Montane Forests

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Introduction

California's montane forests include some of the most productive and diverse temperate ecosystems in the world. They contain the largest single-stem tree (the 1,487 cubic meter General Sherman giant sequoia [*Sequoiadendron giganteum*]) (Van Pelt 2001) and the highest conifer diversity (thirty-plus species in the Klamath-Siskiyou mountain range) (Sawyer 2006) in the world (Table 27.1). Although these forests share some attributes with the Pacific Northwest (i.e., long-lived large trees and some common wildlife species) (North et al. 2004) and Southwest (i.e., historical forests dominated by pine and shaped by frequent fire), their combination of high productivity, strong seasonal drought, and fire dependence distinguish them ecologically from montane forests in these adjacent areas. The distribution of different forest types is strongly influenced by temperature and precipitation gradients associated with elevation and inland distance from the Pacific Ocean. Historically the forests have been logged, but interestingly for the nation's most populous state, some large areas of montane forest—especially in the central and southern Sierra Nevada—remain only lightly affected by human resource use. Management practices in these montane forests have often been controversial, and fire suppression has significantly altered forest conditions such that fires escaping containment are often large and produce extensive areas burned at high severity. Climate change, California's increasing population, and projected increases in wildfire pose challenges that will require collaborative and inventive future management.

In this chapter we focus on montane forest ecosystems in California's Sierra Nevada, Klamath, Cascade, Coastal, Traverse, and Peninsular Ranges. These forests often border, at lower elevations, warmer, drier ecosystems that include oak-savanna and chaparral (see Chapters 24, "Chaparral," and 25, "Oak Woodlands"). At upper elevations, montane forests often border colder red fir and subalpine forests characterized by deeper, more persistent snowpacks (see Chapter 28, "Subalpine Forests").

TABLE 27.1
Characteristics of mature trees for major tree species in California's montane forests at the turn of nineteenth century

Species	Elevation (m)	Height (m)	Diameter at breast height (DBH) (cm)	Mature age (years)
White fir	800–2,300 N: 1,500–2,400 S	53–58 (66)	110–170 (223)	200–300 (372)
Red fir	1,400–2,400 N; 1,700–2,700 S	51–56 (77)	100–180 (295)	250–400 (665)
Incense cedar	600–1,600 N; 800–2,100 S	24–31 (70)	150–210 (456)	250–600 (unk)
Jeffrey pine	1,500–2,400 N; 1,700–2,800 S	34–49 (61)	90–150 (250)	120–350 (813)
Sugar pine	1,000–2,000 N; 1,400–2,700 S	55–61 (82)	120–180 (352)	100–400 (unk)
Ponderosa pine	300–1,800 N; 1,200–2,100 S	45–55 (70)[B]	90–120 (277)[C]	100–350 (907)[A]
Douglas-fir	300–2,100 N; 600–2,100 S	46–53 (92)[A]	120–210 (485)[A]	120–400 (1,350)
Black oak	900–1,500 N; 1,400–2,100 S	28–34 (38)[C]	130–160 (273)[C]	120–400 (unk)
Giant sequoia	900–2,000 N; 1,600–2,700 S	50–75 (94)	400–600 (1,228)	400–1,100 (3,266)

SOURCE: According to Sudworth 1900.
NOTE: In height and DBH columns, values in parentheses are for the largest dimension on record (in van Pelt 2001) and the oldest on record (in The Gymnosperm Database), www.conifers.org.
A. Record holder in Washington State
B. Record holder in Idaho
C. Record holder in Oregon
UNK = unknown

Physiographic Setting

Climate

California's Mediterranean climate, in which 85% of annual precipitation occurs between November and May, significantly influences montane forest composition, distribution, and ecosystem functions (Minnich 2007). Unlike montane weather in much of the Rockies and the Southwest, summer thunderstorms and significant rain events are infrequent and often highly localized in California. During the growing season (generally March through July), plants rely on soil moisture stocks from winter precipitation and melting snow (Major 1977). The distribution of montane forest is influenced by site water availability and evaporative demand and roughly corresponds to an elevation zone with a mean annual temperature of 7°C to 12°C and total precipitation of 800 to 1,800 mm yr[1] (Stephenson 1998, Goulden et al. 2012). In general, the elevation of this zone shifts upward from north to south and coast to inland. For example, mixed-conifer forests in the Klamath Mountains occur between about 1,000 to 2,100 meters in elevation, compared to 1,400 to 2,400 meters in the southern Sierra Nevada (Fites-Kaufman et al. 2007). Temperatures decrease by approximately 4°C to 6°C km^{-1} of elevation gain (Major 1977). Precipitation rises with elevation up to a point then gradually decreases. For example, maximum precipitation in the central Sierra Nevada occurs around 1,900 meters (Armstrong and Stidd 1967, Major 1977).

The percentage of annual precipitation that occurs as snow ranges from approximately 25% to 65% in lower to upper montane forests. Montane forests typically transition to red fir (*Abies magnifica*)–dominated forest types at elevations where winter and spring temperatures ensure that most of the precipitation occurs as snow (Barbour et al. 1991). A large increase in snowpack accompanies the transition from ponderosa pine (*Pinus ponderosa*)–dominated forest through mixed conifer to red fir. For example, in the Pit River basin in northern California, April 1 snow depths below 1,500 meters are minimal (13 centimeters at Burney Springs in ponderosa pine) but reach over 200 centimeters at elevations over 1,950 meters in the red fir zone. In the American River basin of the central Sierra Nevada, similar patterns occur, with 37 centimeters average April 1 snow depth at 1,600 meters eleva-

Photo on previous page: Mixed-conifer forest with a restored fire regime, containing horizontal and vertical structural diversity, in the Illilouette Basin of Yosemite National Park. Photo: Marc Meyer.

tion (pine-dominated, mixed conifer) and 215 centimeters at 2,270 meters (red fir) (WRCC). In red fir forests the deeper snowpack and cooler temperatures substantially reduce the length and magnitude of the summer drought (Royce and Barbour 2001).

On an annual basis, California experiences one of the most variable precipitation regimes in the United States. In montane forests this means snowpack depth (and available water during the growing season) can vary by more than an order of magnitude between years (Mote 2006). The El Niño/Southern Oscillation (ENSO) often drives this interannual variability, but the area affected in any annual event varies across the range of montane forests (Minnich 2007). An El Niño year may produce a deep snowpack in the southern California mountains while northern California experiences normal or below normal precipitation. Patterns vary year-to-year depending on the strength of the ENSO event. California Department of Water Resources splits its Sierra Nevada snowpack assessment into northern, central, and southern zones because winter storms tracking from the Pacific Northwest and southern California might only impact the northern and southern half, respectively, of the state (see Chapter 2, "Climate"). Long-term averages suggest Yosemite National Park might roughly be a transition zone, as montane forest precipitation significantly decreases south of the park coincident with the southern range limit of Douglas-fir (*Pseudotsuga menziesii*) in the Sierra Nevada (Burns and Honkala 1990).

Precipitation patterns within the wet season are also highly variable. A few large winter storms usually account for a third to a half of annual precipitation and can occur over a seasonal total of only five to ten wet days per year. So-called atmospheric rivers (ARs) generate 20% to 50% of the state's precipitation totals (Dettinger et al. 2011). ARs are narrow bands (typically less than 200 kilometers wide) of concentrated water vapor that develop over the oceans and direct large amounts of moisture at continental areas (see Chapter 2, "Climate"). Due to the influence of periodic ARs developing over the tropical Pacific, California experiences more extreme precipitation events than any other part of the U.S., including the hurricane-affected Gulf Coast (Dettinger et al. 2011). ARs in montane forests, such as the New Year's Day storm of 1997, can cause widespread flooding and landslides, reshaping riparian corridors and forest stands on unstable slopes.

Soils

Montane forest soils are generally relatively young and weakly developed because of the recent glaciation of most California mountain ranges (generally higher than 1,400 meters in elevation) during the Late Wisconsin glacial episode (thirty thousand to ten thousand years ago) (Atwater et al. 1986; see Chapter 4, "Geomorphology and Soils"). Soils over granitic parent material, which predominate in montane ecosystems south of the Merced River (O'Green et al. 2007), often are highly porous and well-drained because they contain a substantial fraction of decomposed granite. California's mountains also contain older, metamorphosed rocks invaded by batholithic magma and young volcanic and sedimentary postbatholithic rocks (Harden 2004). Most lower montane soils are ꜰ ꜱᴏ ꜱ and more highly leached ᴛ ꜱᴏ ꜱ and are moderate to strongly acidic. Organic horizons may be deep (often depending on time since last fire) due to low decomposition rates resulting from conifer's poor litter quality and

from minimal topsoil mixing by soil fauna (O'Green et al. 2007).

Microbial activity and organic matter decomposition are also limited by dry conditions during California's annual summer drought. For example, the thick litter layers often found around the base of mid-elevation trees result in part from reduced decomposition rates from rapid drying produced by accelerated snowmelt from solar heating of the tree bole (Johnson et al. 2009). Soil depth varies considerably, strongly affecting water-holding capacity and in turn forest productivity. Maximum clay content may range from 30% to 55% in the lower montane zone, but a significant reduction occurs in soil development above 1,500 to 1,800 meters in elevation, with clay content often dropping to less than 15% (O'Green et al. 2007). ɴ ᴇᴘᴛ ꜱᴏ ꜱ and ɴᴅ ꜱᴏ ꜱ dominate these higher-elevation soils. Generally, such soils are shallow and rich in organic matter with large, unconsolidated fragments and limited soil moisture storage. One study examining soil change along an elevation gradient (200–2,900 meters) found decreasing pH (about two units) and base saturation (90% to 10%) and increasing organic carbon with increasing elevation (Dahlgren et al. 1997). They also found maximum chemical weathering at mid-elevations (ponderosa and mixed-conifer forest types). Aspect and slope position also influence soil development and processes, with more weathering and deeper, richer soils on mesic, northerly aspects and lower-slope positions compared to xeric, south-facing, and upper-slope conditions.

After water, nitrogen is typically the most limiting plant growth resource in temperate zones (Vitousek and Howarth 1991). In California's montane forests mineral soil holds most (65–90%) of the nitrogen (Johnson et al. 2008). Nitrogen loss from fire volatilization increases with fire intensity but is often rapidly replenished by common actinorhizal shrubs such as *Ceanothus* spp. and bear clover (*Chamaebatia foliolosa*) that are associated with nitrogen-fixing bacteria (*Frankia* spp.) (Oakley et al. 2003, 2004; Stein et al. 2010). Ultramafic soils are not widespread in Sierra Nevada montane conifer ecosystems except in the Feather River drainages, but where present they significantly limit plant productivity and species composition as they lack most macronutrients and contain various heavy metals. The Klamath-Siskiyou Mountains have extensive ultramafic soil areas that support many rare plants and plant communities unique to this region of high diversity (Alexander et al. 2007).

