource Area.

D-39 Arizona and New Mexico Mountains is just north of the Mollogon Rim and also stretches in a strip across Arizona into New Mexico, with a few small patches in Central New Mexico. The area includes areas of Cibola, Kaibab, and Gila National Forests as well as the two highest points in Arizona—Baldy Peak (11,403 feet) and Humphrey's Peak (12,670 feet). Again, a vegetation gradient across elevations occurs in this region. At lower elevations of deep soils are grasslands in which gramas, needlegrasses, and June grasses (*Koeleria spp.*) dominate. Mid elevations are shrub-woodland systems comprised of oak, pine, and juniper species. North-facing slopes are dominated by PJ, while south-facing slopes contain PJ intermixed with oak and with understory of fescues, bluegrasses, and brome species. Woodland mixes with pine, which gives way to firs and spruces at higher elevations.

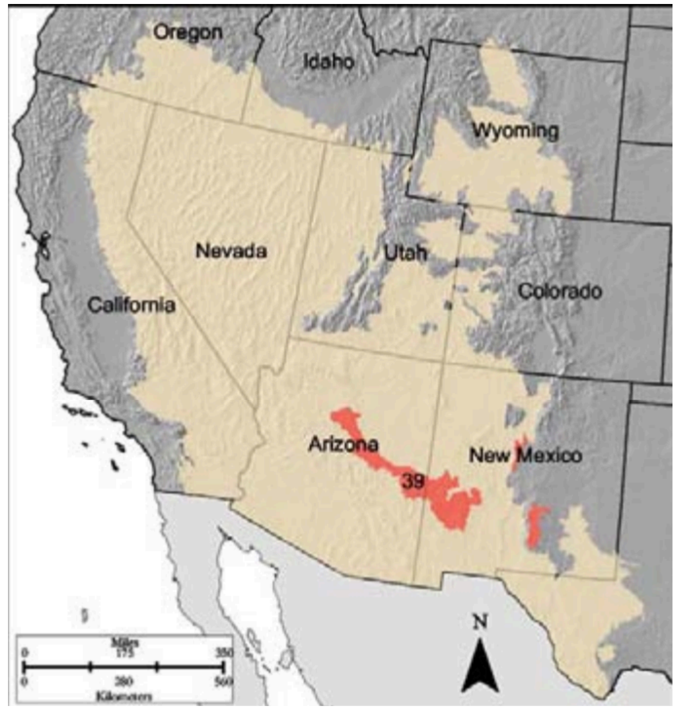


Figure 9.8

E-Region MLRAs

Much of Land Resource Region E is in the rugged areas and valleys of the Rocky Mountains spanning from the Canadian border down through northern New Mexico. Over half of the region is managed by the federal government for timber, grazing, and recreation. This text will focus on two MLRAs in the southern reaches of the region—E-49 and E-51.

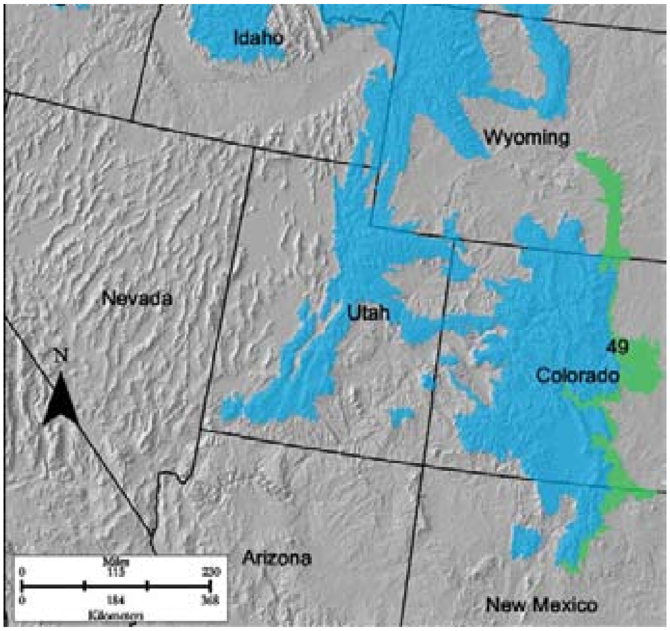


Figure 9.9

E-49 Southern Rocky Mountain Foothills could otherwise be known as the "Front Range" in Colorado. PJ systems in this MLRA are only found at lower elevations in the southern portion, extending down to Santa Fe, New Mexico, mixed with sagebrush, mountain mahogany (*Cercocarpus spp.*), grama and needled grasses, and western wheatgrass. This area is largely undeveloped at the moment, but the heavily traveled corridor of Interstate 25 runs through it. It is dotted with wind farms and grazing operations. The upper elevation forests are national forests and timber extraction operations.

E-51 High Intermountain Valleys is a small patch that largely encompasses the San Luis Valley, with the moderately busy Highway 160 crossing through. This home to the Great Sand Dunes National Park and is bounded by the Sangre de Cristo Mountains and the San Juan Mountains. Agriculture, grazing, and recreation are dominant land uses. The vegetation community is a mosaic of shrub-grasslands and PJ woodlands. Shrubs include greasewood, rabbitbrush, four-wing saltbush, alkali sacaton, and big sagebrush. The understory is a mix of grama and needled grasses and western wheatgrass. Stream areas are lined with cottonwoods.

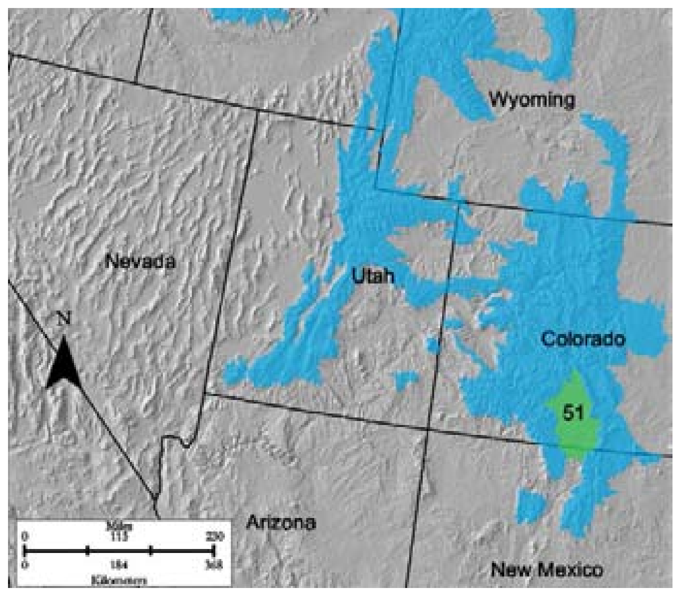


Figure 9.10

Two other MLRAs of note in this land resource area are E-47 Wasatch and Uinta Mountains and E-48A Southern Rocky Mountains (figure x). Both have patches of PJ systems in their respective elevation vegetation gradients from shrub-grasslands to woodlands to pine to alpine systems.

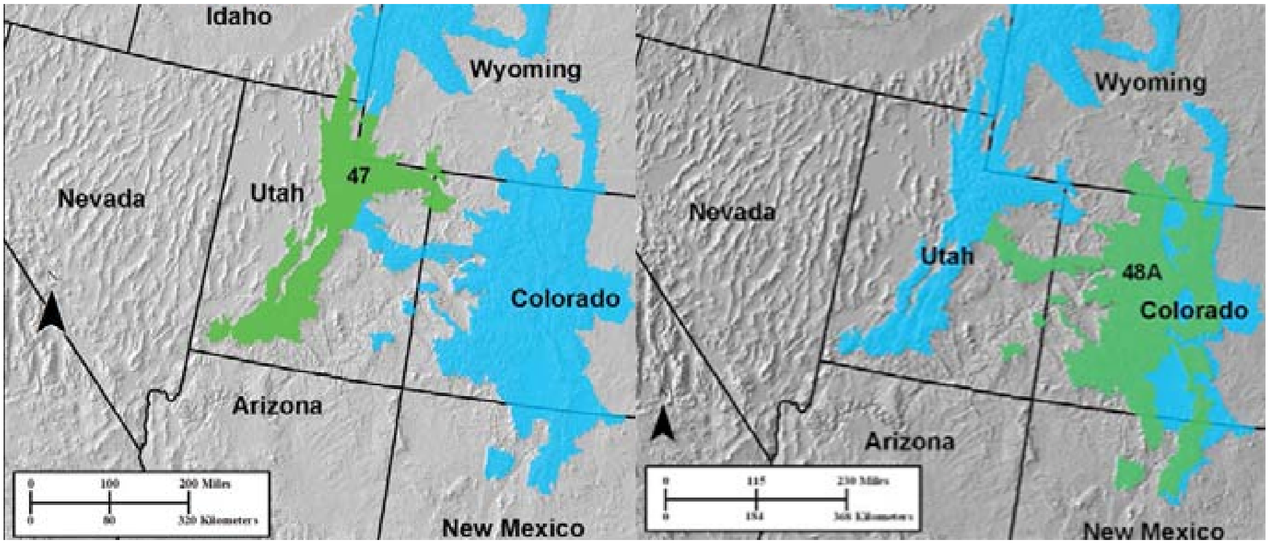


Figure 9.11

Alternative Classifications and Profiles of PJ Systems

In the few studies that have been conducted on PJ systems, most have focused on differences among the systems, and an informal classification scheme of savanna, woodland-shrubland, and persistent woodland has emerged. Table 9.1 differentiates among these three classifications across key variables.

Table 9.1 Pinyon-juniper woodland types

Type	Savanna	Wooded shrubland	Persistent woodland
Precipitation	Receives mainly summer precipitation; bimodal precipitation in some areas	Most often occurring (but not restricted to) areas of winter precipitation	Receives mainly winter precipitation
Soils	Deeper, fine-textured soils support a range of vegetation types	Wide variety of substrates	Shallow, often rocky soils do not support continuous vegetative cover
Terrain	Gentle terrain—valleys, basins, and foothills	Wide variety of topography—plains, valleys, and lower montane	Rugged upland sites and steep, rocky terrain
Stand structure	Open savanna-like stand structure, supports low density of trees and shrubs and dense herbaceous growth: grasses, forbs, and annuals	Areas of woodland expansion and contraction; shifts from herbaceous to shrub to tree dominance over time, in the absence of fire; often shrub dominated, with trees colonizing when growing conditions are favorable.	Multiaged stand structure. Range of tree densities and canopy cover, depending on site conditions
Historical fire regime	Frequent, lower-intensity surface fires maintain grasses and open stand structure; few barriers to fire spread	Infrequent, high-severity fires and patchy, mixed-severity fires	Infrequent high-severity fire. Significant barriers to fire spread: cliffs, canyons, exposed rock, topographic isolation
Impacts: Livestock and fire suppression	Increased density of younger trees, reduced ground cover, and higher-severity fires when they occur	Increased tree density, cover, and canopy closure; decreased shrub density; and larger higher-severity fires when they occur	Little impact to fire frequency and severity; understory species composition altered by livestock grazing

Section 3: Pinyon Pine and Juniper Species

There are several species in each of the *Pinus* and *Juniperus* genera that comprise PJ woodlands and associated systems. There are eight species of true pinyon pine; four species of pinyon (no pine) species, and several bristlecone species. In the United States, there are three species of pinyon pines: single-leaf pinyon pine (*Pinus monophylla*), two-leaf or Colorado pinyon pine (*Pinus edulis*), and Mexican pinyon pine (*Pinus cembroides*). Overall, there are over fifty pinus species, six of which will be covered in this text.

Pinus Species

Single-leaf pinyon pine

Pinus monophylla

Green—subsp. *monophylla*

Blue—subsp. *californiarum*

Red—subsp. *fallax*

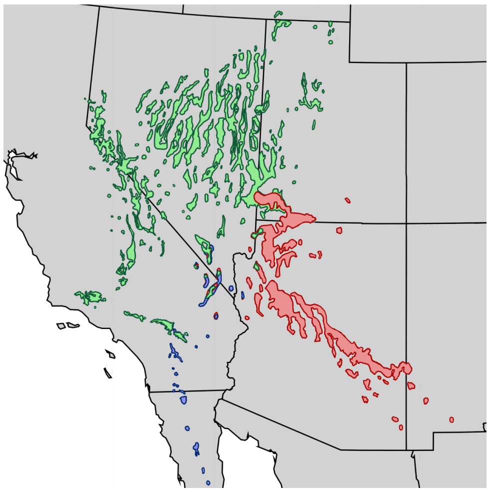


Figure 9.12

Figure 9.13

Two-leaf pinyon pine

(Colorado pinyon pine)

Pinus edulis

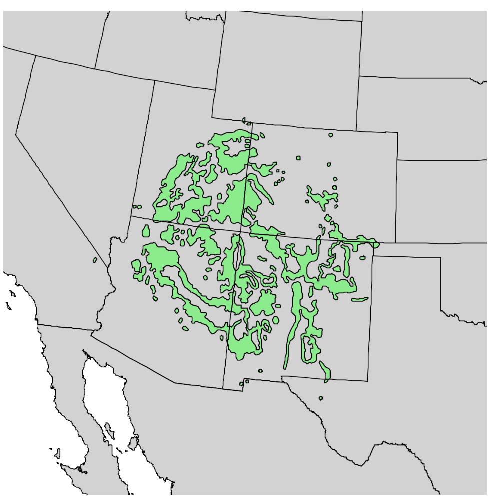


Figure 9.14

Figure 9.15

Mexican Pinyon Pine

Pinus cembroides

Figure 9.16

Figure 9.17

Species in the *Pinus* genus are evergreen trees native to the western United States and ranging in mature height from twenty-five to seventy feet, depending on species; they have long waxy needles in various arrangements and produce small roundish cones. This species is known for its small, round, edible nut production, which has been a dietary staple for many Native American tribes throughout the Southwest. Many people burn pinyon pine as firewood, as it burns hot and has a rich, fragment aroma. Although species in the *Pinus* genus provide habitat to a number of bird and animal species, most notably is the pinyon jay (*Gymnorhinus cyanocephalus*; figure 9.18), which nests in pinyon trees and feeds on the nuts. These jays are a threatened species due to habitat fragmentation as land managers have historically attempted to convert extensive areas of PJ systems to grazing lands.

