TWENTY-EIGHT

# Subalpine Forests

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## Introduction

Subalpine forests in California, bounded by the treeline at their upper margin, are the forest zone influenced primarily by abiotic controls, including persistent snowpack, desiccating winds, acute and chronic extreme temperatures, soil moisture and evapotranspirative stresses in both summer and winter, and short growing seasons (Fites-Kaufman et al. 2007). Subalpine forest species derive their annual precipitation primarily in the form of snow. Disturbances such as fire, and biotic interactions including competition, are less important than in montane forests. Although some subalpine forests are dense and have closed canopies, most are more accurately considered woodlands, with short-statured individuals and wide spacing of young as well as old trees. Subalpine forest stands are commonly interrupted by areas of exposed bedrock, snowfields, and upland herbaceous and shrub types—the latter comprising important components of broader subalpine ecosystems (Figure 28.1; Rundel et al. 1990, Sawyer et al. 2009).

Subalpine forests comprise the highest-elevation ecosystems in California dominated by trees. Although scattered upright trees and wind-swept, shrubby individuals ( RUMM HO ) grow sparsely in the alpine zone, subalpine forests have their upper limit at the alpine-treeline E OTONE. Treeline has long fascinated ecologists for its predominance worldwide, from equatorial tropical forests to polar zones. While many environmental factors mediate the exact location of regional treelines—a "devil-is-in-the-details" that also delights ecologists—a robust unifying theory has been developed to explain the treeline ecotone as the thermal contour (isotherm) on the landscape where average growing-season temperature is 6.4°C (Körner and Paulsen 2004, Körner 2012). In this context "trees" are defined as plants having upright stems that attain height ≥3 meters regardless of taxonomy, and "forest" is characterized as more-or-less continuous patches of trees whose crowns form at least a loose canopy (Körner 2007). Although not without some controversy, the hypothesized mechanism behind the global treeline isotherm relates to the fact that upright trees are more closely coupled with the atmosphere than shorter-statured vegetation types such as those found in the alpine zone. This coupling is tightly interrelated with rooting zone temperatures, tissue thermal capacities, primary production (photosynthesis and carbon allocation), water transport, canopy shade, snowfall filtering, and relationships of incoming solar radiation.

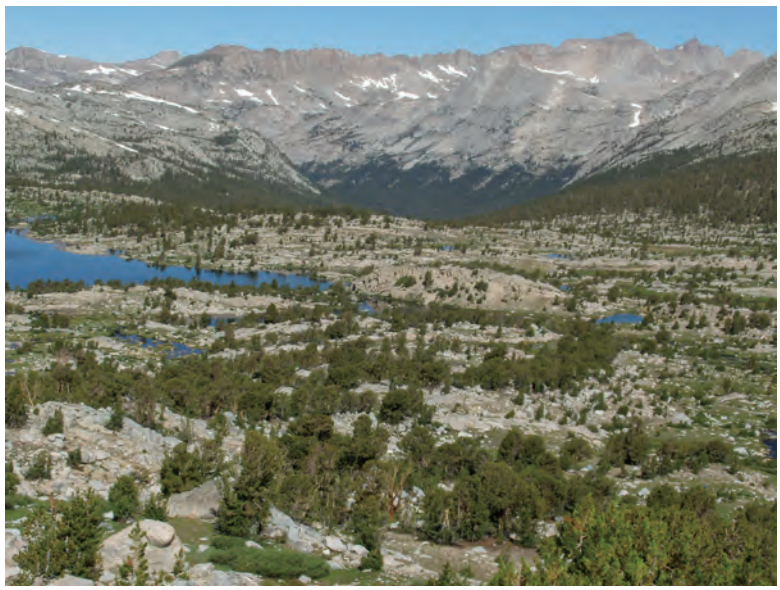

FIGURE 28.1 Typical woodland structure of California's subalpine forest ecosystems, characterized by scattered trees and abundant rocky ground. *Pinus albicaulis* forest type, Humphreys Basin, Sierra Nevada. Photo: Constance Millar.