Montane Forest Types

Several classification schemes exist for montane forest types in California (Critchfield 1971, Davis et al. 1995, Holland and Keil 1995, Barbour et al. 2007, Sawyer et al. 2009). Although each slightly differs in the number and types of forest ecosystems, they generally concur, particularly for the most widely distributed forest types discussed in this chapter. More detailed vegetation information using finer forest-type classifications are available in Barbour et al. (2007) and Sawyer et al. (2009). We generally have used the California Wildlife Habitat Relationships System (Meyer and Laudenslayer 1988) (Figure 27.1), which builds upon the U.S. Forest Service California Vegetation (CALVEG 2013) classification based on existing vegetation (rather than potential natural vegetation). All of the forest types discussed in this chapter could be viewed as related to the mixed-conifer group because they are delineated by changes in
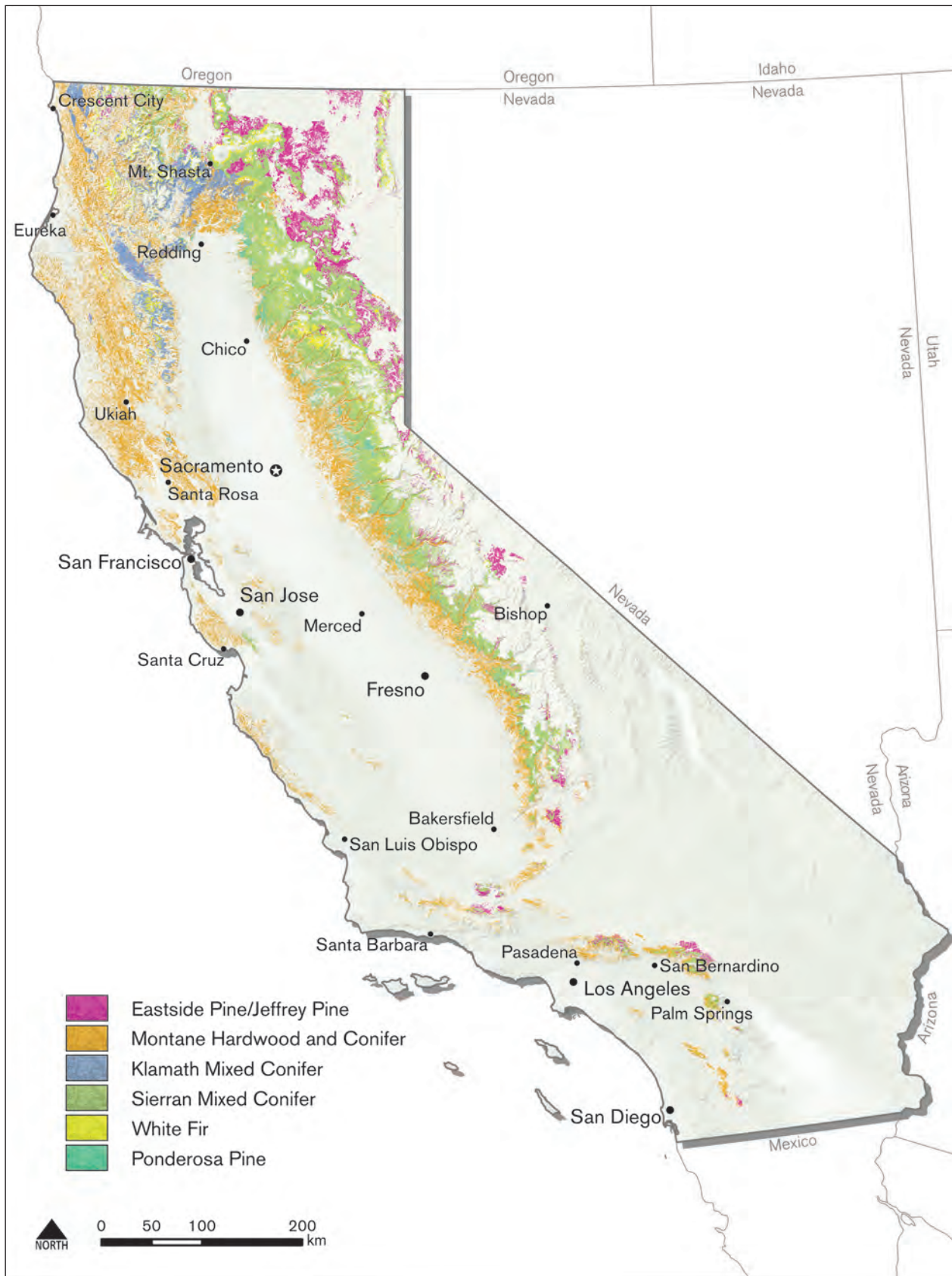
FIGURE 27.1 Distribution of montane forest types in California based on California wildlife habitat and CALVEG classifications. Giant sequoia groves not shown. Data from Cal Fire, Fire Resource and Assessment Program (FRAP). Map: Ross Gerrard, USFS PSW Research Station, and Parker Welch, Center for Integrated Spatial Research (CISR).

environmental or EDAPH conditions that allow one or several typical mixed-conifer species to become dominant.

Mixed Conifer

Mixed conifer (2,484,012 hectares) is one of the most common montane forest ecosystems in California and has the highest diversity among them of vertebrate species (Meyer and Laudenslayer 1988) (Figure 27.2a). Major tree species include ponderosa pine, Jeffrey pine (*Pinus jeffreyii*), sugar pine (*P. lambertiana*), white fir (*Abies concolor*), incense-cedar (*Calocedrus decurrens*), Douglas-fir, and black oak (*Quercus kelloggii*). Red fir, lodgepole pine (*Pinus contorta murrayana*), and western white pine (*Pinus monticola*)—all upper montane species—intermix with mixed conifer at higher elevations and in cold air drainages. Within mixed conifer, species composition can change over small distances, often in response to water availability (i.e., generally transitioning from fir to pine with increasing dryness) and microclimate (i.e., cold air drainages that retain snowpack are dominated by lodgepole pine, and white and red fir). Differences with aspect in temperature and insolation influence the elevations at which different forest types occur (Figure 27.3).

Considering the overwhelming importance of water availability and fire—historic mean fire return intervals (HFRI) averaged eleven to sixteen years (Van de Water and Safford 2011)—to mixed-conifer ecosystems, perhaps the most important distinction within the mixture of species concerns those that are highly tolerant of fire and drought but intolerant of shade (black oak and the yellow pines) and those that are less tolerant of fire and drought but grow relatively well in low-light conditions (white fir, incense-cedar, Douglas-fir) (Table 27.2). Historically, frequent fire kept forests generally open and exposed bare mineral soil, although conditions varied with topography and fire history (Collins, Lydersen et al. 2015, Stephens, Lydersen et al. 2015). These conditions favored pines, which could comprise up to 40–65% of the trees (McKelvey and Johnston 1992, North et al. 2007, Lydersen and North 2012). Fire suppression has significantly increased stem densities and ANOPY OER and reduced understory light, resulting in heavy dominance by fir and incense-cedar and little shrub cover in many mixed-conifer forests today (North, Oakley et al. 2005; Collins et al. 2011; Dolanc et al. 2013; Knapp et al. 2013).

Klamath Mixed Conifer

Mixed-conifer forests in the Klamath Mountains (461,666 hectares) contain many species found in montane ranges in both California and the Pacific Northwest, contributing to high diversity and unique community assemblages (Sawyer 2006) (see Figure 27.2b). The diverse flora has developed over a long period from many biogeographic sources (Whittaker 1960, Briles et al. 2005) including migration from other regions (Stebbins and Major 1965), relictual species such as the recently identified Shasta snow-wreath (*Neviusia cliftonii*) (Lindstrand and Nelson 2006), and newly evolved taxa (Smith and Sawyer 1985). This diversity does not appear to result from the Klamath's fire regimes (HFRI seven to thirteen years) (Fry and Stephens 2006), which are similar to those in the Sierra Nevada, but instead is probably due to its ecotonal location straddling an area where different climate, geologic, and edaphic zones collide. Ultramafic, mafic, granitic, sedi-

mentary, and metamorphic substrates are common (Waring 1969, Kruckeberg 1984), and temperature and precipitation gradients are very steep between the wet, cool western slopes and dry, hot interior areas bordering the Central Valley. Pleistocene glaciation in the Klamath Mountains was primarily confined to higher elevations (Sawyer 2007), and unlike most of the Sierra Nevada, modern streamflow is more driven by rainfall than by snowpack (Miller et al. 2003).

Populations of some conifers in this range are geographically quite distant from their distributions in other mountain ranges, and some endemic conifers occur here as well (Sawyer 2007). Examples of the former include foxtail pine (*Pinus balfouriana*; shared with the southern Sierra Nevada), Engelmann spruce (*Picea engelmannii*), and subalpine fir (*Abies lasiocarpa*—both at their southern range limit in the Klamaths; the latter is exemplified by Brewer spruce (*Picea breweriana*). In addition to thirty conifer species, Sawyer (2007) lists nineteen common hardwood tree species and more than seventy species of shrubs. The rugged topography in these mountains contributes to different fire regimes and forest types associated with aspect, slope position, and elevation (Taylor and Skinner 2003). Because the mountains are discontinuous and highly dissected, forest types tend to occur in patches rather than continuous belts. The rugged topography and lack of a dominant orientation provides many edaphic, microclimate, and disturbance regime differences over fine scales (Skinner et al. 2006). Whereas mixed conifer in the Sierra Nevada may have three to five tree species at any one site, Klamath mixed conifer typically has five to seven or more species growing together. A few sites in the Klamath Mountains apparently support the highest local diversity of conifers in the world. For example, the Sugar Creek drainage in the headwaters of the Scott River contains seventeen conifer species within an area of less than 2.6 square kilometers (Cheng 2004).