Figure 9.18 Pinyon Jay

Juniperus Species

Several of the more than fifty species in the *Juniperus* genus are found in the PJ systems of the western United States. See figure 9.19.

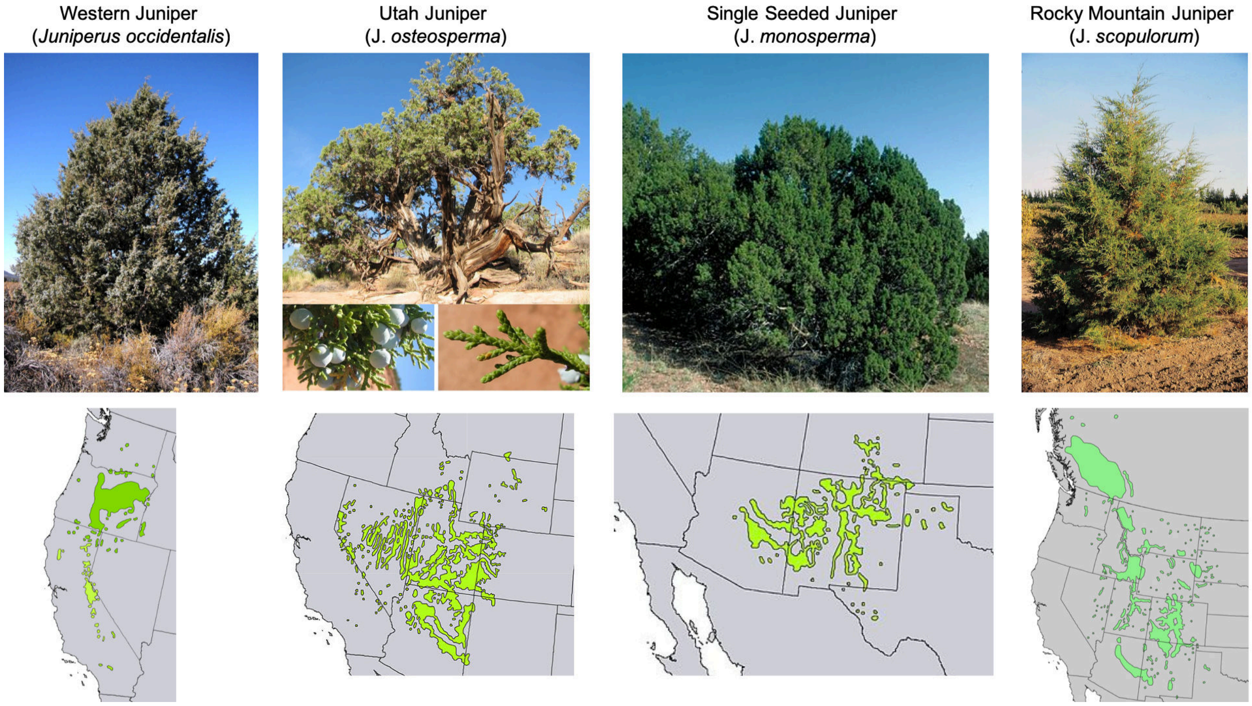


Figure 9.19

Species in the *Juniperus* genus range in mature height from thirty to seventy feet. *Juniperus* species are well known for slow growth habit, longevity, and distinctive twisting trunks (most species) of strong wood. The *Juniperus* genus includes some species that are monoecious (individual with both sexes) and others that are dioecious (single-sexed individuals). In some areas of the western United States, due to fire suppression and overgrazing, juniper is encroaching on grasslands and grass-shrub systems.

Drought Tolerance

Both pinyon and juniper tree species are adapted to tolerate a broad range of environmental conditions, enabling them to compete with a variety of plant communities and achieve wide distribution. Both mature pinyon and juniper trees have rooting systems that allow them to tolerate low moisture levels by extracting moisture through an extensive network of both lateral and taproots root systems (figure 9.20).

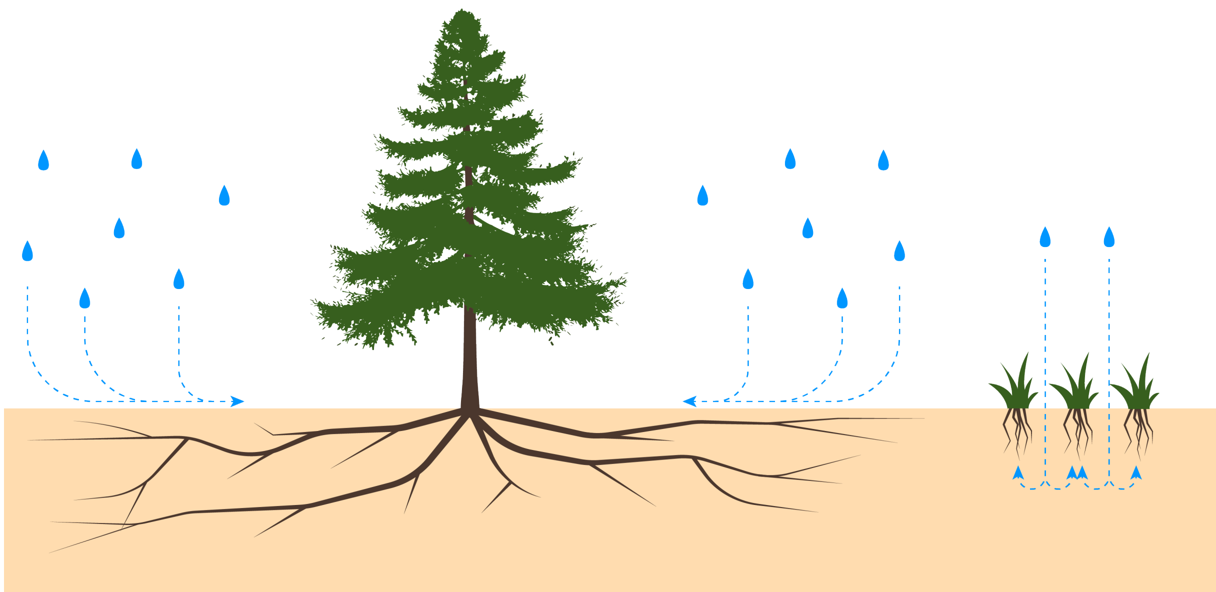


Figure 9.20 Characterization of Pinyon Pine and Juniper Rooting System

The deep taproots access moisture deep belowground that other plants, such as shrubs and grass, are unable to access. Their lateral roots systems, which are close to the soil surface, access moisture from recent precipitation events. The juniper tree species tends to remain at lower elevation levels and can tolerate drought more efficiently than can the pinyon tree species.

Section 4: Succession and Retrogression in Pinyon-Juniper Ecosystems

Expansions and contractions of pinyon-juniper habitat can be driven by factors, or combinations of factors, such as climate, insects, disease, and fire frequency. Climate and fire also influence pinyon pine and juniper succession, since certain conditions are better than others for seed germination and seedling establishment.

Climate and Drought

Moisture availability and temperature are important factors influencing the expansion and decline of pinyon-juniper woodlands. Surges of pinyon pine and juniper seedling recruitment and growth generally correspond with periods of wet climatic conditions, creating higher-density stands with greater fuel continuity.

Figure 9.21 Pinyon pines in New Mexico in 2002, stressed from drought and an associated bark beetle outbreak

Subsequent periods of drought create conditions conducive to large, stand-replacing fires. One of the most severe droughts of the twentieth century occurred between 1950 and 1956 in the southwestern United States and Mexico, causing massive die-off of many types of drought-adapted vegetation, including conifers, grasses, and cacti (Betancourt et al.1993). Two decades of higher than usual precipitation, followed by drought and combined with high winds have fueled six large fires in Mesa Verde National Park since 1996 (Floyd et al. 2000).

Periods of extreme drought intensify a number of other disturbance processes and ecological effects. Shaw et al. (2005) attribute a recent increase in pinyon mortality across portions of the Southwest to "a complex of drought, insects, and disease"—the cumulative effects of multiple mortality agents working in concert.

Endemic Insects and Disease

Pinyon pines affected by moisture stress are more susceptible to outbreaks of disease, parasitism by pinyon dwarf mistletoe (*Arceuthobium divaricatum*), and damage from endemic insects that feed on cones, needles, shoots, roots, and conductive tissue. Bark beetle and other insect outbreaks are closely tied to drought-induced moisture stress (Allen and Breshears 1998). Populations of pinyon tip moth (*Dioryctria albovittella*), pinyon cone moth (*Eucosma bobana*), pinyon Ips (*Ips confusus*), pinyon twig beetles (*Pityophthorus spp.* and *Pityogenes spp.*), pinyon needle scale (*Matsucoccus acalyptus*), and pinyon needle miner (*Coleotechnites edulicola*), normally present in pinyon-juniper woodlands at low levels, can increase dramatically during periods of drought, causing large-scale defoliation, reduced growth and reproduction, tree mortality, and a myriad of other effects. Juniper is also parasitized by its own species of mistletoe, the juniper mistletoe (*Phoradendron juniperinum*).

Fire

Wildfire has played an important role in structuring pinyon-juniper woodlands, with different fire regimes historically present in the three pinyon-juniper woodland types described in table 9.1 in section 2.3. Fires are described in terms of their severity, which is determined by the fire's effect on vegetation and is usually defined in terms of the survival of dominant trees. Three major types of wildfire influence the range, age class, species composition, structure, and density of pinyon-juniper woodlands: (1) low-severity surface fires, (2) high-severity fires, and (3) mixed-severity fires. Low-severity surface fires are fueled primarily by dense herbaceous biomass, leaving most overstory trees alive. High-severity, stand-replacing fires can burn over the surface, or up in the tree crowns (crown fire), killing most trees and initiating stand replacement. Finally, mixed-severity fires are a combination of low-severity surface fires in some areas and high-severity fire in other areas, leaving a patchwork of surviving trees interspersed with patches of tree mortality where shrubs and herbaceous ground cover regenerate first.

Modeling historic fire regimes is difficult in PJ systems as neither pinyon nor juniper reliably forms fire scars as do ponderosa pine and other conifer species. Both pinyon pines and junipers, with thin bark and low crowns, are easily killed by wildfire. With the exception of young alligator juniper, pinyon and juniper species do not resprout after fire as do associated species of shrubs and oaks but take several decades to become reestablished by seed. Although dead juniper snags can be persistent on the landscape, they are difficult for researchers to age.

The introduction and expansion of livestock grazing throughout much of the Southwest removed the fine herbaceous fuels that create a continuous layer of combustible material over the surface of the landscape. Combined with fire detection and suppression efforts in the twentieth century, fire frequency has been reduced, but fires have tended to burn with greater intensity when they do occur. The frequency of large, severe fires has increased over the past twenty years in pinyon-juniper woodlands and other vegetation communities across the western United States (Romme et al. 2008).

Succession

Seed Production and Establishment

Pinyon pine reproduces only by seed, not vegetatively. Heavy crops of pinyon pine cones (called mast crops) vary by species and are produced every two to six years, followed by multiple years of low cone production (Betancourt et al. 1993). On average, mast crops in pinyon pines will occur in one to three out of every ten years (Gori and Bate 2007). The cycle of flowering, fruiting, and seed maturation takes three years, with seedlings becoming established four growing seasons after cone initiation (Betancourt et al. 1993). Pinyon seedlings are shade-tolerant and have the best chance of establishment and survival under the protected microclimates of "nurse plants."

Juniper exhibits a similar seed-production cycle, where heavy (mast) crops of juniper berries/seed are produced every two to five years, interspersed with intervals of low seed production (Gori and Bate 2007). Young alligator juniper trees are able to sprout prolifically after the death of the main trunk, but the ability to resprout declines with age (Gottfried et al. 1995; Tirmenstein 1999). One-seed, redberry, Utah, Rocky Mountain, and mature alligator juniper must rely on seed production and dispersal for reestablishment. For both pinyon and juniper, levels of germination and establishment are highest when a mast seed crop is followed by a period of increased precipitation and the absence of fire (Gori and Bate 2007).

Herbivory and Seed Dispersal

Birds and small mammals, including chipmunks, raccoons, and squirrels feed on and cache juniper berries and pinyon nuts. Birds are considered to be the primary dispersal agents for juniper (Gottfried et al. 1995). Seeds that have passed through birds' digestive tracts germinate faster than uneaten seeds (Johnsen 1962). Bird species responsible for dispersing pinyon seeds include scrub jays (*Aphelocoma californica*), pinyon jays (*Gymnorhinus cyanocephalus*), Steller's jays (*Cyanocitta stelleri*), and Clark's nutcrackers (*Nucifraga columbiana*). Seeds deposited or cached under the protective microclimate of nurse plants or other debris are more likely to germinate and become established than those deposited or cached in the open. One potential advantage of seed masting is that surplus seeds remain after seed predators have consumed a portion of that year's crop.