Two corollaries follow from this treeline mechanism: that mean growing-season temperature mechanistically translates into a life-form boundary (the alpine-forest ecotone), and that treeline should not be strictly related to elevation. Nonetheless, for a particular region, elevation provides a rough proxy for the thermal treeline. The treeline isotherm logically rises where local conditions are warmer (e.g., south slopes), depresses where cooler (north slopes), and varies by latitude as well as regional climate regimes. California traverses more than nine degrees of latitude, and thermal treeline elevations also vary among the mountain regions of the state. They are lowest in the north, where they range from about 2,700 meters near Mount Shasta to 2,800 meters on Mount Lassen. At similar respective latitudes, treeline elevation is slightly lower in the Klamath Mountains to the west and slightly higher in the Warner Mountains to the east due to differing climate regimes and species compositions. In the Sierra Nevada thermal treeline ranges from 2,800 meters in the northern forests; to 3,000 meters near Donner Pass; to 3,200 meters in the Yosemite region; and to 3,500 meters in the southern Sierra Nevada (Rundel 2011). Thermal treeline in the Great Basin ranges to the east of the Sierra Nevada are slightly higher than corresponding Sierran latitudinal positions.

Treeline isotherm is the background regulator for the highest (coolest) occurrence of subalpine forests; however, local environmental factors control the specific position (including elevation) of upper subalpine forests. These include slope and aspect, substrate type and geomorphology, avalanche occurrence, and other disturbance history. This "ecological noise" can be critically important for ecosystem function and diversity and reminds us that changes in treeline position over time (or lack of change) are not necessarily indicators of climate change. Subalpine forests in California include communities dominated by whitebark pine (*Pinus albicaulis*), foxtail pine (*P. balfouriana*), limber pine (*P. flexilis*), western white pine (*P. monticola*), mountain hemlock (*Tsuga mertensiana*), or Sierra juniper (*Juniperus grandis,* formerly *J. occidentalis* var. *australis*). In addition, lodgepole pine (*Pinus contorta*) also commonly occurs in subalpine forests in California, either as the dominant species or intermixed with others. Because it extends across many more environments than subalpine, including elevations down to sea level, lodgepole pine alone is not an indicator of subalpine forests. In addition to these conifers, several very small stands of otherwise wide-ranging subalpine fir (*Abies lasiocarpa*) grow in the Trinity Alps and Marble Mountains of northwest California, and several tiny stands of Alaska yellow-cedar (*Callitropsis nootkatensis*, formerly *Chamaecyparis nootkatensis*) occur in the Siskiyou Mountains; these species are indicators of the subalpine zone at these rare locations. The hardwoods quaking aspen (*Populus tremuloides*) and curl-leaf mountain mahogany (*Cercocarpus ledifolius*) also grow commonly in subalpine environments, but because they extend abundantly to lower montane zones, they are not indicator species.

Whereas the upper bounds of subalpine forests have a robust, thermal delineation and form a visible transition from forest to alpine vegetation, the lower limits of the subalpine zone are less distinct. These generally follow the elevation of snowpack dominance, which strongly influences tree species diversity. The subalpine/montane forest ecotone is also controlled by shifts in fire regimes (Caprio and Graber 2000, Minnich 2007). On the one hand, while the dense canopies and surface fires of lower-elevation red and white fir (*Abies magnifica*, *A. concolor*, respectively) limit establishment of subalpine species, high-intensity fires burning downslope from lodgepole pine or hemlock forests can create openings in the fir forests and expose mineral soils. In these cases, subalpine species can advance downslope until succession of fir regains dominance uphill. As with upper treeline, elevation only roughly defines lower limits of the subalpine zone, and these vary with latitude across the state. Lower boundaries extend to 2,200 meters in the Klamath Mountains; 2,300 meters at Mount Shasta; 2,400 meters in the northern Sierra Nevada; 2,750 meters in the southern Sierra Nevada; 2,900 meters in the southern California mountains; and 3,000 meters in the Great Basin ranges (Griffin and Critchfield 1976, Elliott-Fisk and Peterson 1991, Holland and Keil 1995).