White Fir

Forests in which white fir (379,372 hectares) makes up more 60% of the relative canopy cover are often typed white fir (Sawyer et al. 2009), although other species such as incense-cedar, dogwood (*Cornus nuttallii*), ponderosa and Jeffrey pine, and Douglas-fir may also be present (see Figure 27.2c). Although white fir is more widely distributed than any other fir in California, intermixing with many species, it becomes dominant in mesic areas that have a longer fire return interval (greater than forty-five years) (Van de Water and Safford 2011), where regenerating trees can grow large enough to survive low- to moderate-intensity fire. White fir forests may be intermixed with or adjacent to mixed conifer and usually indicate an A OT shift toward cooler, wetter conditions. However, white fir is also found in drier interior ranges including the Warner Mountains (1,550–1,850 meters) in northeastern California and the Clark, Kingston, and New York Ranges (2,300–2,900 meters) (Paysen et al. 1980) in the Mojave area.

The dominance of a shade-tolerant species creates high canopy cover and multilayer stands with less fine-scale variability in microclimate, habitat, and understory conditions. Few openings and low understory light conditions reduce shrub and herbaceous cover; reduced fire frequency can produce thick litter and duff layers, higher fuel loads, and more snags and coarse woody debris than are common in mixed conifer. Heart rots are common, producing snags for cavity-
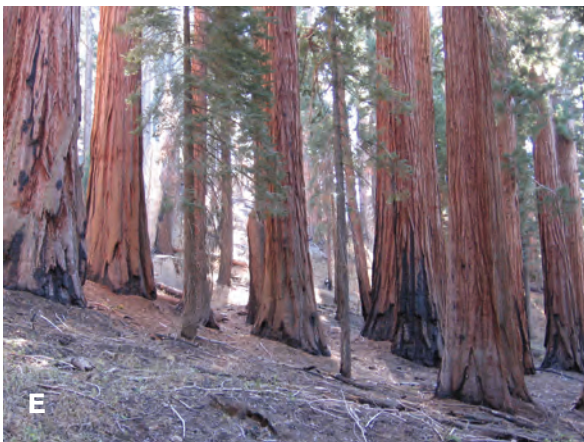
FIGURE 27.2 Forest types.

A   Mixed conifer (Photo: Malcolm North)

B   Klamath mixed conifer (Photo: Carl Skinner)

C   White fir (Photo: Malcolm North)

D   Montane hardwood-conifer (Photo: Carl Skinner)

E   Giant sequoia (Photo: Nate Stephenson)

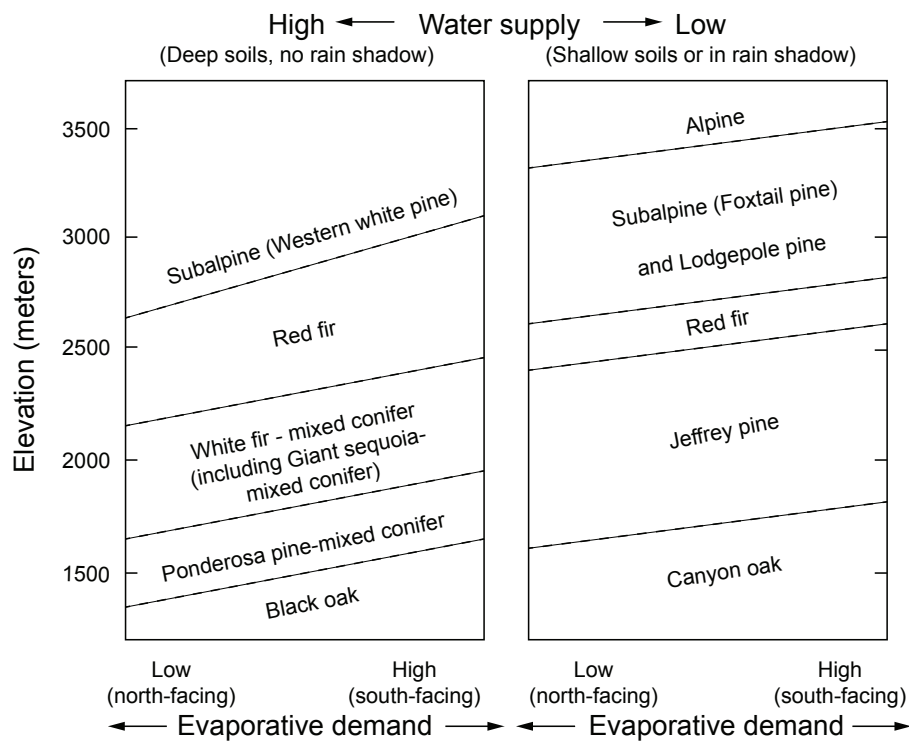F   Eastside pine (Photo: Malcolm North)

FIGURE 27.3 The approximate distribution of forest types in the southern Sierra Nevada relative to elevation (y-axis), evaporative demand (x-axis), and water supply (compare left and right panels). Source: Fites-Kaufmann et al. 2007.

dependent wildlife and large logs that can be used as runway structures for small mammals. White fir is the preferred tree species for several insect-gleaning birds, including yellow-rumped warblers (*Setophaga coronate*), western tanagers (*Piranga ludoviciana*), mountain chickadee (*Poecile gambeli*), chestnut-backed chickadee (*Parus rufescens*), golden-crowned kinglet (*Regulus satrapa*), and black-headed grosbeak (*Pheucticus melanocephalus*) (Airola and Barrett 1985).

Montane Hardwood-Conifer

There are many variations of montane hardwood-conifer (2,484,012 hectares), sometimes called mixed evergreen, which is characterized by composition including at least one-third hardwoods and one-third conifer (Anderson et al. 1976) (see Figure 27.2d). Hardwoods are usually dominated by species from the oak family, such as interior live oak (*Quercus wislizeni*), canyon live oak (*Q. chrysolepis*), tanoak (*Notholithocarpus densiflorus*), California black oak, Oregon white oak (*Q. garryana*), and golden chinquapin (*Chrysolepis chrysophylla*). Other hardwood associates include Pacific madrone (*Arbutus menziesii*) and big-leaf maple (*Acer macrophyllum*), while common conifers are Douglas-fir, ponderosa pine, white fir, incense-cedar and sugar pine, and in central coastal and southern California, bigcone Douglas-fir (*Pseudotsuga macrocarpa*) and coulter pine (*Pinus coulteri*) (Meyer and Laudenslayer 1988).

The overstory canopy (30–60 meters) is often dominated by conifers, especially where fire has been lacking for many years. Hardwoods comprise a lower layer (10–30 meters) above a shrub layer that can be sparse (in stands with high total canopy cover) to impenetrable (following fire). Although

present in all of California's mountain ranges, the montane hardwood-conifer type is most extensive in the Klamath and North Coast Ranges and the northern Sierra Nevada and is often transitional between dense coniferous forests and mixed chaparral, open woodlands, or savannas. The mix of species can be highly variable, but some general patterns are apparent. Tanoak is a significant component in more mesic areas in the northern and western montane areas of California, and Douglas-fir is a local dominant in the same areas. Both species are absent in the southern Sierra Nevada and south Coast Ranges. Drier inland regions tend to have more black and canyon live oak, with the latter particularly found on steep slopes with thinner soils where sparse fuel accumulation reduces fire frequency and intensity. A recently introduced pathogen, sudden oak death (*Phytophthora ramorum*), has spread throughout many coastal montane hardwood-conifer forests within the moist fog belt, whose conditions favor the disease's dispersal. Tanoak experiences almost 100% mortality to sudden oak death. Although the pathogen rarely kills California bay (*Umbellularia californica*), research has identified it as the best predictor of the disease's presence (Rizzo and Garbelotto 2003).

Many of these hardwood species benefit from severe fire because they resprout. Warming temperatures, increasing precipitation, and increasing nutrient inputs from air pollution enhance their competitiveness with conifers. Lenihan et al. (2008) projected a notable increase in the area of hardwood forest by the end of the twenty-first century as a result of climate change. A recent study comparing forest structure between the 1930s and 2000s found that stem densities in Sierran montane hardwood forest have increased more than in any other forest type and that the proportion of plots dominated by montane hardwood species increased

TABLE 27.2
Comparative ecological tolerances of common tree species in California's montane forests

Species arranged from low tolerance (top) to high tolerance (bottom)

Shade	Frost	Temperature[A]	Drought	Fire[B]
Black oak/western juniper	Madrone	Lodgepole pine	Red fir	Lodgepole pine
Ponderosa pine/giant sequoia	Douglas-fir	Red fir	White fir	Sugar pine/white fir
Lodgepole pine	White fir	Jeffrey pine	Sugar pine/ giant sequoia	Incense cedar/ Douglas-fir
Sugar pine	Sugar pine/giant sequoia	White fir/giant sequoia	Douglas-fir	Jeffrey pine/ponderosa pine/giant sequoia
Incense cedar	Incense cedar	Douglas-fir/sugar pine/ incense cedar	Lodgepole pine/ incense cedar/ madrone	
Douglas-fir	Ponderosa pine/ Jeffrey pine/red fir	Ponderosa pine/black oak/ madrone	Ponderosa pine	
Red fir	Lodgepole pine		Jeffrey pine	
White fir			Black oak	

SOURCE: Data from Minore 1979, Burns and Honkala 1990, and the Fire Effects Information System (FEIS).

A. Least heat tolerant/most cold tolerant on top.

B. Fire tolerance of mature trees. Fir and Douglas-fir seedlings and saplings are less tolerant of fire than yellow pine and sugar pine.

by almost 100% between the two time periods (Dolanc et al. 2013).

Giant Sequoia

Giant sequoia occurs naturally in roughly seventy relatively small, scattered groves (total area of 14,600 hectares) along the western slope of the Sierra Nevada, mostly south of the Kings River (Stephenson 1996, Fites-Kaufman et al. 2007) (see Figure 27.2e). The eight groves north of the Kings River span elevations of 1,370 to 2,000 meters, while those to the south are mostly found between 1,700 and 2,250 meters in elevation. Within these groves, giant sequoia usually dominates ASA AREA, but by stem frequency and composition the groves would be considered mixed conifer. Grove locations are usually characterized by deep, well-drained soils with relatively high water availability. Although the trees can grow rapidly, typically to 400–800 centimeters in diameter and 65–80 meters tall, they are also long-lived, reaching ages of one thousand years or older.

More than any other tree species in the Sierra Nevada, giant sequoia is a pioneer species requiring disturbance for successful regeneration (Stephenson 1994). In the past, frequent, moderate-intensity fires burned through sequoia groves, creating occasional gaps in the forest canopy in locations where these fires burned at high severity. These canopy gaps, with their greatly reduced competition for light and water, are the sites of virtually all successful sequoia regeneration (Stephenson 1994, York et al. 2011, Meyer and Safford 2011). Following Euro-American settlement, more than a century of fire exclusion led to a nearly complete failure of sequoia regeneration. Where fire has subsequently been reintroduced, sequoia

regeneration has been restored (Stephenson 1996, Stephenson 1999, York et al. 2013).