Succession after Fire

Generally, after a stand-replacing fire, succession begins with the establishment of annual grasses and forbs for several years, followed by perennial grasses and forbs. Shrubs are the next cover type to become established, utilizing the increased humidity and buffering from the sun and wind provided by perennial vegetation. In the absence of fire, juniper and pinyon will become the climax species, but they may take several decades or longer to become established. As canopy cover increases, shrubs and herbaceous cover tend to decrease in density and abundance. Shrubs may remain a component of pinyon-juniper woodland indefinitely or may eventually be suppressed by the slow-growing overstory, which takes hundreds of years to reach the "open" old-growth stage.

After a low-severity surface fire, surviving shrubs may regenerate quickly by resprouting. Frequent low-severity fires can eliminate pinyon and juniper seedlings and maintain shrub-dominated plant communities.

State and Transition Model

In 2006, the Nature Conservancy undertook an initiative to understand and model historic, current, and potential vegetation changes over time throughout the Southwest under the impact of varying fire intensities and concomitant impacts of drought and insect infestation. The initiative looked at a spectrum of systems from semidesert grasslands to shrublands to woodlands to forested systems. As a product of this initiative, state and transition models such as the one below were produced.

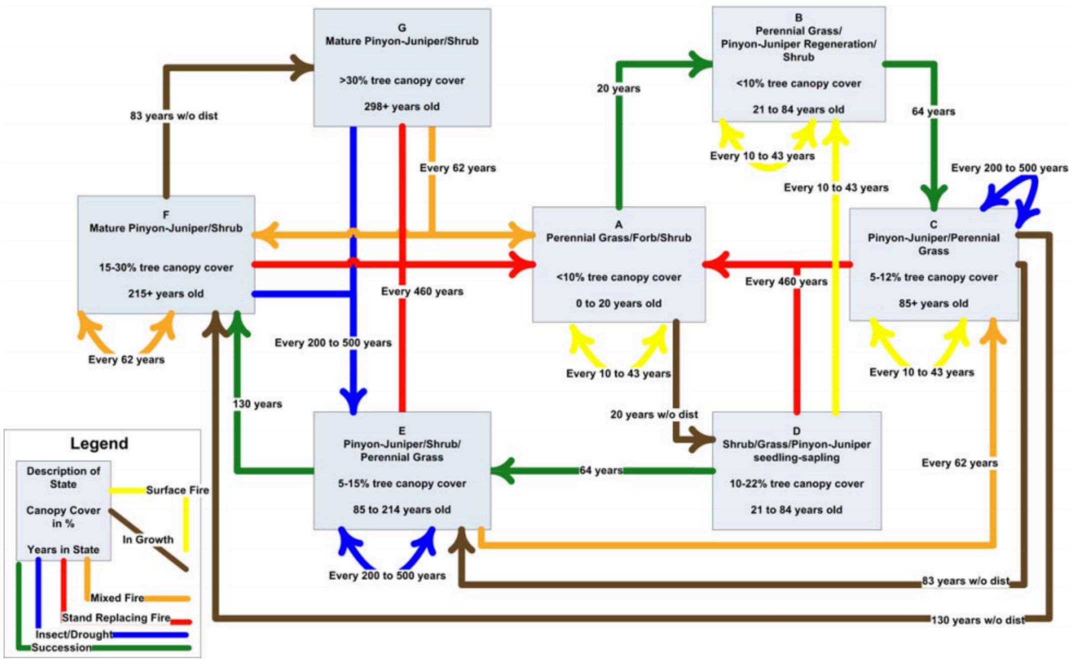


Figure 21-1. Conceptual Historic state and transition model for the pinyon-juniper savanna vegetation type. Frequency of transitions are noted when this information is supported by published sources; where no or conflicting information exists on the frequency of transitions, unknown is the notation.

Figure 9.22 From Gori, D., and J. Bate. 2007. Historical Range of Variation and State and Transition Modeling of Historical and Current Landscape Conditions for Montane Grassland for the Southwestern U.S. Prepared for the USDA Forest Service, Southwestern Region by the Nature Conservancy, Tuscon, AZ. Accessed September 2008. http://azconservation.org/projects/southwest_forest_assessment.

One can read this state-and-transition model (STM) from a number of different perspectives depending on management objectives and the associated desired vegetative community. From an overall rangeland health perspective aimed at an ecosystem that supports biotic integrity, soil stability, and hydrologic function, management objectives may cycle through states A: Perennial Grass/Forb/Shrub, B: Perennial Grass/PJ/Shrub, C: PJ/Perennial Grass, and D: Shrub/Grass/PJ Sapling. If management aims are to maintain habitat for pinyon jays and other species, achieving states with >15 percent tree cover would be the target. A balance among rangeland health attributes and habitat is ideal, however, so the sweet spot of states in the model above may be C: PJ/Perennial Grass (10–12 percent tree cover) and E: PJ/Shrub/Perennial Grass.

Section 5: Current Environmental Anthropogenic Stresses

What is not reflected in the STM above are the current environmental and anthropogenic stresses of livestock grazing, invasive grasses, timber harvest, and mining activities, all of which are covered in the final section of this chapter.

Livestock Grazing

A marked increase in pinyon-juniper tree density and extent over the past century has been attributed by many researchers to a combination of livestock grazing and the disruption of historical wildfire regimes (Gori and Bate 2007; Gottfried et al. 1995). Some have hypothesized that livestock grazing has aided the spread of juniper into grasslands by reducing the density of grasses and palatable shrubs that compete with juniper seedlings for soil moisture, nutrients, and other limiting factors (Johnsen 1962). Livestock overgrazing has modified fire regimes and erosion processes across multiple spatial scales by altering the density and spatial patterning of ground cover (Allen 2007). More trees survive in the absence of fire, further reducing vegetative ground cover by outcompeting grasses and forbs for limited soil moisture. Livestock can also transport nonnative, invasive weed seed from weed-infested rangelands into more pristine areas, where they, too, can outcompete native grasses and forbs.

Erosion

Pinyon-juniper ecosystems in the southwestern United States are particularly susceptible to erosion. When fire, livestock grazing, or drought reduces the amount of vegetative ground cover and organic litter, rates of soil erosion during and after precipitation events can increase dramatically. Where appropriate grazing management systems are not implemented, livestock grazing contributes to soil erosion by compacting the soil. Soil compaction reduces the amount of water that filters down through the soil (infiltration) and increases surface water runoff. As a result, topsoil is lost, and large quantities of sediment are deposited by surface runoff into rivers and streams, negatively impacting water quality and aquatic habitat.

Furthermore, livestock, off-road vehicles, hikers, and other types of mechanical disturbance damage biological soil crusts (communities of bacteria, cyanobacteria, lichens, mosses, algae, and/or fungi on the soil surface). These crusts reduce erosion from wind and water, hold nutrients and moisture, enrich the soil via atmospheric nitrogen fixation, and initiate primary succession by recolonizing disturbed areas (Gottfried et al. 1995). Biological soil crusts play an important role in reducing surface runoff and erosion, but they are fragile and can be slow to recover after disturbance (Belnap and Eldridge 2001).

Invasive Plants

Some invasive plants that cause concern in PJ ecosystems include cheatgrass (*Bromus tectorum*), knapweeds

(*Centaurea spp.*), thistles (*Cirsium spp.*, *Carduus spp.*, and *Onopordum spp.*), mustards (*Sisymbrium spp.* and *Brassica spp.*), and Dalmatian toadflax (Linaria dalmatica). These species have established and proliferated in PJ systems through vectors such as drought, fire, timber harvest, mining activities, livestock grazing, road construction, and erosion, all of which create conditions that allow nonnative invasive species to become established. Once established, many nonnative invasive plants can outcompete native vegetation for space, moisture, nutrients, and other limiting factors. They spread aggressively and are difficult to control, as they have few natural enemies in their new environment.

Mining Activities

Natural gas extraction is a primary industry in southern Colorado and New Mexico. Maps such as the one shown in figure 9.23 below are typical for large areas throughout the state. This map represents a small portion in the northwest corner of New Mexico, and each red dot is a natural gas well-pad site. There are hundreds of thousands of natural gas well-pad sites throughout PJ ecosystems.

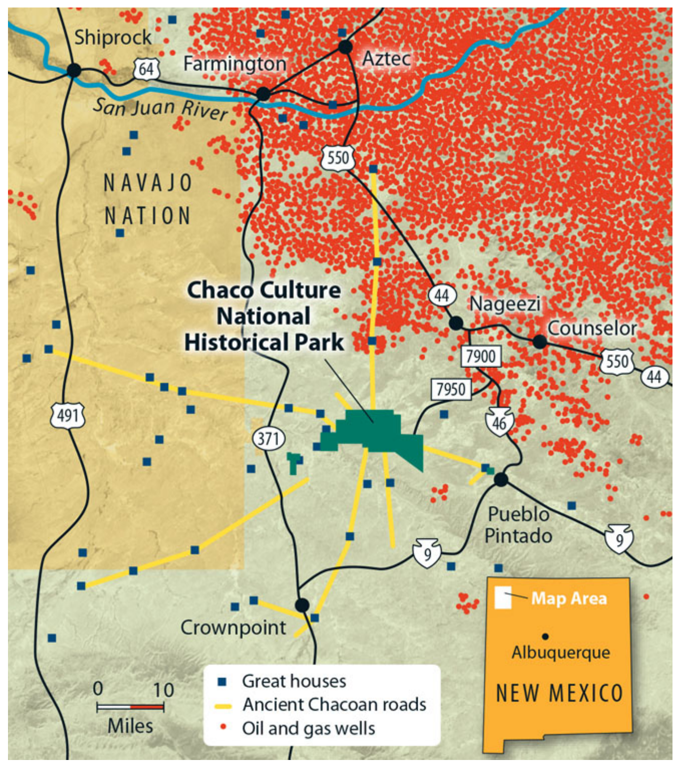


Figure 9.23 Map of natural gas well-pad sites in a small section of northern New Mexico—representative of many areas throughout PJ ecosystems

The footprint and ecological impacts of natural gas extraction are severe and far-reaching. Given the number of well-pad sites and associated networks of roads (figure 9.24) simply establishing and maintaining the extraction site is a substantial disturbance. Plant material is removed, and soil is moved to create roads and lay pipeline. This opens niches for invasive species to make their way into the area through natural dispersal and on vehicles coming and going to service equipment. All that traffic compacts and erodes the soil of roads and adjacent areas. During precipitation events, the networks of roads prevent adequate overland water flow.

Figure 9.24 Example of distribution and road network of natural gas extraction areas

Further, vegetation clearing fragments and destroys wildlife habitat. This may be through removal of the primary forage or browse plant of a wild herbivore or by altering the plant community structure (height and density) vital for nesting or cover. Some wildlife species require a mosaic of plant types and plant community structures, such as dense shrubs for nesting and open areas for foraging and mating. To some species, such as a small mammal, the width of a road is an uncrossable distance. Disturbed areas become sites for invasive species establishment, and the high degree of vehicle traffic to and from the site serves as a vector of introduction.

Mojave Desert Ecosystems

The Mojave Desert is the driest of the North American deserts, so after adequate winter precipitation spring wildflower blooms like the one in the image above are a spectacular event. This desert is one of the top destinations for tourists visiting the western United States, with some six million visitors annually to destinations such as Joshua Tree National Park, Lake Mead, and Death Valley, as well as the largest off-road vehicle area in the world in Johnson Valley. One-third of the species in the Mojave Desert are endemic. Increasing the pressure on this extremely arid and sensitive desert area are the impacts of urbanization, heavy recreational and military uses, mineral extraction, and large-scale alternative energy production.

Section 1: Physiography

Geographic Location and Topography

The Mojave Desert extends over roughly 50,000 square miles largely located in California with a small area in Nevada, and even smaller areas in Utah and Arizona. It is bordered by the Sierra Nevada Mountains to the northwest; the San Miguel and San Bernadino Mountains to the west; the Sonoran Desert to the southeast; the Colorado Plateau to the east; and the Great Basin to the North (figure 10.1). Its elevation goes from approximately 280 feet below sea level at Death Valley to just over 11,000 feet at its highest point—Telescope Peak, also in Death Valley. Average elevation in the Mojave Desert ranges from 2,000 to 5,000 feet. Its position on the landscape and its precipitation regime result in a desert not of general characteristic vegetation but rather of ecotones (i.e., transitions).

Figure 10.1 (a) Map of geographic location of Mojave Desert; (b) topography and physiographic regions surrounding Mojave Desert

Climate and Vegetation

Death Valley is well known for its extreme temperatures and aridity. In 1913 the temperature at Furnace Creek, Nevada, hit 134°F, which to this day is the hottest temperature ever recorded on Earth. Average monthly temperatures range from the upper sixties to over 100°F, with seven months out of the year in the 100° range. Less than two inches of rainfall on the Mojave Desert annually; this is largely in the form of winter storms, except in the southern areas, which are impacted by the summer monsoonal effect. The ecotone gradient, underlain by the boundaries of mountainous topography and precipitation, has resulted in the Mojave Desert having 1,700 to 2,000 endemic plant species.

Section 2: Classifications

Given the strong presence of ecotones, researchers and naturalists have divided the Mojave Desert into regions or series, depending on perspective. This section will review portions of all three Mojave Desert classification schemes: series, regions, and two Major Land Resource Areas (MLRAs).