In California today, subalpine forest ecosystems conservatively extend over 390,270 hectares of California (Figure 28.2,

Photo on previous page: Long-lived bristlecone pines of the White Mountains are emblematic of subalpine forest ecosystems in California. Photo: Constance Millar.


FIGURE 28.2 Distribution of subalpine forest ecosystems in California. Source: Data from U.S. Geological Survey, Gap Analysis Program (GAP). Map: P. Welch, Center for Integrated Spatial Research (CISR).

TABLE 28.1
Area and percentage of total subalpine forests in California by mountain region

| Mountain region | Area (hectares) | Percentage of total |
|---|---|---|
| South Cascades[A] | 284 | 0.1 |
| Great Basin North[B] | 3,494 | 0.1 |
| Klamath Mountains[C] | 77,920 | 20.1 |
| Sierra Nevada | 290,830 | 75.2 |
| Great Basin, Central[D] | 10,590 | 2.7 |
| Great Basin, Southern[E] | 376 | 0.1 |
| Southern California[F] | 6,777 | 1.7 |
| TOTAL | **390,271** | **100** |

Data from U.S. Geological Survey, Gap Analysis Program (GAP).
A. Mounts Shasta and Lassen
B. Warner Mountains
C. Marble Mountains, Trinity Alps, Salmon Mountains, Yolla Bolly Mountains
D. Sweetwater Mountains, White-Inyo Range
E. Panamint Range
F. Tehacapi Mountains, San Gabriel Mountains, San Bernardino Mountains, San Jacinto Mountains

Table 28.1; Davis et al. 1998) and occur in the Klamath Mountains, including the Marble Mountains, Trinity Alps, Mount Eddy, Salmon Mountains, and North and South Yolla Bolly Mountains; southern Cascade Range, including Mounts Shasta and Lassen; Sierra Nevada; Great Basin ranges, including the Warner Mountains, Carson Range, Zunamed Mountains (Charlet 2014), and Sweetwater Mountains; Glass Mountains, Mono Craters, White-Inyo Range, and Panamint Range; and southern California ranges, including the Tehachapi Mountains, San Gabriel Mountains, San Bernardino Mountains, and San Jacinto Mountains (Griffin and Critchfield 1976). Forests types differ across mountain regions of the state in overall tree species diversity as well as species dominance, diversity of affiliated nonarboreal vegetation, faunal relations, climate interactions, productivity, and biogeochemistry. Although subalpine forests commonly occur on all slope aspects of California mountain ranges, they are limited to wetter aspects in more arid regions such as southern California and the Great Basin. These usually include western slopes in southern California (Holland and Keil 1995) and northern slopes in the Great Basin (Elliott-Fisk and Peterson 1991).

The large majority of subalpine forest ecosystem in California occurs in the Sierra Nevada, with more than 75% of the total (see Table 28.1). Subalpine forests dominate in a broad band on the gradual west slope of the Sierras and in a narrow, less diverse and more scattered band on the steep eastern escarpment. The areas high enough to support subalpine forest in the jumbled Klamath Mountains of northwest California collectively amount to the second largest region, with 20% of the state's total. The southern Cascades support a deceptively small amount of subalpine forest (less than 1%), which results from the narrow perimeter area around Mounts Shasta and Lassen. The remaining mountain regions of the Great Basin and southern California each also contain less than 1% of the total subalpine forest in the state (see Table 28.1).

## Environmental Controls

### Geology, Geomorphology, and Soils

The environmental context for California's subalpine ecosystems derives from the unique sequence of historical geologic processes that gave rise to its upland regions (see Chapter 8, "Ecosystems Past: Vegetation Prehistory"). Subalpine forests have shifted greatly in diversity and geography over the past thirty million years as topography changed in the California region. Prior to that time, California was mostly under water and/or characterized by lowlands with subtropical climates. Mountain ranges of the pre-Sierra/Cascade cordillera first emerged as eruptive centers along the subduction plate boundary that defined the Pacific margin of North America more than seventy-five million years ago (Millar 2012). Tectonic action related to plate boundaries led to emplacement of magmatic batholiths (subsequently granitic rocks) deep below the continent. Plate-boundary tectonics also catalyzed extensive aboveground volcanoes that defined the Nevadan and Sevier orogenies and led to development of the extensive Nevadaplano, with high-elevation summits that extended across present-day eastern California and Nevada.