Ponderosa, Jeffrey, and "Eastside" Pine

Sometimes collectively called the "yellow pines," ponderosa and Jeffrey pine are closely related (both in the subgenus Pinus, section Pinus, subsection Ponderosae) and occasionally hybridize (Baldwin et al. 2012). Ponderosa pine, one of the most widely distributed pine species in North America (327,778 hectares), is found throughout the mountainous regions of the western U.S., whereas Jeffrey pine is primarily a California tree, with a few occurrences in westernmost Nevada, southwestern Oregon, and northern Baja California, Mexico (see Figure 27.2f). Of the two species, Jeffrey pine is more stress-tolerant and replaces ponderosa pine at higher elevations, on poorer soils, and in colder and/or drier climates (Haller 1959, Stephenson 1998, Barbour and Minnich 2000). Ponderosa pine–dominated forests can occur from approximately 300 to 1,800 meters and 1,200 to 2,100 meters in northern and southern California, respectively (Fites-Kaufman et al. 2007). Jeffrey pine–dominated forests occur mostly between 1,500 and 2,400 meters and 1,700 and 2,800 meters in northern and southern California (with the highest elevations usually on the east side of the Sierra Nevada), respectively (Fites-Kaufman et al. 2007, Barbour and Minnich 2000). Both yellow pine species also occur in other forest types including mixed conifer, where they were dominant in many places before logging and fire suppression.

A large area of the northern Sierra Nevada east of the crest supports a mixed yellow pine forest, sometimes called "eastside pine," with co-dominance by ponderosa and Jeffrey pine

(782,526 hectares of Jeffrey and eastside pine area combined). Like white fir forests, forests dominated by ponderosa and Jeffrey pine are closely intermingled with mixed conifer, in this case indicating a shift toward drier, warmer (ponderosa) or drier, colder (Jeffrey) site conditions. Historically these forests had very frequent fires that supported low-density openstand conditions characterized by shrub patches, sparse litter cover, and relatively high diversity of herbs and grasses.

Forest Structure and Function

In the nineteenth century John Muir wrote, "These forests were so open, early travelers could ride a horse or even pull wagons through [them]." An early timber survey in the northern Sierra Nevada noted the same conditions and lamented that fire kept the forest at only 30% of its potential lumber stocking (Lieberg 1902). Historically these low-density, large tree–dominated forests had an almost flat D AM ETER D STR UT ON (an equal abundance of all tree sizes) in contrast to the reverse J-shaped distribution (tree abundance rapidly decreases in larger-size classes) many early foresters were familiar with from forests with more infrequent disturbance regimes (North et al. 2007). Based on detailed timber surveys conducted by the Forest Service in the central Sierra Nevada in 1911, tree densities ranged from 40 to 80 trees ha^{-1} and estimated canopy cover was 17–24% (Collins et al. 2011). These open conditions were maintained by frequent surface fires that consumed surface fuels and small-diameter trees, providing a pulse of nutrients to the soil, creating patches of bare mineral soil for seed establishment, and reducing competition for soil moisture (Gray et al. 2005, Zald et al. 2008). Without fire, forest structure becomes more homogeneous, and some ecosystem functions "stall" (Ma et al. 2004, North and Rosenthal 2006) (Figure 27.4).

Frequent fire creates structural diversity at fine (stand) and coarse (landscape) scales associated with several ecosystem processes. The within-stand structure has been characterized as containing three main conditions: individual trees, clumps of trees, and openings or gaps (ICO) (Larson and Churchill 2012, Lydersen et al. 2013, Fry et al. 2014). Stand-level average canopy cover under frequent-fire conditions is typically low (20–45%) compared to modern, fire-suppressed conditions (typically 55–85%). However, within a stand, ICO conditions produce heterogeneity such that ANOPY OSURE (a point-level measure) (Jennings et al. 1999, North and Stine 2012) is highly variable, providing a scattering of dense areas for wildlife cover. Several studies suggest this fine-scale heterogeneity affects ecosystem conditions and functions, producing a wide range of microclimates (Rambo and North 2009, Ma et al. 2010), a diversity of understory plants (Wayman and North 2007) and soil invertebrates (Marra and Edmonds 2005), variation in soil respiration (Concilio et al. 2005, Ryu et al. 2009), and limits to pest and pathogen spread (Maloney et al. 2008). In addition, modeling efforts that have compared fire-suppressed forest conditions with two different fuel reduction treatments found higher avian richness in forests treated to create variable canopy closure and increase structural heterogeneity (White et al. 2013a, b).

At a larger scale, models suggest that fire created a mosaic of different forest SERA conditions that diversified landscape structure (Kane et al. 2014). For example, modeling by the LANDFIRE program (Rollins and Frame 2006, Rollins 2009) predicts that under an active fire regime, 10–20% of yellow and mixed-conifer forests in California would have been in early seral stages (herbs, shrubs, seedlings/saplings) with approximately 30–40% in areas dominated by trees between 10 and 53 centimeters dbh (diameter at breast height) (5–21"), and 40–60% in areas dominated by larger trees (higher than 53 centimeters dbh). Furthermore, the models indicate that most of the landscape was under open forests of less than 50% canopy cover ("open" stages), especially in the yellow pine and drier mixed-conifer types (Rollins 2009). This is quite different than modern forest conditions where 85% of montane forests are dominated by 10–53 centimeter trees and canopy cover averages greater than 65%.

Water availability appears to be one of the strongest influences on ecosystem function. At fine scales, functions such as decomposition, nutrient cycling, and soil respiration vary strongly within forest stands by patch type (North and Chen 2005) and their different levels of available soil moisture (Erickson et al. 2005, North, Oakley et al. 2005, Concilio et al. 2006). At larger scales, forest greenness (Trujillo et al. 2012), CO_2 uptake, and evapotranspiration (Goulden et al. 2012) are correlated with elevational differences in snowpack depth and total precipitation.

Fauna

Montane forests in California support at least 355 vertebrate species (Verner and Boss 1980). The high species richness of montane forests probably stems in part from changing habitat conditions created by frequent fire and seral development. For example, a study of the avian community between a burned area and neighboring unburned forest in the Sierra Nevada found that over a third of species occurred only in the burned area (Bock and Lynch 1970). In addition, a study of breeding birds observed over a twenty-five-year period found that bird community guild structure shifted among species with different foraging strategies (i.e., foliage searching to bark gleaning) as forest succession progressed (Raphael et al. 1987).

Concern has often focused on species that might be affected by modern changes in forest conditions that differ from their historical analogs or that have become increasingly rare (North and Manley 2012, Stephens et al. 2014). For instance, some songbirds are strongly associated with shrub patches (Burnett et al. 2009) now uncommon in the low-light understory of fire-suppressed forests (Knapp et al. 2013). The most widely known sensitive species, however, are associated with old forest conditions such as the northern (*Strix occidentalis caurina*) (Moen and Gutierrez 1997, North et al. 1999) and California spotted owls (*S. o. occidentalis*) (North et al. 2000, Lee and Irwin 2005), northern goshawk (*Accipiter gentilis*) (Morrison et al. 2009), fisher and marten (*Martes pennanti* and *M. martes*) (Zielinski et al. 2004a, b), southern red-backed vole (*Clethrionomys gapperi*) (Sullivan and Sullivan 2001), and northern flying squirrel (*Glaucomys sabrinus*) (Meyer et al. 2005, 2007; Meyer, North, and Kelt 2007) (Figure 27.5). The California spotted owl and fisher have been studied more extensively than other species because both are considered threatened. Guidelines for maintaining and improving their habitats strongly affect forest management on public lands (North, Stine et al. 2009; Roberts and North 2012). Both species are associated with large, old structures that contain high levels of canopy closure to use for nesting and resting. This has often resulted in minimal or no fuels removal in these areas, which in turn makes these sites prone to burning at

Historic pine-dominated mixed conifer

Low-intensity fires kill most fir ①

Pine-dominated forest type persists ②

① Selective logging of mature pines

② Fire-suppression allows fir to establish

③ Shift to fir-dominated forest type

Pine-dominated
fire active + unthinned

Fir-dominated
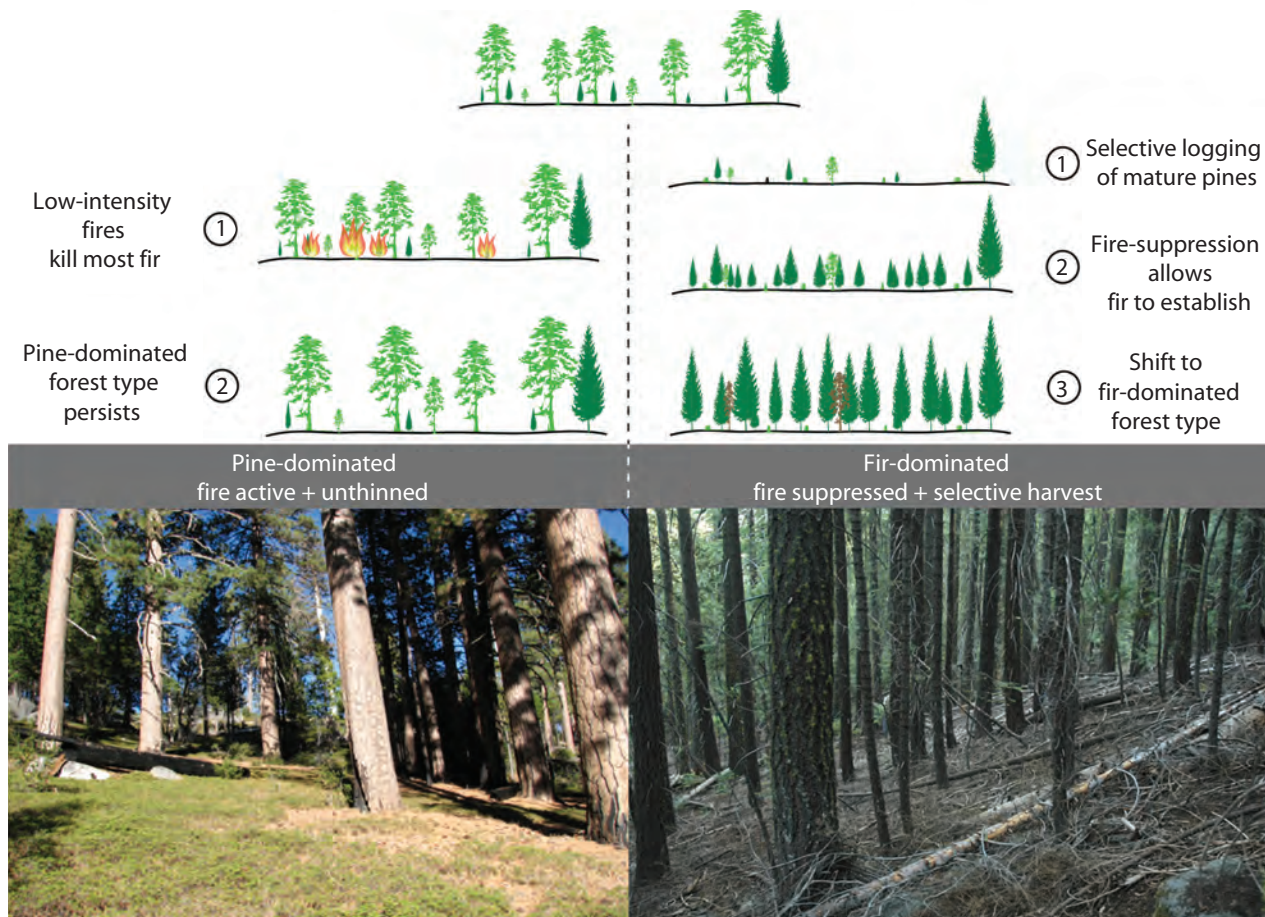fire suppressed + selective harvest