Mojave Desert Series

Scientists Vasek (1980), then Turner and Brown (1982) outlined a classification system: creosote bush series; shadescale series; saltbush series; blackbrush series (*Coleogyne spp.*; all of which are distinctive in some areas but generally fill out a gradient based on elevation), and Joshua tree series.

Creosote bush (*Larrea tridentata*) and white bursage (*Ambrosai dumosa*) cover over two-thirds of the Mojave. This species association mixes in four-wing saltbush (*Atriplex confertifolia*) in valley areas and lower portions bajadas. On calcareous soil, there is often a creosote-saltbush association.

The Joshua tree series is defined by its namesake species, the Joshua tree (*Yucca brevifoia*). Joshua trees are generally found on the moister, cooler sites of higher elevations. At higher elevations this series transitions into pinyon-juniper woodland and in the southern portion it transitions into the Sonoran Desert with a mix of saguaro cacti (*Carnegiea gigantea*), paloverde (*Parkinsonia spp.*).

Mojave Desert Regions

Using topography and the precipitation gradient across the Mojave Desert, Rowlands et al. (1982) proposed six general regions: northern, eastern, western, central, south-central, and southeastern (figure 10.2), all of which will be briefly reviewed in this section.

Figure 10.2 Mojave Desert regions (Rowlands et al. 1982)

Northern Mojave is a large broad ecotone dominated by creosote and bursage assemblages and that transitions to Nevada's Great Basin. In the southern portions of the region, Joshua tree assemblages dominate Death Valley.

Eastern Mojave, the largest of the six regions, is topographically diverse and is bounded by the Great Basin to the North; Colorado Plateau to the East; and Sonoran Desert to the South. The region is influenced by both winter precipitation and summer monsoons. Given the size, topography, and precipitation of this region, the mosaic of plant communities is substantial. In the northern high elevation areas, creosote-bursage assemblages dominate and give way to pinyon-juniper woodlands to the north and east. Southern areas are dominated by Joshua tree associations that mix with cacti and Northern Sonoran Desert plant assemblages. The region includes Las Vegas, the Mojave Natural Preserve, and the Lake Mead Recreational Area and abuts the Grand Canyon.

Southeastern Mojave is the generally topographically homogenous area bounded by the Hualapai Mountains on its eastern border. Vegetation in this region is a mix of characteristic Mojave Desert plant assemblages intermixed with northern Sonoran Desert plant assemblages, particularly in the southeastern corner, where there is a mix of both Joshua tree and saguaro cactus.

Central Mojave is the terminus of the Mojave River drainage. Topographically it is a mix of playas and broad, high-elevation valleys. Given the homogeny of topography of this area and its geographic location, it has the lowest levels of diversity found in the Mojave Desert.

South Central Mojave is bounded by the San Bernadino Mountains to the southwest and the Sonoran Desert to the south and southeast. This region is influenced by a rainfall gradient of winter storms in the west to summer monsoons in the south and east. Vegetation assemblages vary in association with the precipitation gradient, with more diversity as the region transitions to the Sonoran Desert assemblages with species such as palo verde and ironwood (Olneya tesota) mixing among Joshua trees. Given the region's proximity to Los Angeles, impacts of urbanization, particularly in the Coachella Valley, and deposition from smog are substantial influences. Additionally, this region is home to the tourist attraction Joshua Tree National Park and a large Marine base near Twentynine Palms.

Western Mojave is bounded by the San Gabriel Mountains to the south, the Sierra Nevada to the west, and the Great Basin to the north. Given its western geographic location and proximity to mountains, it receives the greatest amount of winter precipitation of all the Mojave Desert regions. The vegetation assemblages transition from Joshua tree to pinyon-juniper woodlands.

MLRAs

The Mojave Desert is within the D Land Resource Region; an overview of the region appears in chapter 8. Given the size and location of the Mojave Desert, only two MLRAs apply to the area: D29 and D30.

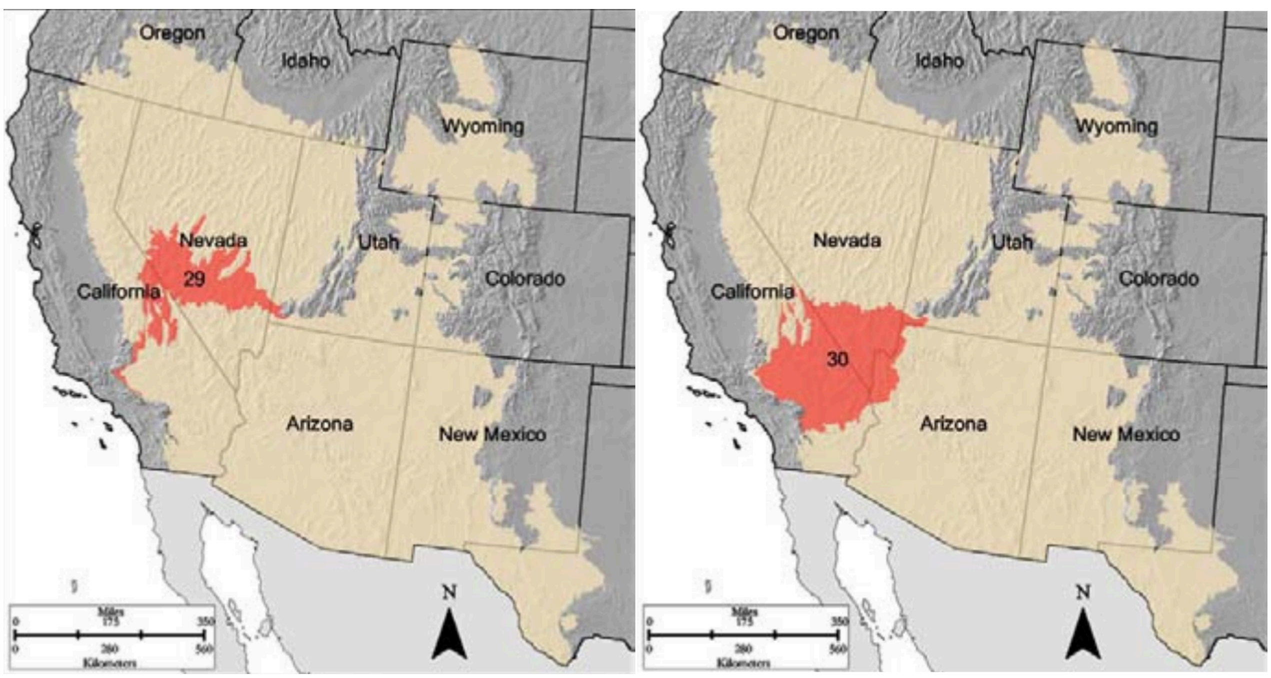


Figure 10.3

The D29 Southern Nevada Basin and Range is mostly outside of the Mojave Desert, except for a small sliver that is part of the Death Valley National Monument. This small area reflects the "shadescale series" noted above.

D30 Mojave Desert is entirely comprised of the Mojave Desert, split between the Great Basin Province to the north and the Sonoran Desert Province to the south, and is largely federally managed. Notable regarding this region is the number of closed basin playas that are often rimmed by mounds of wind-driven erosion. The playas' bottom surfaces often have buildups of salts and minerals as a result of the quick evaporation of their shallow pools formed by winter storms or summer monsoons. Groundwater in the area generally has a high concentration of dissolved solids and high chloride levels. Soils throughout the region have what is called a thermic (warm) soil temperature regime, meaning they range from 15°C to 22°C (59°F to 71°F), another factor underlying the endemism and diversity of the region. The Mojave River flows through the region, providing, along with the Colorado, a large portion of the public water.

Section 3: Current Anthropogenic Stresses

Although the Mojave Desert is arid and hot, human presence is firmly established and continues to grow and intensify. This section will outline major areas and installations of human presence and land use, before discussing the impacts from larger issues: recreation and off-road vehicles; mineral extraction and energy production; and urbanization and atmospheric deposition. Human land uses all have the same general impacts; this section, therefore, begins with a brief, high-level overview of the extent of the human footprint in the Mojave Desert, continues with highlights from several specific types of land use, and concludes with an overview of the ecological impacts.

Human Footprint and Major Areas of Land Use

Despite the Mojave Desert being hot, dry, and water limited, over two million people reside there in several dozen cities (the largest are listed in table 10.1); about a dozen US government facilities are located within its boundaries (the largest are listed in table 10.2); several dozen energy companies have facilities there (the largest and most notable appear in table 10.3); and it contains a couple dozen heavily visited recreation and off-road vehicle areas (the most notable are in table 10.4).

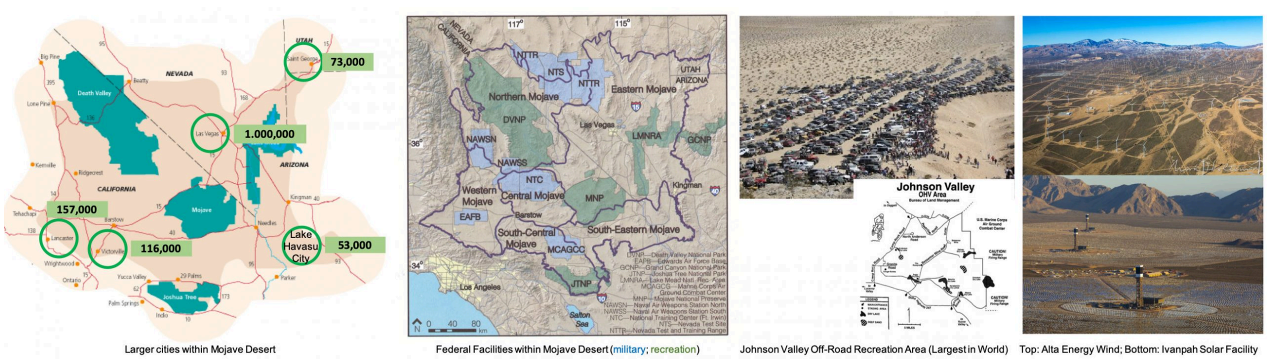


Figure 10.4

Table 10.1 Cities (population)

Las Vegas Metro Area (1,000,000)	Palmdale, CA (153,000)
Victorville, CA (115,000)	St. George, UT (73,000)
Apple Valley, CA (70,000)	Lake Havasu City, AZ (53,000)
Pahrump, NV (43,000)	Kingman, AZ (30,000)

Table 10.2 Military Bases and Government Facilities

Edwards Air Force Base	Fort Irwin National Training Center
Marine Corps Base—Twentynine Palms	Marine Corps Base—Barstow
Naval Air Weapons Stations (North and South)	Nevada Test Site

Table 10.3 Solar and Wind Power Installations

US Department of Energy Solar One	US Department of Energy Solar Two
Copper Mountain Solar Facility	Nellis Solar Power Plant
Mojave Solar Project	Antelope Valley Solar Ranch
Ivanpah Solar Power Facility	Desert Sunlight Solar Farm
Tehachapi Pass Wind Farm	Alta Wind Energy Center

Table 10.4 Tourist and Recreation Destinations

Joshua Tree National Park	Mojave National Preserve
Lake Mead National Recreation Area	Death Valley
Las Vegas Strip and Hoover Dam	Red Rock Canyon National Conservation Area

Off-Road Vehicles and Recreation

Outdoor recreation countrywide is more than $6 billion industry and growing. Of that $6 billion, approximately $300 million to $500 million annually is spent directly throughout the Mojave Desert, making it one of the nation's top outdoor recreation and tourist destinations. Many consider outdoor recreation the antithesis of being tied to electronic devices, social media networks, and video games: they see it as a means of reconnecting with nature. A closer look at the ecological impacts of outdoor recreation may tell a different story, however.

Johnson Valley

Johnson Valley, California, is the largest off-road vehicle recreation site in the world. Throughout each spring and summer, tens of thousands of off-road vehicles (ORV) and motocross enthusiasts descend on Johnson Valley to zoom every which way across the landscape and camp out in expansive minivillages (figure 10.5).

Figure 10.5 (a) Expansive ORV enthusiast minivillages; (b) example of crisscrossing ORV trails

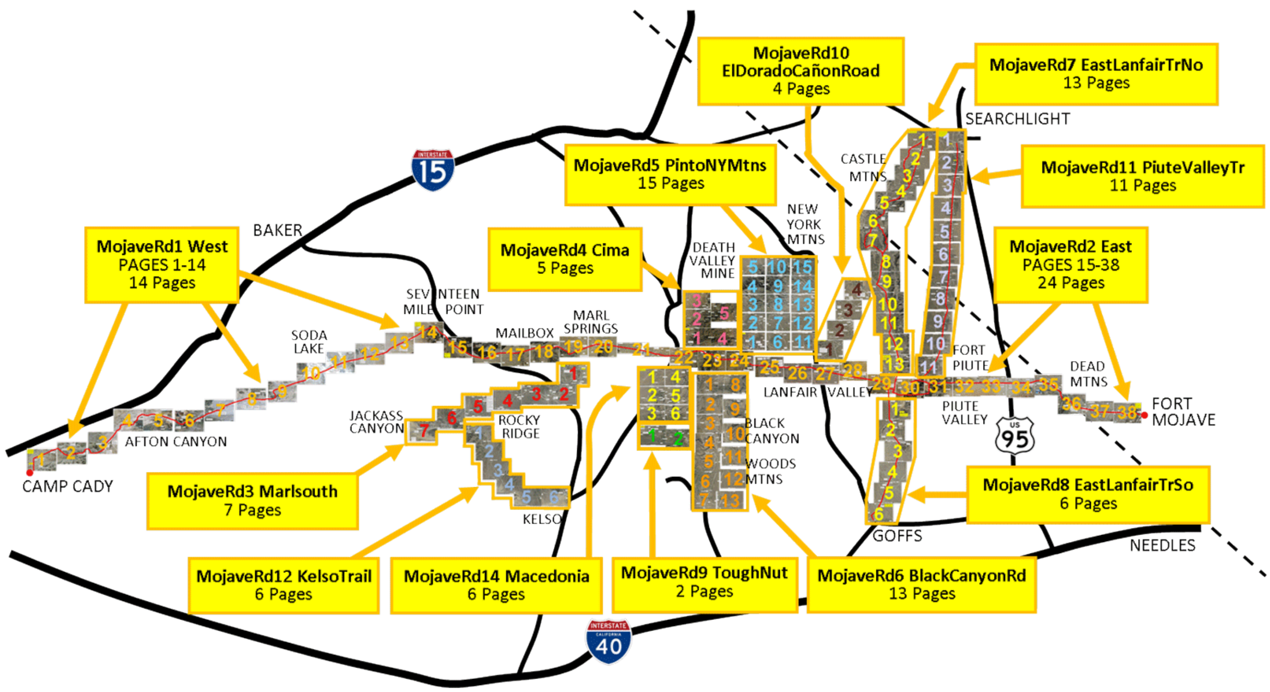


Figure 10.6

The recreational off-road vehicle industry is expected to climb from a $7 billion industry to an $11 billion industry in the next five years. Maps such as the one in figure 10.5 are a dime a dozen as more and more ORV recreationists cut trails across areas of the Mojave Desert. This map alone includes 114 ORV trails just between I-15 and I-40 outside of Needles, Arizona.

Red Rock Canyon

Figure 10.7 Traffic on Red Rock driving loop

Located only seventeen miles outside of Las Vegas, Nevada, Red Rock Canyon is easy to access, and once inside the conservation area a single one-way loop winds through breathtaking geologic formations.

This popular tourist destination is often packed with cars, so much so that traffic backups in the park can extend for several miles (figure10.6). Approximately two million people visit Red Rock Canyon annually, and most are limited to the one-way loop. Some, however, enter by bicycle or aim for a parking area for backcountry hiking or rock climbing.

Death Valley National Park

Figure 10.8 Wind-driven dust storm in Death Valley

A visit to Death Valley may be considered a badge of honor, whether to see spring wildflowers, if winter storms produced enough precipitation, or to muddle through the sweltering temperatures of late spring through fall. This national park, which is located more than 120 miles from any sizable city, sees approximately one million visitors annually, and with them have come invasive species and air quality issues. Particulate matter from the Los Angeles metro area is carried by wind to settle in the lower-elevation valley of the park. This is exacerbated by the dust particulate matter produced by vehicular traffic and by the continued loss of vegetation or changes in vegetative communities that reduce soil stability, making it more susceptible to wind erosion.

Lake Mead National Recreation Area (LMNRA)

Figure 10.9

Seven to eight million people visit Lake Mead annually, many of whom boat on the 290 square miles of water. As a result, quagga mussels (*Dreissena bugensis*) have been established and proliferate in both Lake Mead and Lake Mohave. Not only has an invasive species become firmly established in the lakes, but fountain grass (*Pennisetum setaceum*) has been established on the land. As visitors to LMNRA increase, so too does the area's litter problem. The Park Service is so overwhelmed with the volume of litter that in the last decade it developed several programs to address the issue (i.e., prisoner cleanup and adopt-a-cove programs). Although the programs are proving successful to some degree, the issue persists.

Mineral Extraction and Energy Production

Mineral Extraction

The Mojave Desert has a long history of mineral extraction dating back to the mid-1850s. A truly remarkable amount and variety of minerals have been removed from the area, including gold, silver, lead, zinc, copper, tungsten, vanadium, iron, clay, and cinders. Discovery, exploration, and development of the area's rich mineral potential was facilitated by the lack of vegetation, which tended to obscure mineral deposits in more temperate locations. Molycorp is one of the largest mineral extraction companies in the Mojave Desert.

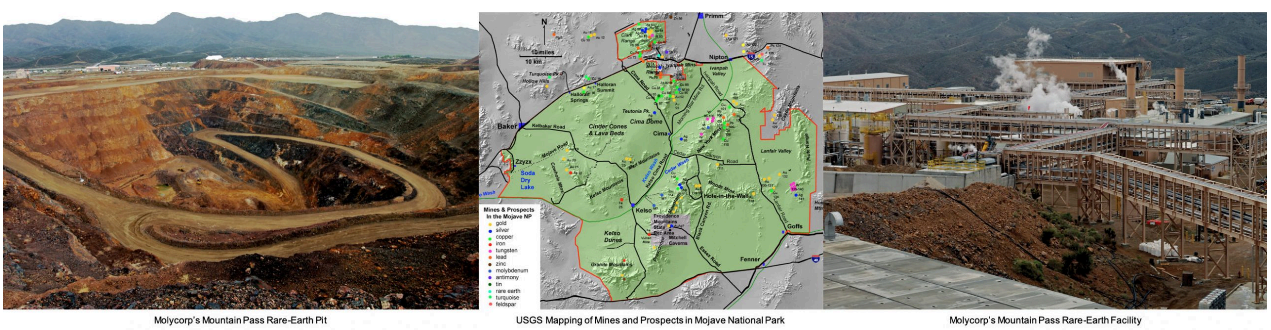


Figure 10.10

Energy Production

The vast open spaces of the Mojave Desert support large alternative energy installations. Looking at the map in figure 10.10, it's clear that the latitude and climate of the Mojave Desert make it an ideal location for industrial solar-array complexes. The Mojave Desert, as of 2014, was the location of the largest capacity of solar power in the world, with the combined power of the SEGS (Solar Energy Generating Systems) comprising nine solar power plants and the Ivanpah Solar Power Facility. Newer, larger-capacity plants have recently come online and more will in the near future as part of California's attempt to obtain 100 percent of its electricity from carbon-zero sources.

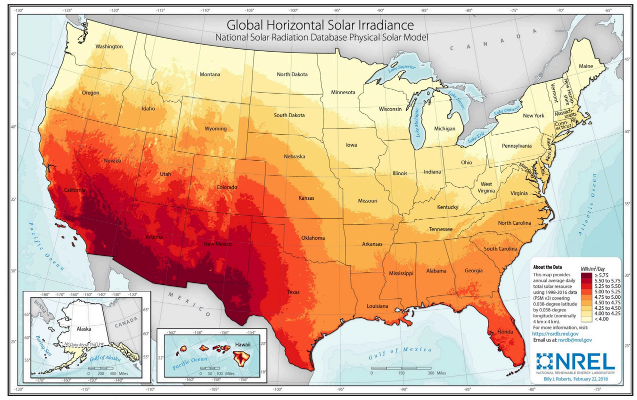


Figure 10.11 Distribution of solar radiation

Urbanization

Approximately fifteen million people inhabit the Mojave Desert, and population growth continues at around a rate of 3 to 5 percent annually. Growth is concentrated in the western regions near Palmdale and the desert suburbs of the Los Angeles metropolitan area and the Las Vegas Region. Urban centers are increasingly surrounded by planned communities with amenities that insulate inhabitants from the desert aridity. Most people in the Mojave Desert are linked by highways, utility corridors, railroads, and the goods required for life and living are imported by aqueducts, powerlines, pipelines, and commercial transport vehicles (i.e., trains and trucks).

Overall Ecological Impacts of Land Use in the Mojave Desert

Ecological impacts are similar, although they vary in intensity and impact, across Mojave Desert land uses. For all the land uses in the Mojave Desert, a project lead by the Nature Conservancy to identify conservation targets found that large swaths of the desert reflected high landscape integrity to support conservation (figure 10.12).

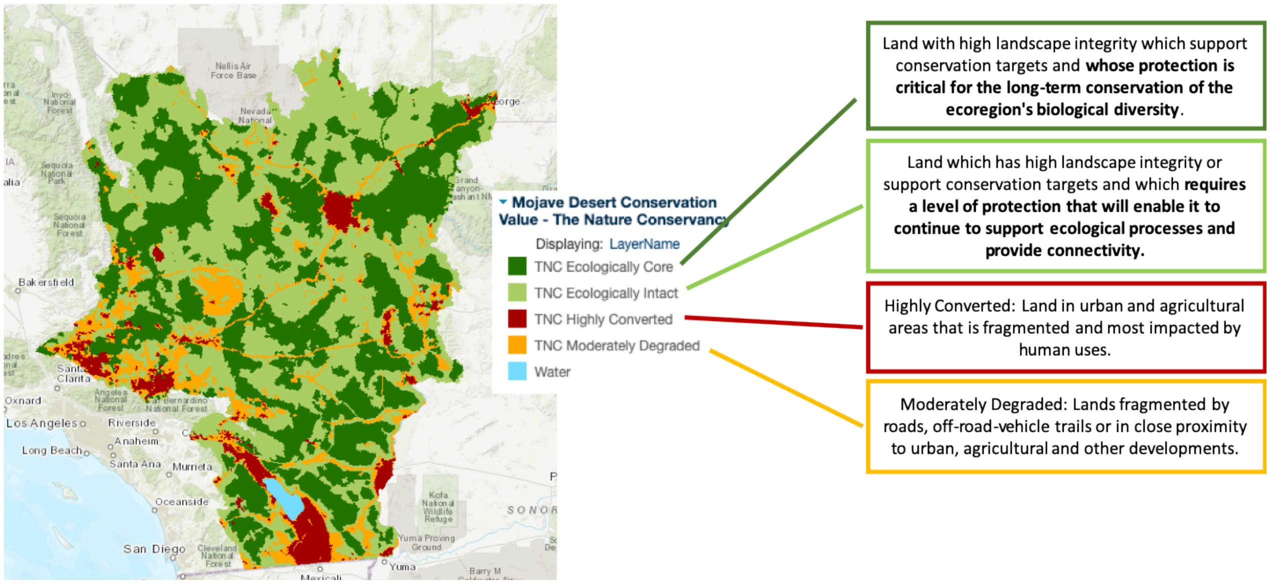


Figure 10.12 Mojave Desert conservation value, The Nature Conservancy (TNC)

This does not mean, however, that the Mojave Desert does not experience ecological impacts or that those impacts are limited to the red- and orange-shaded areas. Ecological impacts can vary in scale from microsites to local landscapes to large regional areas. Likely the most pervasive and persistent impacts include, but are not limited to, habitat alternation, invasive species proliferation and fire regime shifts, loss of biotic crusts, and reduced soil stability.

Habitat Alteration

Recall that approximately one-third of the species in the Mojave Desert are endemic, so they likely have specific habitat requirements and fairly restricted ranges. Roads, infrastructure, alternative energy installations, heavily used recreation areas all fragment habitat. The desert tortoise (*Gopherus agassizii*) is a species whose habitat has been greatly impacted by land uses throughout the Mojave Desert region, particularly by vehicular traffic on-road and off-road.

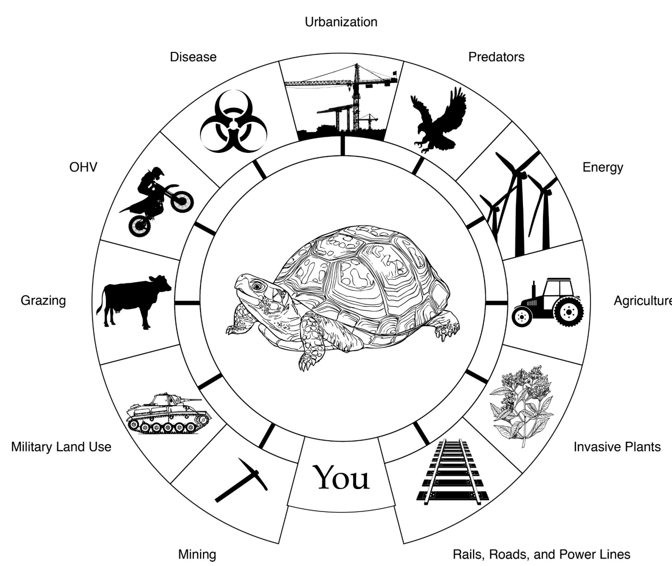


Figure 10.13

Tortoises move slowly across the landscape, and they often become casualties when run over. Surprisingly, trash from ORV mini-villages accounts for a fair number of tortoise deaths, as the tortoise mistakes brightly colored trash, such as small plastics, balloons, and bags, for flowers (food); because they are unable to digest trash it remains in their digestive system until they are ill and starving. Trash also attracts and supports higher than normal raven populations, a species that predates juvenile tortoises.