FIGURE 27.4 Two generalized successional pathways for historic mixed-conifer forests (top). The left side shows how an active-fire regime maintains a resilient composition and structure dominated by a low density of large pine. The right side shows how past selective logging and fire suppression can lead to a high-density, white fir–dominated forest stand. This right side is a common condition in many montane forests and can be very susceptible to high-intensity fire and drought mortality. Source: Earles et al. 2014.

high severity in the event of a wildfire and to subsequent loss of nesting and resting habitat (North et al. 2010). For foraging, however, both species use a variety of habitat conditions, possibly because they have broad prey bases that include several small mammal species associated with a range of forest and shrub conditions (Innes et al. 2007, Meyer et al. 2007).

Some controversy has focused on the black-backed woodpecker (*Picoides arcticus*), a species associated with large, recently dead (four to eight years old) trees and often found foraging in "snag forests" produced by stand-replacing fires (Saab et al. 2007, Hanson and North 2008). The black-backed

woodpecker might seem like an unlikely candidate for sensitive species status. With fire suppression, although the extent of wildfire has decreased, increased fire severity has kept the area of snag forests at levels consistent with estimates of historical conditions (though patch size has significantly increased) (Miller et al. 2009, Mallek et al. 2013). The concern with black-backed woodpecker habitat is not an areal decrease but a reduction in habitat suitability if many snags are removed by postfire salvage logging.

In addition to reduced old forest conditions, some special habitat elements (e.g., "defect" trees) may have declined

FIGURE 27.5 Sensitive species that affect land management in California's montane forests: (A) fisher resting on a large black oak limb, (B) a northern flying squirrel holding a truffle (its primary food source), (C) northern goshawk, (D) a California spotted owl, and (E) a black-backed woodpecker on a snag.

in abundance (Bouldin 1999). Large defect trees and snags are often rare in managed montane forests because they are removed for worker safety, and past stand "improvement" practices removed "defect" structures that did not contribute to wood production. Trees and snags selected by primary cavity nesters, woodpeckers, and nuthatches (*Sitta* spp.) could be particularly important because the cavities, once vacated, are used by other birds and mammals (Bull et al. 1997). Several studies have found that cavity availability can limit abundances of some of these species in managed forests (Carey et al. 1997, Carey 2002, Cockle et al. 2011, Wiebe 2011).

Ecosystem Characteristics

Drought, Pests, and Pathogens

Although montane forests are adapted to annual drought stress characteristic of Mediterranean climates, periods of multiple, consecutive dry years can have large impacts (e.g., see Guarin and Taylor 2005). For example, a massive die-off of conifer trees took place in the San Bernardino Mountains after the drought of the late 1990s and early 2000s. In the absence of frequent fire, increases in forest density result in

greater competition for scarce water (Innes 1992, Dolph et al. 1995). Potential increases in older tree mortality are a major concern because large trees are often more prone to drought-induced mortality (Allen et al. 2010). Some studies have found higher than expected mortality rates in large trees (Smith et al. 2005, Lutz et al. 2009), suggesting that a "leave it alone" forest management approach that does not reduce stand density might actually contribute to the loss of old-growth trees.

Drought itself is usually not the proximal cause of tree mortality, however, as drought-induced stress also leads to greater insect and disease susceptibility (Savage 1994, Logan et al. 2003, Fettig et al. 2007, Allen et al. 2010). In general, open stands with a mix of species have had more localized damage and mortality, while the scale and extent of mortality have been greater in dense, single-species stands and plantations (Stephens et al. 2012). Beetles are probably the greatest source of stress and mortality. Some beetle species are specialists focused primarily on one or two species, such as western (*Dendroctonus brevicomis*) and Jeffrey pine (*D. jeffreyi*) beetles primarily affecting ponderosa and Jeffrey pines, respectively. Mountain pine beetle (*D. ponderosae*) and California five-spined ips (*Ips paraconfusus*), however, are more generalist and affect most of the conifers in California's montane ecosystems (Fettig 2012). Several pathogens also notably influence montane tree mortality. White pine blister rust (*Cronartium ribicola*) has been devastating to sugar pine since the disease entered northern California around 1930, and impacts to western white pine are also locally severe (Maloney et al. 2011). Pathologists and foresters have widely collected sugar pine seeds and conducted nursery experiments to identify blister rust–resistant individuals to help regenerate the species (Kinloch 1992). Root rot (*Heterobasidion* spp.) disease is also widespread, particularly in fir-dominated forests. Some evidence suggests that forest thinning can accelerate spread of root rot because the disease's windblown spores can colonize tree stumps (Rizzo and Slaughter 2001).

Fire

Under presettlement conditions, most of California's montane forests supported fire regimes characterized by frequent, predominantly low- to moderate-severity fires (Agee 1993, Sugihara et al. 2006, Barbour et al. 2007) (see Chapter 3, "Fire as an Ecosystem Process"). Historically these fire regimes were limited principally by the amount of available fuels rather than by fuel moisture during the summer drought. As elevation increases, the role of fuel moisture becomes more important, gradually supplanting fuel availability in red fir and higher-elevation forest types (Agee 1993, Miller and Urban 1999a, Sugihara et al. 2006, Van de Water and Safford 2011).

Historically ignitions originated with Native American burning or lightning. Oral history suggests that many groups used fire to produce more open forest conditions favorable for foraging and hunting (Anderson et al. 1997). Whether these ignitions were concentrated in a few favored places or broadly used has been debated (Parker 2002; see Chapter 10, "Indigenous California"). In contrast, areas of heavy lightning activity are more easily identified. In a statewide analysis (van Wagtendonk and Cayan 2008), strikes increased with elevation up to 2,400 meters, had the highest monthly totals from June through the end of September, and occurred most between the hours of 1400 and 1900. Fire ignitions from lightning likely varied substantially from year to year. For the

period between 1985 and 2000, van Wagtendonk and Cayan (2008) found a fivefold difference between the years with the highest and lowest number of strikes.

Across the state, fire return intervals (FRIs) averaged eleven to sixteen years in yellow pine and mixed-conifer forests, with a mean minimum and maximum FRI of five and forty to eighty years, respectively (Van de Water and Safford 2011; North, Van de Water et al. 2009). Presettlement fire frequencies were higher in the drier, lower-elevation forest types (yellow pine and dry mixed conifer) and lower in moister and higher-elevation montane forests (Caprio and Swetnam 1995, Sugihara et al. 2006, Fites-Kaufman et al. 2007). Fire frequencies and patterns of fire severity were also influenced by local topographic variables. Several studies have documented longer FRIs and greater proportions of high severity on cooler, more mesic slopes (mostly north-facing), with the opposite pattern on warmer, more xeric slopes (mostly south-facing) (Kilgore and Taylor 1979, Fites-Kaufman et al. 1997, Taylor 2000, Beaty and Taylor 2001). Riparian areas also followed this pattern, with forests around smaller, headwater streams having a similar fire regime to adjacent uplands while larger streams (generally third order or greater) had longer fire return intervals (Van de Water and North 2010, 2011).

In the absence of fire, many modern forests have unusually high fuel loads with much greater potential for high-severity, crown fires (Brown et al. 2008, Taylor et al. 2013). These conditions have shifted the fire regime from "fuel-limited" to "climate-limited" or "weather-limited" (Miller and Urban 1999b, Running 2006, Morgan et al. 2008, Collins et al. 2009, Miller et al. 2009, Steel, Safford et al. 2015). Adding to this trend is a policy of fire suppression on many forested lands, causing most wildfires to occur when they escape containment during extreme weather conditions (i.e., low humidity and high temperatures and wind speeds). In most montane forests the proportion and area of stand-replacing fire area and the sizes of stand-replacing patches are increasing (Miller et al. 2009, Miller and Safford 2012; however, see Miller, Skinner et al. 2012). These increases may be problematic because most of California's montane trees species do not have direct mechanisms to regenerate following stand-replacing fire (e.g., serotiny, vegetative sprouting) (Goforth and Minnich 2008, Keeley 2012). This is particularly a concern in large stand-replacing patches, where the likelihood of wind-blown seed establishing is low (McDonald 1980). Conifer regeneration in stand-replacing patches can be highly variable. However, a recent study found that it was completely absent in nearly three-quarters of sampled high-severity patches, at least in the short term after fire (less than ten years) (Collins and Roller 2013).