Invasive Species Proliferation and Fire Regime Shifts

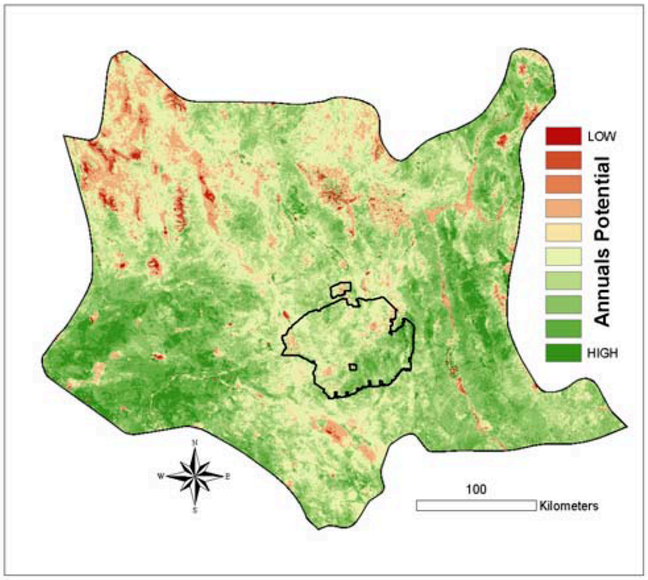


Figure 10.14 Mojave Desert potential of annuals

The National Park System leverages a citizen science approach to monitor for fifty invasive species. As with most ecosystems in the western United States, annual species, particularly bromes, are the most serious threat. In 2008 researchers (Wallace and Thomas 2008) mapped the potential of annual invasions throughout the Mojave Desert (green areas are high); not only is the overall potential of invasion high, but areas of greatest risk for invasion correlate to urban and tourist concentrations are as well (figure 10.13). Due to increased densities of brome species, particularly red brome (*Bromus rubens*), and intensifying land use, the fire regime in the Mojave Desert is becoming more frequent and increasing in severity. Desert plant species are not fire dependent like adjacent chaparral communities to the west. In fact, desert postfire recovery is a long process, particularly for the shrubs that dominate this desert system, which can take up to fifty years to reestablish. Postfire soils are highly susceptible to wind erosion and form physical crusts in the arid conditions of the desert that further challenge the system's ability to recover.

Saltcedar (*Tamarix chinensis*) is another invasive species exacerbating the fire regime, altering hydrology, and increasing water and soil salinity. Saltcedar establishes and invades riparian areas, outcompeting native cottonwoods and willows. The species, reproducing vegetatively, grows in dense thickets, altering the flood regimes that native species require and extracting large quantities of scarce water while depositing large quantities of salt into the soil. Saltcedar is highly flammable, but its ability to reproduce vegetatively allows it to quickly reestablish postfire.

Loss of Biotic Crust and Reduced Soil Stability

Biotic crusts in desert ecosystems serve a critical role in stabilizing soil, particularly given the strong winds that blow across the region; the crusts also facilitate water infiltration and provide a source of nitrogen in desert ecosystems. In the late successional stages of biotic crust, lichens and mosses establish that provide the level of soil stability and fertility required to support diverse native plant communities. Disturbance by fire, plant invasion, or recreational activities (ORV, hiking, etc.) reduces biotic crust cover, which in turn reduces the fertility of the system and its ability to maintain soil resources.

Recovery and establishment of biotic crust to support diverse communities post-disturbance takes decades and is dependent on elevation, climate, and soil chemistry (figure 10.15). Organisms of biotic crusts are only metabolically active when moisture is available due to precipitation and air temperature conditions. Temperature is important in allowing biotic crust organisms to take advantage of a precipitation event: evaporation rates need to be low at the time of the event. Fine-textured soils have great water-holding capacity and facilitate rooting better than coarse-textured soils, making biotic crust recovery faster. Higher levels of salinity, phosphorus, and manganese also contribute to faster recovery rates.

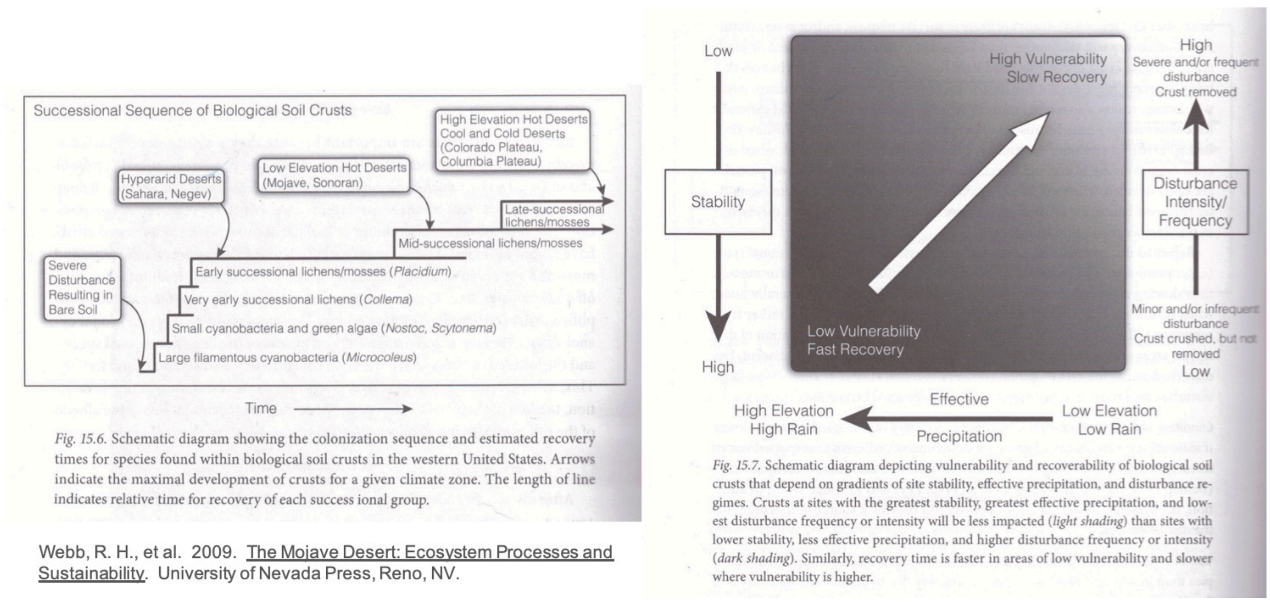


Figure 10.15 (a) Successional trajectory of biotic crust; (b) vulnerability and recovery influences of biotic crust

Restoration and Conservation Efforts

In one of the benefits of being an iconic western landscape, a great deal of focus and energy is being put into mitigation and restoration efforts in the Mojave Desert. As noted above, citizen science is leveraged to monitor invasive plants. Federal agencies, land conservation NGOs (e.g., the Nature Conservancy, Center for Biological Diversity, etc.), and scientists are working together to balance the land-use pressures and preserve the Mojave Desert ecosystem. Much of the restoration effort focuses on native seed programs (e.g., "Right Seed, Right Place"). These programs are critically important as soil seedbanks are depleted in many areas due to wind erosion and establishment of prolific seeding by annual invasive plant species. The "Right Seed, Right Place" aims not only to seed native species but also to do so strategically, so that seeded species and microclimate align for the greatest chance of success.

Figure 10.16 Mojave Desert Land Trust (MDLT) conservation target map

Guided by the Nature Conservancy's conservation target mapping (figure 10.11 above), the Mojave Desert Land Trust is working tirelessly to place biologically sensitive and culturally important areas under more stringent conservation restrictions (figure 10.15). Part of their efforts in this pursuit is land acquisition and trade with private landowners and federal land management agencies.

The Center for Biological Diversity (CBD) supports numerous ongoing projects to support desert tortoise protection and habitat restoration. CBD also focuses on the Mojave River and riparian areas, which provide habitat to six species of endangered fish.

Wildlife Defenders are leading efforts to protect bighorn sheep habitat and migration corridors at higher elevations.

Sonoran Desert Ecosystems

The Sonoran Desert could be referred to as one of the most architecturally varied natural environments in the world, with its towering saguaro cacti, barrel species, furry teddy bear cholla, sprawling ocotillo, branched paloverde species, and understory of grasses and colorful flowering forbs, as depicted in the image above. This complex of life-forms is a product of abiotic variables: soil, climate (specifically biseasonal precipitation), community ecology, evolution, and environmental gradients. The extensive niches in this system provide habitat to hundreds of species of birds, bees, butterflies, mammals, hummingbirds, and reptiles. Like the Mojave, the Sonoran also has a respectable number of endemic species and is under considerable human land-use pressures.

Section 1: Physiography

Geographic Location

The Sonoran Desert spans approximately one hundred thousand square miles split fairly evenly between the US and Mexico. Most of the US portion of the desert is located in the southern portion of Arizona (figure 11.1). It is a mosaic of isolated mountain ranges with bajadas that flow into flat valley areas.

Figure 11.1 Map of the Sonoran Desert

Climate

Most of the Sonoran Desert, at least the area with which we are most familiar, is influenced by biseasonal precipitation: winter frontal storms and summer monsoons. Winter storms develop in the Pacific Northwest, and because westerly winds drop to about thirty-five degrees latitude in the winter, it generally isn't enough to bring precipitation to the Sonoran Desert; however, occasionally, low-pressure troughs develop that push the storm fronts farther south into the Sonoran Desert.

Summer monsoons are a product of moist air off the Gulf Coast circling inland and buffered by dry air off the Pacific Coast, and when it hits the mountains, the orographic effect comes into play, and it rains intensely for short durations of time (figure 11.2).

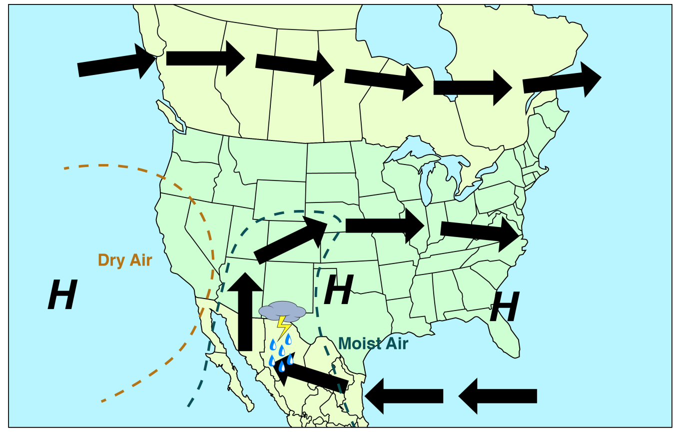


Figure 11.2 Summer monsoon effect

To an outsider, the Sonoran Desert is simply just hot and dry, and there is little to no seasonality, but to someone who lives there, it may be argued that there are five seasons:

- *Summer monsoon*: early July to mid-September
- *Autumn*: October through November, characterized by warm temperatures and low humidity
- *Winter*: December through January, characterized by mostly sunny mild days with frontal storms
- *Spring*: February through April, characterized by mild temperatures, minimal precipitation, winter annuals flower
- *Foresummer*: May through June, characterized by high temperatures and aridity with most flowering perennials blooming in May

Sky Islands, Elevation, and Gradient of Biomes

The Sky Island Region is about forty-five thousand square miles of sixty-five isolated mountain ranges rising up from the desert as a result of the convergence of several major biogeographic areas (Chihuahuan Desert, Sonoran Desert, Colorado Plateau, Southern Rocky Mountains, and the Northern Sierra Madre Mountains; figure 11.3). This convergence, in conjunction with the elevation gradient of the Sky Islands, results in extreme biodiversity across the region, to the degree that the International Union for the Conservation of Nature has declared it an area with the greatest plant diversity outside of the tropics.

One mountain within the region provides habitat to more than 50 percent of the bird species and the greatest diversity of mammal species in the US. It is estimated that more than 150,000 invertebrates, 100 mammals, over 2,100 plant species, and hundreds of species of bees inhabit the Sky Island Region. It is an area that is an active range to about a dozen endangered mammals, including the jaguar.

Figure 11.3a, b, c Convergence of biogeography, Sky Islands 2-D relief, sixty-five Sky Island ranges

Eight biomes are present along the elevation gradient (figure 11.4). As with each one-thousand-foot elevation gain, the temperature generally drops four degrees, and precipitation increases by 4.5 inches due to the orographic effect.

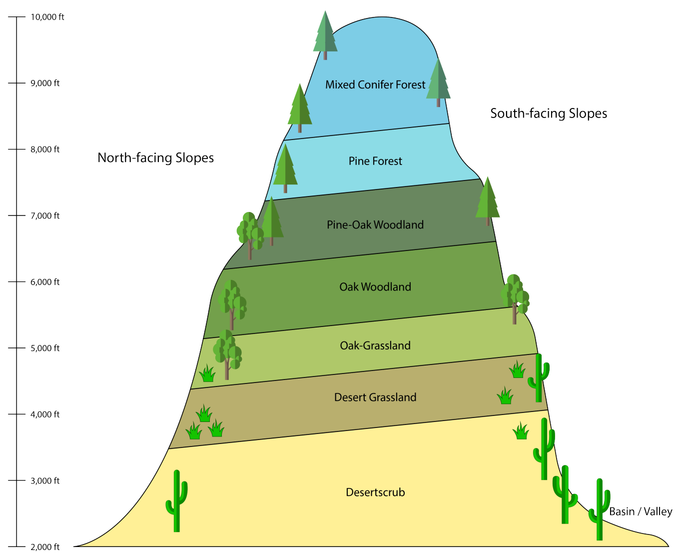


Figure 11.4 Vegetation across elevation gradient

Section 2: Classifications

Like the Mojave Desert, the Sonoran Desert is not short on classifications schemes that reflect the diversity of systems spanning over 100,000 square miles (~50,000 square miles in the US). One group has divided the Sonoran Desert up into "subdivisions," another group into "regions," and of course we have Major Land Resource Areas (MLRAs); however, only two encompass the Sonoran Desert.

Subdivisions

There are six Sonoran Desert subdivisions, of which two are present in the US and the remainder on the Baja Peninsula and Northern Mexico in the Sonoran Province (figure 11.5).

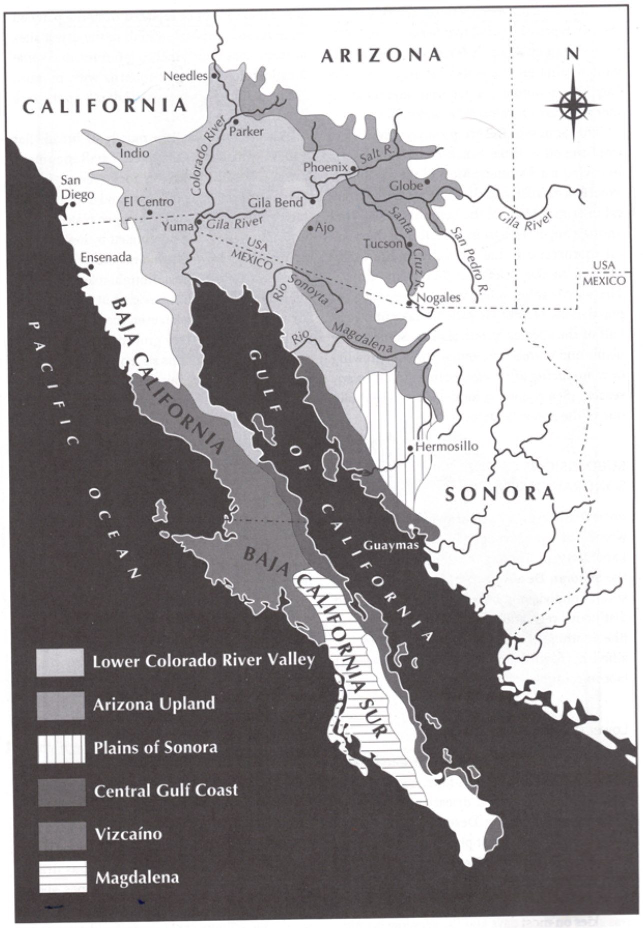


Figure 11.5 Map of Sonoran Desert subdivisions

Lower Colorado River Valley is the largest subdivision, with the Colorado River cutting through it. It is the most arid subdivision with low precipitation distributed irregularly across the subdivision, as such vegetation diversity is low and largely dominated by creosote (*Larrea tridentata*) and white bursage *(Ambrosia dumosa*). Soils in the Lower Colorado Valley subdivision are products of alluvium fans, wind erosion, and drought. Large soil extents have a caliche layer and/or desert pavement (covered in the section below). Extensive sand dunes stretch across the subdivision, connected to a system of flats populated with perennial grasses and shrubs. Washes and riparian areas have the highest levels of biodiversity, which include palo verde, perennial legumes, and mesquite species. In more saline soils of riparian areas, Atriplex species occur. Low-lying mountains support a variety of cacti-shrub communities.

Arizona Upland encompasses some of the wettest, coldest, and highest-elevation portions of the Sonoran Desert, and as such, it has a high degree of biodiversity. Rainfall in this subdivision is biseasonal, with relatively equal amounts distributed between winter storms and summer monsoons. Creosote and white bursage interspersed with acacias species dominate valleys and lower portions of bajadas. Ascending in elevation subtrees such as mesquites, paloverde species and ocotillos are intermixed, which give way to paloverde—saguaro cactus forests (figure 11.6).

Magdalena Plain is the southernmost subdivision located on the Baja Peninsula. Creosote is dominant, but several species of cacti, paloverde, and *Opuntia* species have a strong presence.

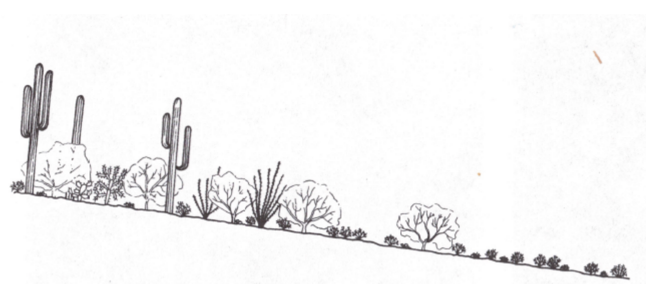


Figure 11.6 Elevation vegetation gradient, Arizona Upland subdivision, Sonoran Desert

Plains of Sonora is the smallest subdivision, located in the Sonoran Province of Mexico. It is dominated by randomly dispersed clusters of small trees, shrubs, and columnar cacti species, including ironwood (*Olneya testa*), paloverdes, mesquites, and brittlebush (*Encelia spp.*).

Central Gulf Coast is split on either side of the Gulf of California and has a north-south vegetation gradient; further, the Baja-side vegetation is more diverse than the mainland side. Vegetation is a sparse mix of subtrees and tall cacti with shrubs mixed in across rocky soils.

Vizcaino borders the Pacific Ocean to the west, which influences a lessening diversity vegetation gradient from coast to inland areas. Boojum cacti (*Fouquieria columnaris* visually dominates across the subdivision, while ragweed (*Ambrosia chenopodiifolia*) and Shaw's Agave (*Agave shawii*) generally dominate in density. Variations of associated species are related to the vegetation gradients across this subdivision.

Subregions

Author's note: Given the varying classification schemes applied to the Sonoran Desert, this section outlining subregions will briefly geographically place the subregion, provide any interesting facts, and focus mostly on images of the region.

Colorado Desert aligns with MLRA D31 and the Lower Colorado River Valley subdivision. It is roughly seven million acres and encompasses the agricultural production strongholds of the Coachella and Imperial Valleys.

Figure 11.7 Colorado Desert, Algodones Dunes, Salton Sea, Big Horn Sheep, Desert Lily, Nolina bigelovii, Pygmy Cedar, Ocotillo Wells ORV Recreation

Gran Desierto de Altar is a small region in Northern Mexico just over the US-Mexico border. It is a region with the only active erg dunes in North America. Erg dunes are those that are continuously being formed and reshaped by wind and are generally devoid of vegetation. This region also encompasses a UNESCO World Heritage Site—El Pinacate y Gran Desierto de Altar Biosphere Reserve. The mountains of this area are volcanic chains.

Figure 11.8 Map of Gran Desierto de Altar region, Erg Dune in Gran Desierto de Altar region, UNESCO World Heritage Site: El Pinacate y Gran Desierto de Altar Biosphere Reserve

Lechuguilla Desert is a small region on the north side of the Gran Desierto de Altra in Arizona. The region is named for the extensive presence among creosote and bursage of *Agave lechuguilla*, which is generally found in the Chihuahuan Desert.

Figure 11.9 Lechuguilla Desert, view from mountains looking toward valley. Lechuguilla Agave in center.

Tonopah Desert is only about thirty miles long and is just south of the intersection of the Gila and Hassayampa Rivers. It is in MLRA D40 and the Lower Colorado Yuha Desert. Conservation efforts continue to protect and recharge the overdrawn Tonopah Aquifer that lies below this region.

Figure 11.10 Tonopah Desert, one of the aquifer recharge sites

The region in the Imperial Valley of California along the border with Mexico once was the lake bed of the ancient Lake Cahuilla. It is also the site of the passage of the de Anza expedition. Culturally, archeologically, and ecologically, the Yuha Desert is a critical area that is currently under extensive conservation status.

Figure 11.11 Yuha Desert, Yuha Desert, life at the bottom of a lake bed, strong wind-driven dust storm

Yuma Desert is a largely barren, wind-blown desert that is highly irrigated to produce crops in the valley areas located between the Gila and Colorado Rivers in Southern Arizona. Most of the irrigation water comes from a heavily dammed Lower Colorado River, which largely prevents water flow to the lower reaches in Mexico. The military has a large presence in this area.

Figure 11.12 Yuma Desert, Laguna Diversion Dam, Irrigated crop field in Yuma Desert

MLRAs

Figure 11.13

D31 Lower Colorado Desert is largely in California, situated south of the Salton Sea, with numerous wilderness areas and Native American reservation lands. The topography is a mix of mountains, alluvial fans, and valleys. Elevation ranges from 275 feet below sea level to elevations above 1,650 feet. It is within the Lower Colorado River Valley subdivision. Vegetation patterns reflect the intense competition for water and resources. Although this region has low precipitation, irrigated agriculture production is a major land use.

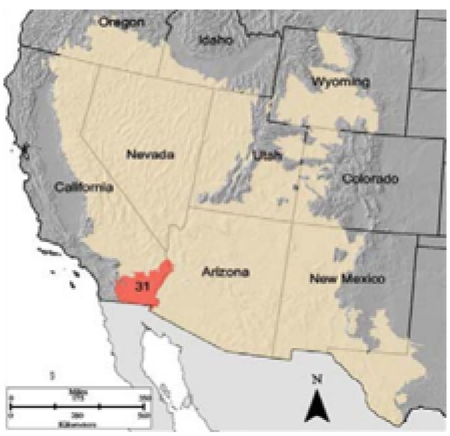


Figure 11.14

D40 Sonoran Basin and Range is extensively in Arizona, encompassing the major cities of Yuma, Phoenix, and Tucson as well as two major Native American reservations (Gila Indian River Community and Tohono O’Odham). Its topography is a mix of fault-block mountains ranging in elevation from 1,000 to 4,600 feet and valleys. Most of the valleys are covered with young deep alluvium washed out from surrounding mountains. The area has experienced intense volcanism in the geologic past, with some granite outcrops over one billion years old. Three major rivers flow through this region: Lower Colorado, Gila, and Salt. Most of the population of Arizona lives in this MLRA, and as such, over six million gallons of water are withdrawn daily (40 percent ground; 60 percent surface). Like many areas in the West, about 50 percent of this MLRA is federally managed. Major conservation concerns are water scarcity, soil stability, and biodiversity.

Section 3: Soils

Many soils through the valleys of the Sonoran Desert are the result of alluvium washouts, with three commonly occurring characteristics: calcic and argillic horizons, areas of desert pavement, and soil crusts, which were discussed in chapter 10.

Calcic Horizon

This is the buildup of calcium carbonate into a layer within the soil profile. Precipitation regime is the driving factor determining the depth of the calcic horizon; the more precipitation, the greater the depth. Calcic horizons take a long time to form; figure 11.15 depicts the formation process. For many years, the source of calcium was a bit of a mystery, as the parent material doesn't contain high quantities of calcium. It was determined that a predominant source of calcium was a result of wind-driven deposition. This accumulation of calcium carbonate results in soil pH levels above 7 (which means more alkaline).

Figure 11.15 Calcic horizon formation process

Argillic Horizons

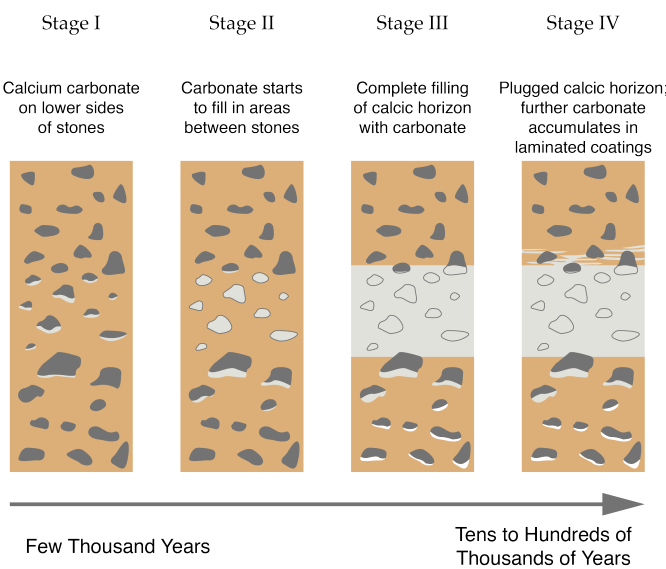


Figure 11.16 Argillic horizon

Clay-rich layers, often rusty red in color, are referred to as argillic horizons (a.k.a. claypans; figure 11.16). The reddish colors are a result of the oxidation of iron-bearing minerals. These horizons are also formed over a long period of time as a result of water carrying clay particles that accumulate. Desert soils of Pleistocene deposits generally have argillic horizons, while those formed in the Holocene do not or have weak argillic horizons because their time in residence has not been long enough. Soils with a high calcium carbonate concentration do not have argillic horizons, as calcium carbonate causes clay particles to clump together rather than disperse in water. These claypan horizons can impede water movement and rooting depth.

Desert Pavement

Desert pavements are areas of small packed stones that make a relatively flat surface devoid of vegetation (figure 11.17). Most desert pavements are in the most arid locations and develop on stony alluvial fans. They, like most soil characteristics, form over time, driven by physical processes (figure 11.18).