Topography's Influence

Slope aspect, through its effects on insolation and hence the evaporative demand experienced by plants, has a relatively modest influence on montane forests and mostly affects the elevation at which particular forest types are found (Stephenson 1998, Fites-Kaufman et al. 2007, Lydersen and North 2012). For example, in the Sierra Nevada a given montane forest type can generally be found a few hundred meters higher on south-facing (sunward) slopes than on north-facing (shaded) slopes (see Figure 27.3). Water availability has more dramatic effects (Tague et al. 2009). For instance, firs are usually most abundant where water availability is high (such as on deep soils, with their high water-holding capaci-
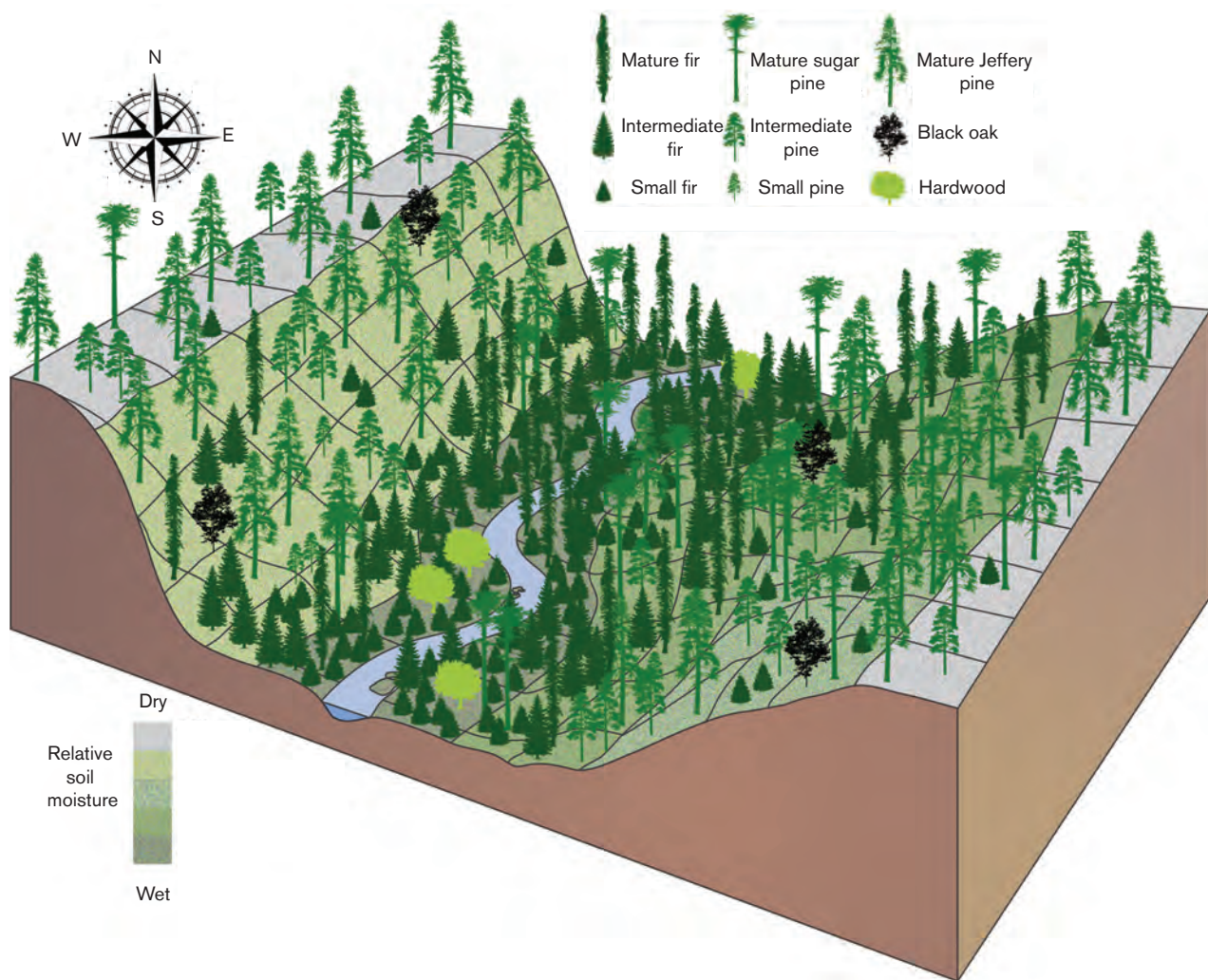
FIGURE 27.6 Landscape schematic of variable mixed-conifer conditions produced by an active fire regime. Forest density and composition vary with topographic features such as slope, aspect, and slope position. Ridgetops, with drier soils and higher fire intensity, have lower stem density and a higher percentage of pine than more mesic riparian areas with lower-intensity fire. Midslope forest density and composition vary with aspect: density and fir abundance increase on more northern aspects (right side) and flatter slope angles. Illustration by Steve Oerding.

ties), whereas pines are most abundant where water availability is low (such as on shallow soils or in rain shadows) (Stephenson 1998; Fites-Kaufman et al. 2007; Meyer, North, Gray et al. 2007). Slope steepness and slope position (e.g., ridgetop, midslope, valley bottom) also affect the reception and retention of both meteoric waters and water flowing above, within, and beneath the soil.

The influence of topography can be twofold, affecting both productivity and fire intensity (Figure 27.6) (Kane et al. 2015). Topographic locations that contain more mesic, productive sites (i.e., lower slope and riparian areas) were associated with greater densities of large, overstory trees, high total basal area and canopy cover, and an abundance of large snags and logs. This high-biomass forest structure existed in these topographic positions regardless of recent fire history. Outside of mesic sites and in forests that still have an active fire regime (i.e., no suppression), recent fire history was found to have the strongest influence on understory conditions (Lydersen and North 2012). Small tree density decreased and shrub cover increased with increased fire intensity and frequency, which in turn tended to occur on upper slope and ridgetop

locations. These findings suggest that topography, fire history, and their interaction produce the heterogeneity characteristic of montane forest landscapes (Taylor and Skinner 2003, Lydersen and North 2012).

Wind

Overall, few historical accounts exist of large wind events in montane forests. In at least one study, the random direction of downed trees in old mixed conifer suggested that big wind events were not a significant driver of mortality (Innes et al. 2006). According to maps (Peterson 2000), California and neighboring states are subject to fewer major wind events like tornados and convective events ("downbursts") than any other part of the contiguous United States. However, winds can have strong local effects. Very high winds can be common when winter storms arrive at the Sierra Nevada crest, but these elevations generally support subalpine forests. One recent event in fall 2011 in Devil's Postpile National Monument in the upper San Joaquin River basin had winds exceed-

ing 145 kilometers per hour (Hilimire et al. 2012). Thousands of mature trees were downed—mostly red fir, white fir, and lodgepole pine—but areas of Jeffrey pine were also impacted. In some areas more than 70% of live trees were downed. Large trees and snags were more susceptible to uprooting than smaller ones, and effects were distributed fairly evenly across species. This size-dependent response to wind has a very different impact on forest structure than does fire, which preferentially kills smaller trees.

Forest Turnover

Montane forests are more dynamic than forests found at higher elevations. For example, tree turnover rates (the average of tree recruitment and mortality rates) for old-growth Sierra Nevada forests are roughly three times greater in montane forests than in subalpine forests at treeline (Stephenson and van Mantgem 2005). The strong decline of forest turnover rates with increasing elevation may be related to parallel declines in forest productivity (Stephenson and van Mantgem 2005).

Background tree mortality rates in montane forests generally can be higher in fire-suppressed forests than in contemporary forests with a more intact fire regime, possibly due to reduced competition among trees in burned stands (Ansley and Battles 1998, Maloney and Rizzo 2002, Stephens and Gill 2005). Similarly, modern plantation studies show much higher annual mortality in high-density than in low-density stands. In ponderosa pine, one study found annual mortality rates of between 0% and 0.8% in thinned stands of less than 332 trees per hectare, versus rates of 0.6% to 2.3% in stands of more than 2,450 trees per hectare (Zhang et al. 2006). Recent studies (van Mantgem and Stephenson 2007, van Mantgem et al. 2009) found that tree mortality rates in western U.S. forests have roughly doubled over the past few decades—an apparent consequence of warming temperatures.

Ecosystem Services

The Millennium Ecosystem Assessment defines ecosystem services as the direct and indirect benefits people obtain from ecological systems (MEA 2005). California's montane forests contribute to quality of life for millions of people, many living at some distance from the state's mountain ranges. Ecosystem services are broadly categorized as provisioning (e.g., water, timber, fuels, food); regulating (e.g., carbon sequestration, erosion control, water quality); cultural (e.g., recreation, spiritual enrichment, educational opportunities); or supporting (biological diversity, nutrient cycling, etc.). All of these services are important, but we focus here on water, recreation, and carbon because of their particular relevance to California policies and economic development.

WATER

By one estimate, about 246,700,000,000 cubic meters (200 million acre feet [maf]) of precipitation falls annually on California, of which about 92,500,000,000 cubic meters (75 maf) is unimpaired runoff available for management and use (Energy Almanac 2014). About two-thirds of this annual runoff comes from one-fifth of California's land area—the mountains in the northern half of the state. A substantial portion of this water originates from precipitation in forested watersheds within the montane forest zone. Most of this water is eventually used by agriculture (41,900,000,000 cubic meters, or 34 maf). Furthermore, most montane rivers are highly engineered with multiple dams and impoundments that contribute to California's greater than 13,725 gigawatt hours of hydroelectric power capacity (meeting about 8% of California's electricity demand).

A recent assessment of forested watersheds found the greatest threats to water quality and fisheries were concentrated in north coast watersheds. These threats stemmed from erosion following forest management activities, development, mass wasting, and high-severity wildfire (California Department of Forest and Fire Protection 2010). The high canopy cover in these forests caused by fire suppression might reduce water runoff because less snow reaches the ground and more is caught in the canopy, where it can sublimate directly back into the atmosphere (Golding and Swanson 1986, Essery et al. 2003). Climate change is expected to increase the percentage of precipitation that occurs as rain rather than snow (Hunsaker et al. 2012). This is expected to accelerate snowmelt and to challenge current reservoir capacity.

RECREATION

Montane forests are used heavily for a wide range of recreational activities. In 2010, Yosemite National Park alone drew four million visitors and provided more than $350 million in tourism revenue. Surveys on National Forest land in California found that the most popular activities were relaxing (52%), viewing natural features (52%), hiking and walking (47%), viewing wildlife (38%), and downhill skiing (36%), with an average of one to five trips per visitor annually (U.S. Department of Agriculture, Forest Service Region 2012). For the Sierra Nevada one study estimated an average rate of fifty million to sixty million annual visitor days for public forestlands alone (Duane 1996). Giant sequoia groves are probably among the most visited forest ecosystems in the world, and their appeal was instrumental in halting logging of the groves and establishing federal protection in the 1890s.

CARBON STORAGE

Through the long-lived nature of many trees, global forests store twice as much carbon as Earth's atmosphere. Global forest growth is a significant net carbon sink, adding 2.4±1.0 Pg C year[1] to biomass storage (Pan et al. 2011) and helping to offset anthropogenic emissions of CO_2. Although developing countries often reduce their carbon stores when forestland is converted to other uses, California's forest acreage has not changed appreciably over the past fifty years. Most montane forests in the state have been net carbon sinks in the last century due to regrowth from past harvesting and ingrowth from fire suppression (Hurteau and North 2009). California forests (all types and ownerships) are estimated to store 2.3 Pg of carbon (Fried and Zhou 2008). However, loss due to fire and conversion of forests due to development could offset, or even exceed, carbon stored from tree growth (Battles et al. 2013, Gonzalez, Battles et al. 2015). Thus the long-term stability of these carbon stores in forest is a key concern.

There has been substantial debate about whether carbon loss through fuels treatment (mechanical thinning and/or

prescribed fire) in fire-prone forests is offset by a reduction in later carbon emissions if the treated stand is burned by wildfire (Hurteau et al. 2008, Hurteau and North 2009, Mitchell et al. 2009, Hurteau and North 2010, North and Hurteau 2011, Campbell et al. 2012, Carlson et al. 2012). In general, treating forests leads to net carbon loss because of the low current probability of wildfire burning the treated area, the modest reduction in wildfire combustion and carbon emissions, and the need to maintain fuels reduction through periodic, additional carbon removal (Campbell et al. 2012).

The concept of carbon carrying capacity (Keith et al. 2009) could be particularly relevant to California's montane forests. Carbon carrying capacity emphasizes the level of stable carbon storage that a forest can maintain over the long term. In the absence of disturbance, a forest can "pack on" more carbon as tree density and size increase (Hurteau and North 2009, Hurteau et al. 2013). Many montane forests are in this state today. This additional biomass, however, makes the forest prone to disturbances—such as drought stress, pests, pathogens, and higher-severity wildfire—that increase tree mortality. Mortality reduces carbon stocks as dead trees decompose and much of the carbon returns to the atmosphere through efflux. Carbon carrying capacity, therefore, is lower than the maximum storage potential of a forest but represents the biomass that can be maintained in the context of disturbance and mortality agents characteristic of a particular ecosystem. In California's forests with historically frequent fire and drought events, carbon carrying capacity is the amount that a forest can store while maintaining low levels of mortality in response to periodic disturbances. In general, forests managed so that growth and carbon accumulation are concentrated in large trees will provide longer, more secure carbon storage than forests where growth is concentrated in a high density of small trees prone to pest, pathogen, and fire mortality (North, Hurteau et al. 2009; Earles et al. 2014). Recent research shows that large trees have remarkably high growth rates, giving them a more dynamic role in forest carbon storage than had been previously appreciated (Stephenson et al. 2014).

Human Impacts

Although American Indians used trees for a variety of purposes, large-scale timber harvest did not begin until after widespread Euro-American settlement (circa 1850). Most logging before the 1900s was done to support mining operations. Timber was cut to build homes and commercial buildings, tunnels, mine and ore processing infrastructure, and railroad lines. It was also the fuel for heating, railroad engines, and other machines, and the various types of mills used for processing ore. In some areas a very valuable market in sugar pine shakes (for roofing or siding) also arose (McKelvey and Johnston 1992). The majority of timber harvests before and after 1900 occurred in yellow pine and mixed-conifer forest and often selected the largest, most valuable pine trees (Sudworth 1900, Leiberg 1902).

Between the 1890s and 1920s, railroad lines were extended throughout the state's lower- and middle-elevation forests to access timber resources beyond the reach of animal-drawn transport. After the Second World War, dramatically increasing wood demand from federal lands led the Forest Service to greatly expand their sale of timber. For example, harvest on the Eldorado National Forest averaged approximately 3.8 million board feet per year between 1902 and 1940 but increased to 35.1 million board feet during the war, and to over 56 million board feet per year between the end of the war and 1959 (Beesley 1996). Harvest techniques were more industrial than before the war, and large areas of forest were clearcut. Since the 1960s, national legislation, regulations, changing economics, and environmental concerns have acted in concert to greatly reduce the amount of logging occurring on California public land, although private lands have made up some of the difference (see Chapter 36, "Forestry").

In the end, Barbour et al. (1993) estimated that half the original area of California's mixed-conifer forest had been cut at least once in the past 150 years. The Sierra Nevada Ecosystem Project executive summary (SNEP 1996) has a succinct summary of the impacts of European settlement on montane ecosystems (Figure 27.4): "The primary impact of 150 years of forestry on middle-elevation conifer forests has been to simplify structure (including large trees, snags, woody debris of large diameter, canopies of multiple heights and closures, and complex spatial mosaics of vegetation), and presumably function, of these forests. By reducing the structural complexity of forests, by homogenizing landscape mosaics of woody debris, snags, canopy layers, tree age and size diversity, and forest gaps, species diversity has also been reduced and simplified." Livestock grazing did not widely affect montane forests because, with the exception of scattered meadows, forage in these ecosystems is scarce, and most sheep and cattle concentrate their summer grazing in alpine meadows. Some areas of montane forests, however, are heavily affected by air pollution (see Chapter 7, "Atmospheric Chemistry").

Current Management Strategies

Fuels Treatment

Fuels treatment is becoming the dominant forest management activity on public lands throughout the montane forest region of California. Mechanical thinning, prescribed fire, or combinations of both are most often used to reduce fuels (Safford et al. 2009; Safford, Stevens et al. 2012). Although controversy has persisted over the ecological effects of these treatments, a recent article synthesizing published studies found "few unintended consequences, since most ecosystem components (vegetation, soils, wildlife, bark beetles, carbon sequestration) exhibit very subtle effects or no measurable effects at all" to treatments (Stephens et al. 2012). Aside from controversy, limited budgets and other regulatory constraints have significantly reduced the pace and scale of fuels treatments (North et al. 2015). First-priority actions usually treat areas near homes in the wildland-urban interface (or WUI). With increasing home construction in these areas, more fuel treatment effort has been concentrated in these areas and correspondingly less in the larger forest matrix (Theobold and Romme 2007). One study of federal forestlands in the Sierra Nevada compared current levels of all fuels reduction treatments (including wildfire) to historical levels of fuel reduction from frequent fire. The study's authors found that fewer than 20% of forests needing treatment were actually treated each year (North, Collins et al. 2012). They also calculated that at current rates more than 60% of the forest would never get treated, as maintenance of existing treatments would eventually subsume all of the fuels reduction effort.

In mechanical fuels reduction, two measures are commonly used for implementing treatments: maximum tree diameter

FIGURE 27.7 A pine plantation forest managed to maximize tree growth rates. A single tree species is planted at regular spacing, producing a simplified stand structure. Photo: Malcolm North.

FIGURE 27.8 A prescribed burn at Blodgett Experimental Forest burning at low intensity and effectively reducing fuel loads. Photo: Kevin Krasnow.

removed ("diameter limits") and minimum residual canopy cover. These metrics are set by the standards and guidelines in planning documents (e.g., SNFPA 2004). Diameter limits and canopy cover requirements are intended to ensure that treatments will move forest structure toward an "old forest" condition. If the diameter limit is set too high, large trees that do not substantially affect fuel conditions might be removed (Bigelow and North 2012). If the diameter limit is set too low, treatment might not produce the open conditions described by studies of historical forest structure (Beaty and Taylor 2007, 2008, Collins et al. 2011, Taylor et al., 2013) or create enough openings to regenerate shade-intolerant, fire-resistant species such as pines (Bigelow et al. 2011).

Fire, as both prescribed burning and managed wildfire, is generally underused for fuels treatment (Figure 27.8). Although ecological restoration of these forests requires fire, numerous constraints limit its use (Collins et al. 2010; North, Collins et al. 2012). These include impacts to local communities from smoke production, reduced recreation opportu-

nities, inadequate personnel to conduct and monitor fires, liability for fire escapes, and risk-adverse policies and institutions. Many concerns about fuel treatment intensity and fire use are inherently social in nature (McCaffrey and Olsen 2012). Addressing these issues will require more focused engagement and education of local communities and the general public to balance shorter-term impacts with the potential for longer-term benefits.

Increasing Forest Heterogeneity and Resilience

Efforts to increase FOREST RES EN E have emphasized management strategies that work with and adapt to dynamic ecological processes at different scales (North et al. 2014). Management is now often focused on restoring heterogeneous forest conditions consistent with how productivity and historical fire intensity affected stand- and landscape-level forest conditions (North and Keeton 2008, Lydersen and North

2012) (see Figure 27.6). Forest managers use existing stand conditions and topography as a template to vary treatments in order to simultaneously achieve objectives such as fire hazard reduction, provision of wildlife habitat, and forest restoration (Knapp et al. 2012; North, Boynton et al. 2012). Within stands, thinning treatments attempt to create the ICO (individual tree, clumps of trees, and openings) structure that would have been created by frequent fire. Managers vary the proportions and sizes of these three structural conditions with small-scale changes in soil moisture and microclimate conditions (North, Stine et al. 2009, North 2012). At a larger scale, managers try to produce the forest density and composition associated with different slope positions and aspects that affect productivity and would have influenced fire severity (Underwood et al. 2010; North, Boynton et al. 2012).

Restoration Successes

Several national parks in California have recognized the importance of fire in montane forests and been able to overcome the many challenges associated with managing fire. Two of the most notable examples are the Illilouette basin in Yosemite National Park and the Sugarloaf basin in Sequoia–Kings Canyon National Park. In both areas, lightning-ignited fires have been allowed to burn relatively unimpeded since the early 1970s (see Lead Photo for this chapter). Although both areas experienced several decades of fire suppression, fire occurrence since the onset of natural fire programs in the 1970s is similar to that in the historical period (1700–1900, prior to fire suppression) (Collins and Stephens 2007). In addition, fire effects and interactions among fires in the program are consistent with our understanding of how historical fires burned in these landscapes (Collins et al. 2007, Collins et al. 2009, Collins and Stephens 2010, van Wagtendonk et al. 2012).

This suggests that fire in both areas might approximate a restored regime. This type of restoration cannot likely take place across much of the montane forest region with managed fire alone. However, the examples of Sugarloaf and Illilouette basins, as well as other areas with successful managed fire programs such as Lassen Volcanic National Park, illustrate the potential to expand fire use to meet restoration objectives. An important objective of these programs is to allow fires to burn under a range of fuel moisture and weather conditions rather than only under the fairly extreme conditions associated with "escaped" wildfires common on Forest Service land managed for fire suppression (Miller, Collins et al. 2012; North, Collins et al. 2012, Lydersen, North et al. 2014). The Forest Service and other landowners sometimes object to wider use of fire. Their reasons can include pursuit of multiple objectives, air quality restrictions, and lack of budget and personnel.