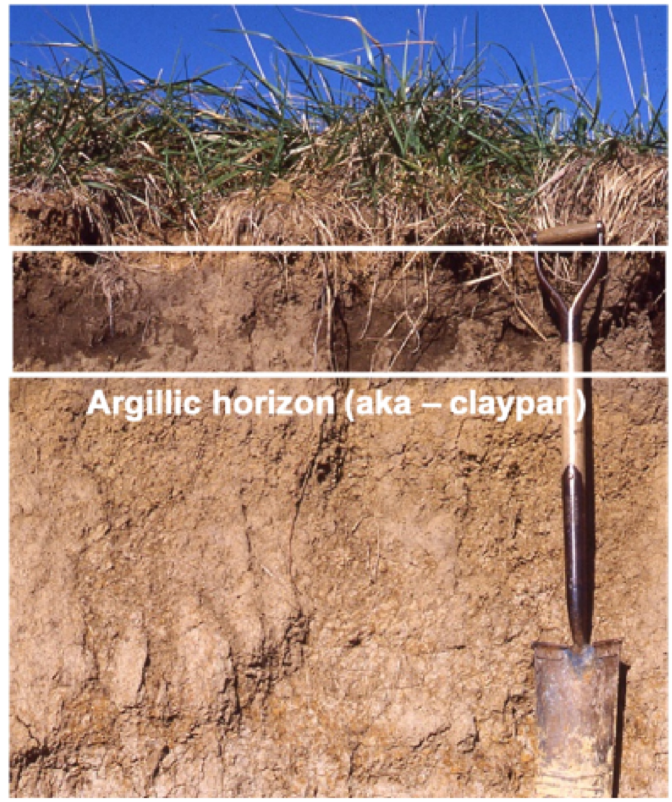


Figure 11.17 Area of desert

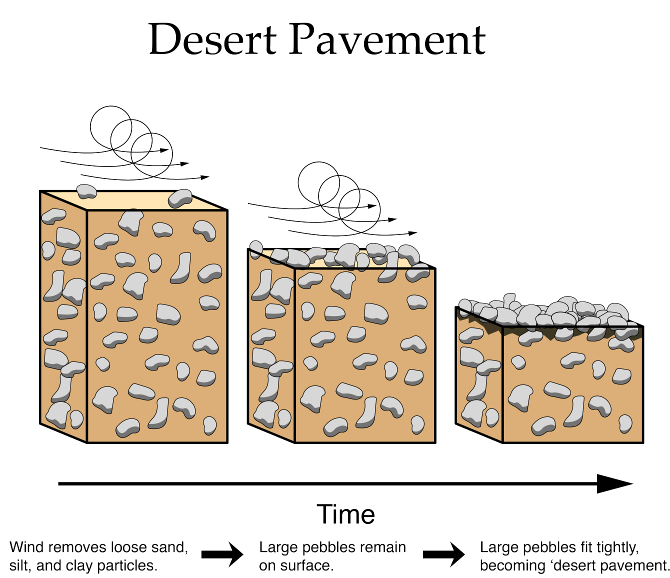


Figure 11.18 Desert pavement formation process

Section 4: Biodiversity

If there is one word to describe the Sonoran Desert, it may be *diversity*. Estimates vary, but in general, there are likely well over five thousand species throughout the Sonoran Desert.

The concept of biological diversity (a.k.a. biodiversity) was first defined by E. O. Wilson. His perspective of the concept was the degree of interconnectivity within an ecosystem, which is more complex than what is generally inferred by the term *biodiversity* today—species richness. To understand the complexity of the Sonoran Desert across spatial and temporal scales; the context of its rich history of native cultures, geologic events, and modern-day human impacts; and the biology and ecology of thousands of native and/or endemic species, we require Wilson's perspective of biodiversity, which encompasses genetic diversity, species diversity, interaction diversity, ecosystem diversity, and cultural diversity.

Genetic diversity in the Sonoran Desert is extensive given the number of species within each taxon. For example, there are over one hundred to two hundred butterfly species and five to ten times the number of moth species. It is estimated that one-third of the species native to the Sonoran Desert are endemic, meaning they only inhabit the Sonoran Desert. On the Baja Peninsula alone, there are approximately 550 endemic plant species.

Species diversity—the number of species in a given area and their relative abundance—across the Sonoran Desert and within ecosystems is considerably high, particularly given the gradient of ecosystems. The biseasonal precipitation also is a substantial factor influencing species diversity. For example, in the Tucson Basin, researchers found twenty species of wildflowers within a single square yard and seventy-five to one hundred native plant species sharing roughly a quarter acre.

Often not considered but a strong diversity factor across the Sonoran Desert is functional or interaction diversity—the multitude of niches occupied and roles species play as well as the number of species filling those functional roles within the cycles of the ecosystem. For example, pollination is a widespread functional activity throughout the Sonoran Desert. In the Huachuca Mountains, hummingbirds, bees, butterflies, and bats all share the pollinating function. Another example that is multilayered, reflecting the complexity of Sonoran Desert ecosystems, revolves around the life of the saguaro cactus. A nurse plant facilitates the beginning of the life of a saguaro cactus by providing shelter and protection, only to have the tables turned when the saguaro cactus overtakes the nurse plant and increases competition for the plant, often outcompeting the plant. When a Gila woodpecker (*Melanerpes uropygialis*) excavates a nest in the upper third of a mature saguaro and then abandons it, other birds utilize the cavity for nesting or as a source of food. Some hawk species use areas where saguaro arms branch out to build nests, and other raptors use the cactus as a hunting perch. Not to mention all the insects that feed off areas where the outer layer of the cactus has been removed or damaged.

As noted above, there is an elevation gradient of ecosystem diversity, particularly in the Sky Island regions where scrub desert transitions to woodlands to conifer forests. There is also ecosystem diversity across the Sonoran Desert, from coastal areas to inland mountains. Areas around water bodies often have a diversity of ecosystems ranging from rivers to riparian and wetland areas to saltgrass flats transitioning to woodland areas or agricultural fields, such as the case in the Colorado River Delta in the southern reaches of Arizona and Northern Mexico.

The cultural diversity of the Sonoran Desert may be the greatest in the US, with seventeen Native American tribes, all sovereign entities with rich cultural histories and traditional ecological knowledge guiding land and resource management. This is in addition to Anglo and Hispanic presence and management approaches.

The high degree of biodiversity across the Sonoran Desert is threatened by an estimated 350+ invasive species, resulting in approximately 60 percent of the desert area no longer covered with native species. Buffelgrass is of serious concern as well as Africanized bees and cowbirds (parasitic bird species that take over the nests of native bird species). Urbanization, recreation, and water development projects have fragmented the habitat and are placing a great deal of stress on water resources throughout the desert. More water is being pumped out of aquifers than is recharged to support urban development and agriculture, and this lowers the water table, making water inaccessible to many plants.

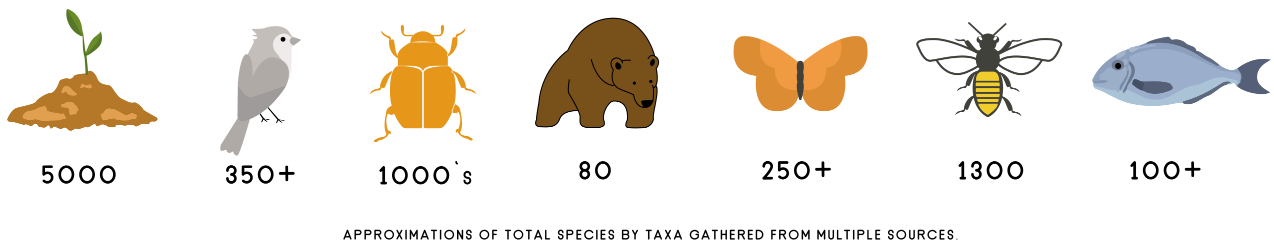


Figure 11.19 Approximations of total species by taxa gathered from multiple sources

Section 5: Current Anthropogenic Stresses and Conservation

As noted throughout the chapter, the Sonoran Desert is under the same types of pressures as the Mojave Desert: invasive plants, land conversion, habitat fragmentation and destruction, off-road vehicle traffic, recreation, drought, and water and resource management. One stress generally missing from the mix is mineral extraction; however, as noted above, water extraction is such that its impacts are substantial on ecosystems, particularly those in the Phoenix-Tucson-Southwest Arizona regions. Of particular concern are the impacts on the vast array of pollinator species throughout the Sonoran Desert, species that not only pollinate native plants but are vital for agricultural production.

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Species list: Plants

Common Name	**Scientific Name**
Brittlebush	Encelia farinosa
Creosote Bush	Larrea tridentata
Bursage	Ambrosia dumosa
Burrobrush	Hymenoclea salsola
Mormon Tea	Ephedra viridis
Mesquite	Prosopis glanduous
Big Basin Sagebrush	Artemisia tridentata
Dandelion	Taraxacum officinale
Cheatgrass	Bromus tectorum
Idaho Fescue	Festuca idahoensis
Bluebunch Wheatgrass	Pseudoroegneria spicata
Wyoming Big Sagebrush	Artemisia tridentata wyomingensis
Western Wheatgrass	Pascopyrum smithii
Yellow Rabbitbrush	Chrysothamnus viscidiflorus
Rubber Rabbitbrush	Ericameria nauseosa
Alfalfa	Medicago sativa
Barrel Cactus	Ferocatus
Saguaro Cactus	Carnegiea gigantea
Western Juniper	Juniperus occidentalis
Needle-And-Thread Grass	Hesperostipa comata
Antelope Bitterbrush	Purshia tridentata
Silver Sage	Salvia argentea
Aspen Species	Populus spp.
Douglas Fir	Pseudotsuga menziesii
Shadscale	Atriplex confertifolia
Budsage	Artemisia spinescens
Thurber's Needlegrass	Achnatherum thurberianum
Sandberg Bluegrass	Poa secunda
Curly Leaf Moutain Mahogany	Cercocarpus ledifolius
Snowberry	Symphoricarpos albus

Common Name	**Scientific Name**
Ceanothus Species	Ceanothus
Black Sage	Artemisia nova
Gardner's Saltbrush	Atriplex gardneri
Indian Ricegrass	Oryzopsis hymenoides
Greasewood	Adenostoma fasciculatum
Winterfat	Krascheninnikovia lantana
Cottonwood Species	Populus spp.
Willow Species	Salix
Utah Juniper	Juniperus osteosperma
Saskatoon Serviceberry	Amelanchier alnifolia
Black Grama	Bouteloua eriopoda
Blue Grama	Bouteloua gracilis
Gambel Oak	Quercus gambelii
Moutain Big Sagebrush	Artemisia tridentate vaseyana
Scabland Big Sagebrush	Artemisia rigida
Low Sagebrush	Artemisia arbuscula
Bigelow Sagebrush	Artemisia bigelovii
Fringed Sagebrush	Artemisia frigida
Crested Wheatgrass	Agropyron cristatum
Ponderosa Pine	Pinus ponderosa
Galleta	Hilaria rigida
Fourwing Saltbush	Atriplex canescens
Alkali Sacaton	Sporobolus airoides
Mountain Muhly	Muhlenbergia montana
Mexican Pinyon Pine	Pinus cembroides
Mexican Blue Oak	Quercus oblongifolia
New Mexico Locust	Robinia neomexicana
Buckbrush	Ceanothus cuneatus
Manzanita	Arctostaphylos
Jojoba	Simmondsia chinensis

Common Name	Scientific Name
June Grass	Koeleria
Single-Leaf Pinyon Pine	Pinus monophylla
Two-Leaf Pinyon Pine	Pinus edulis
Pinyon Dwarf Mistletoe	Arceuthobium divaricatum
Juniper Mistletoe	Phoradendron juniperinum
Knapweeds	Centaurea
Thistles	Cirsium, Carduus, Onopordum
Mustards	Sisymbrium, Brassica
Dalmatian Toadflax	Linaria dalmatica
White Bursage	Ambrosia dumosa
Joshua Tree	Yucca brevifolia
Palo Verde	Parkinsonia
Ironwood	Olneya tesota
Fountain Grass	Pennisetum
Red Brome	Bromus madritensis rubens
Saltcedar	Tamarix chinensis
Pipe Cacti	Stenocereus thurberi
Pricky Pear Cacti	Opuntia
Desert Ironwood	Olneya tesota
Wooly Plantain	Plantago patagonica
Desert Indian Wheat	Plantago insularis
Mediterranean Grass	Schismus barbatus
Texas Filaree	Erodium texanum
Mediterranean Storksbill	Erodium malacoides
Spring Pygmy Cudweed	Diaperia verna
Woolly-Head Neststraw	Stylocline micropoides
Mojave Desert Star	Monoptilon bellioides
Wooly Daisy	Eriophyllum wallacei
Curvenut Combseed	Pectocarya recurvata

Plants

Species list: Animals

Common Name	Scientific Name
Javelina	Pecari tajacu
Coyote	Canis latrans
Desert woodrat	Neotoma lepida
Jackrabbit	Lepus californicus
Vulture	Cathartes aura
Pronghorn	Antilocapra Amerciana
Kangaroo rat	Dipodomys deserti
Great Basin sage grouse	Centrocercus urophasianus
Gunnison sage grouse	Centrocercus minimus
Wolf	Canis lupus
Elk	Cervus canadensis
Great Basin spadefoot toad	Spea intermontana
Fox	Vulpes vulpes
Hare	Lepus
Lynx	Lynx canadensis
Black-tail deer	Odocoileus hemionus
Prairie dogs	Cynomys
Black bears	Ursus americanus

Animals

Species list: Birds and Insects

Common Name	Scientific Name
Vulture	Cathartes aura
Great Basin sage grouse	Centrocercus urophasianus
Gunnison sage grouse	Centrocercus minimus
Great Basin spadefoot toad	Spea intermontana
Mountain pine beetle	Dendroctonus ponderosae
Pinyon jay	Gymnorhinus cyanocephalus
Pinyon tip moth	Dioryctria albovittella
Pinyon cone moth	Dioryctria albovittella
Pinyon Ips	Ips confusus
Pinyon twig beetle	Pityophthorus
Pinyon needle scale	Matsucoccus acalyptus
Pinyon needle miner	Coleotechnites edulicola
Scrub jays	Aphelocoma californica
Stellar's jay	Cyanocitta stelleri
Clark's nutcrackers	Nucifraga columbiana
Quagga mussels	Dreissena bugensis
Desert tortoise	Gopherus agassizii
Sonoran desert cicada	Diceroprocta apache
Sonoran mud turtle	Kinosternon sonoriens

Birds, Insects, etc.

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