Future Scenarios

Drought and Bark Beetles

Warming temperatures will probably reduce the depth and duration of montane snowpacks, lengthening and deepening the summer drought. This will likely increase moisture stress for many forests (Safford, North et al. 2012, McDowell and Allen 2015) (Figure 27.9). Climate models currently do not agree on future precipitation patterns in California, but they all predict temperature increases and greater year-to-year

variability. This will likely mean more pronounced El Niño/La Niña cycles that drive cycling between moderate snowpacks and potentially none at all for montane forests. These drought cycles could become bottlenecks for forest regeneration, killing most seedlings and saplings in dry conditions that are pronounced and/or occur in sequential years (Gray et al. 2005; North, Hurteau et al. 2005).

Climate change could also increase bark beetle populations because warming can allow extra generations to complete their life cycles each year and adult beetle emergence and flight to occur early in the season and to continue further into the fall (Fettig 2012). Mountain pine beetles will likely become especially damaging to higher-elevation conifer forests (Bentz et al. 2010). Large, warming- and drought-driven beetle outbreaks have recently occurred in the U.S. and Canadian Rockies (Kurz et al. 2008) and might occur in California's montane forests in the future. Bark beetle populations currently restricted to the southwestern U.S. and Mexico will also likely move northward as climates warm.

Fire

The combination of warmer climate and possibly increased fuel production (due to lengthened growing seasons) will likely cause more frequent and extensive fires throughout western North America (Price and Rind 1994, Flannigan et al. 2000, Committee on Stabilization Targets for Atmospheric Greenhouse Gas Concentrations et al. 2011, Yue et al. 2013). A recent study from the northern Sierra Nevada indicates noticeable increases in the occurrence of high-to-extreme fire weather since the mid-1990s (Collins 2014). These increases, which are expected to continue at least into the near future, are likely contributing to the rising incidence of large fires in the region (Collins 2014, Lydersen, North et al. 2014). Fire responds rapidly to changes in climate and could overshadow the direct effects of climate change on tree species distributions and migrations (Flannigan et al. 2000, Dale et al. 2001). Under most climate change projections, fire will increase in frequency, size, and severity (Flannigan et al. 2009). The human population of California is expected to increase to more than fifty million by 2050 with a large increase in wildland/urban interface settlements. While educational efforts can help to reduce fire ignitions and improve public safety, more people usually leads to more fire (Syphard et al. 2009). Increased frequencies and intensities of fire in coniferous forest in California will almost certainly drive abrupt changes in tree species compositions and will likely reduce the size and extent of old-growth forest conditions (McKenzie et al. 2004, Stephens et al. 2013).

Species Distribution

Projected changes in California's terrestrial avifauna and flora are likely over the next century. Stralberg et al. (2009) developed current and future species distribution models for sixty focal bird species and found that novel avian assemblages with no modern analogy could occupy over half of California. This implies a dramatic reshuffling of avian communities and altered pattern of species interactions, even in the upper elevations of the Sierra Nevada, where only a modest proportion of novel avian communities were projected. A similar study projected that 66% of California's native flora will experience greater than 80% reduction in range size within a cen-
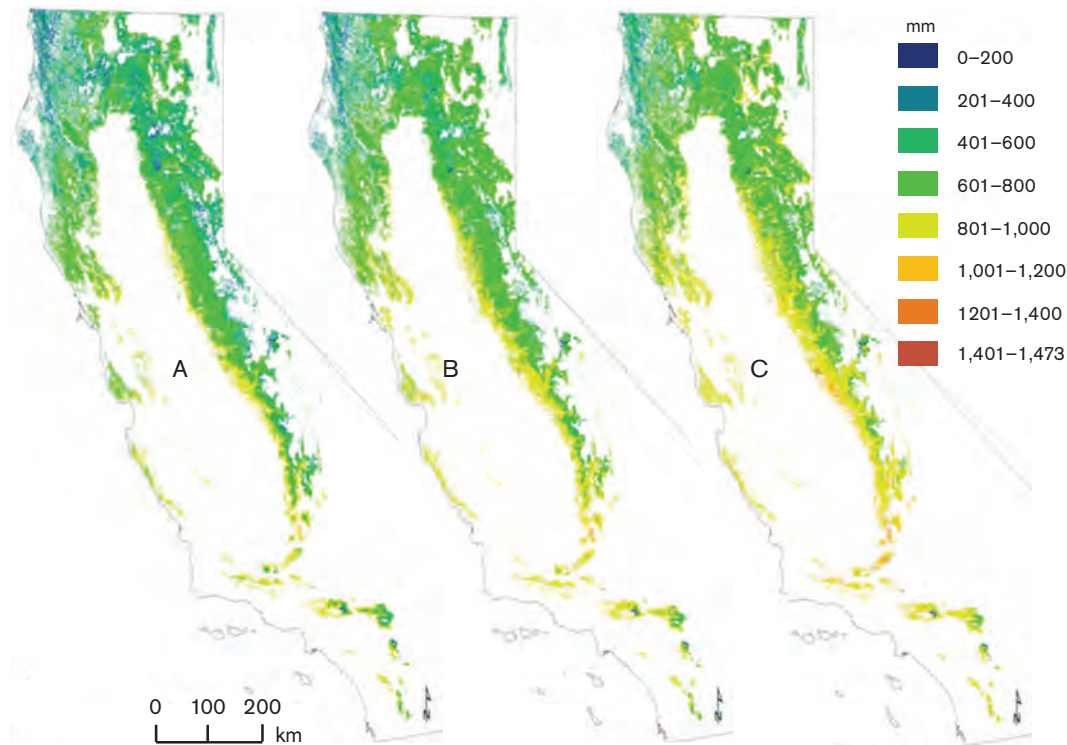
FIGURE 27.9 Current (A) and future (B, C) projections of climatic water deficit for California's montane forests. Climatic water deficit is the amount of water (scaled in millimeters [mm]) by which potential evapotranspiration exceeds actual evapotranspiration indicating relative drought stress. Projections based on (B) the Parallel Climate Model (PCM) and (C) the Geophysical Fluid Dynamics Laboratory CM 2.1 model (GFDL), using the A2 (medium-high) CO_2 emissions scenario. Illustration by Jim Thorne.

tury (Loarie et al. 2008). Their study identified the southern Sierra Nevada and the coastal mountains of northwest California as climate change refugia, defined as areas projected to harbor species with shrinking ranges (presumably retaining subsets of regional species assemblages over time). Loarie et al. (2008) recommended novel adaptive management approaches and large-scale planning efforts that promote landscape and regional habitat connectivity. They also recommended serious consideration of human-assisted dispersal of California's flora and prioritization of climate change refugia for conservation and restoration.

California's montane forests have withstood the pressures of the state's burgeoning human population, frequent droughts and the long-term, general absence of its keystone process—frequent, low-intensity fire. Yet the future promises that these stressors will persist and possibly be amplified by climatic change. The challenge to conserving California montane forests into the future is to increase their resilience while sustaining the old growth, wildlife, and ecosystem services that make them so unique among the world's temperate forests.

Summary

The strong, seasonal drought and historically frequent fire associated with a Mediterranean-type climate shape the composition and distribution of California's montane forests. Differences in fire intensity and soil moisture availability associated with small- and large-scale topographic features such as drainages, aspect, and slope position affect ecosystem pro-

ductivity and processes as well as ecosystem resilience to the most common stressors: fire, drought, and bark beetles. The resulting forest is highly heterogeneous, and the range of habitats—from dry, open woodlands with understory shrubs to dense, mesic, multistory stands—supports the highest vertebrate diversity of California's forest types. Sensitive and threatened species are most associated with forest structures and habitat that have become increasingly rare after a century of logging and fire suppression.

Management of these forests on public lands tends to focus on reducing densities of trees and fuels accumulated from fire suppression and increasing frequency and extent of low-intensity burns. This type of burning has demonstrated potential to restore many ecosystem processes that have stalled in the long absence of fire and to increase forest resilience to stresses likely to increase under climate change, such as drought and pests. Montane forests provide important ecosystem services to the state's large and growing population, including much of its water, hydroelectric power, and substantial carbon storage, which can help offset human CO_2 emissions. Although many challenges confront montane forests as human population and rural home construction increase, lessons learned from past forest management and progressive use of fire by the National Parks provide future pathways for sustaining and improving the ecological resilience of these forests.

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Recommended Reading

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Glossary

ABIOTIC Not associated with or derived from living organisms. Abiotic factors in an environment include factors such as sunlight, temperature, wind patterns, and precipitation.

ALFISOLS One of twelve soil orders in the U.S. Soil Taxonomy, Alfisols make up 9.6% of global soils. They are primarily in cool, moisture regions of the Northern Hemisphere and have sufficient water to support at least three consecutive months of plant growth. They have high-to-medium base saturation, are moderately weathered, and are rich in iron and aluminum.

ANDISOLS One of twelve soil orders in the U.S. Soil Taxonomy, Andisols account for only 0.7% of soils globally. They are formed from volcanic parent material, are high in organic matter content and phosphorous, and have a low bulk density.

BASAL AREA A sum of the cross-sectional area of trees stems, measured by the diameter at breast height (dbh) (1.3 meters above the ground) and standardized to a hectare or acre area. It is a commonly used forestry measure that indicates the relative amount of biomass (and by implication resource use) of different sizes and species of trees within a stand.

CANOPY CLOSURE This is a point measure of how much of the sky hemisphere is obscured by vegetation.

CANOPY COVER This is a stand-level average of how vertically porous a forest canopy is.

DIAMETER DISTRIBUTION The number of trees in different diameter-size classes. It is a widely used measure in forestry that provides insight into a stand's structure and disturbance history.

EDAPHIC Produced or influenced by the soil.

FOREST RESILIENCE The capacity of a forest to absorb disturbance and reorganize while still retaining its essential structure, composition, and ecological functions.

INCEPTISOLS One of twelve soil orders in the U.S. Soil Taxonomy, Inceptisols (9.9% globally) often lack distinctive subsurface horizons. Inceptisols are generally found in landscapes with continuously eroded conditions or areas with young deposits.

SERAL A phase in the sequential development of a community.

ULTISOLS One of twelve soil orders in the U.S. Soil Taxonomy, Ultisols (8.5% globally) have low base saturation at depth.

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