This early volcanism largely defined the stage for subsequent bedrock exposures, soil development, and geomorphic conditions supporting subalpine forests in California today. On the highest ranges and especially in the arid ranges where erosion has been minimal (e.g., the White-Inyo Range and parts of the southern Sierra Nevada), highly metamorphosed rocks called roof pendants occur and date to times when California was submerged under sea. These rocks are often characterized by complex, colorful, and tortuously folded strata, including formations of limestone, marble, and other carbonate substrates. Where they are exposed, unusual chemical compositions and pH levels constrain plant growth to species able to tolerate these conditions, with bristlecone pine on dolomite substrate as an example. Also dating to these eras are exposures of ultramafic and serpentine rocks, with patchwork soils of complex origin primarily derived from former oceanic terranes subsequently accreted into California. Soils derived from these rocks also present nutritional limitations for plant growth and exclude many taxa. Tolerant subalpine species such as foxtail pine and western white pine can be found on these soils in the few locations where they are exposed at high elevations, primarily in northwest California. In eastern California hydrothermal alteration of volcanic rocks created substrates with another type of unique chemistry limiting plant growth. Subalpine conifers such as lodgepole pine and limber pine are able to grow on these soils, and are often found on these substrates in very disjunct locations and at much lower elevations than usual, in zones otherwise dominated by montane or woodland conifers.

Far more extensive substrates underlying California subalpine forests are granitic rocks and associated soils that derive from the early magmatic plutons of subduction plate dynamics. These were exposed over subsequent eras during the processes of mountain-building and erosion by glaciers, water, and wind. Granitic rocks create soils that favor growth of many subalpine conifer species, with characteristics such as coarse grain that enable drainage yet adequate water-holding capacity, intermediate to moderate acidity, and a sufficient balance of vital plant nutrients. In some regions, such as the Great Basin ranges, southern Cascades, and eastern Sierra Nevada, geologic hot spots occur where range-front faulting

is active or magmatic centers are shallow. In these locations volcanism has continued from the late Tertiary into present times. Soils that develop in these regions, especially from Quaternary eruptions such as Mounts Shasta and Lassen and the Glass Mountains in eastern California, are poorly developed and challenge plant growth.

## Current Climate and Climate Variability

Although subalpine forest ecosystems in California lie within the general Mediterranean-climate regime of the state, high elevations modify its influence. For instance, as elevation increases, temperatures and evaporative demand decrease, reducing the stress of the otherwise long summer drought. The subalpine forest zone in California is characterized by short growing seasons (six to nine weeks), prolonged winter snowpack (usually deeper than 2 meters except in the Great Basin ranges), and cool summer and winter temperatures with frost possible any month (Agee 1993, Fites-Kaufmann et al. 2007). Proximity to the Pacific Ocean and dominance of prevailing storms from the west protect these high-elevation ecosystems from extreme cold, although the Great Basin ranges of eastern California experience more continental climates. These include greater extremes, especially of cold temperatures in winter, than other mountain regions in the state experience. Annual and monthly temperatures tend to be cooler as the subalpine zone rises in elevation (i.e., with decreasing latitude) and in interior ranges, regardless of latitude (Table 28.2; PRISM climate model, Daly et al. 1994).

Precipitation falls on subalpine forests mostly as winter snow. Summer precipitation derives from local convectional storms, which vary in intensity and abundance across the range of subalpine forests as well as by topographic position within ranges (Fites-Kaufman et al. 2007). Gradients of precipitation occur in both latitude and longitude. Annual precipitation, including winter snowfall, is generally highest in the northern mountains, including the Klamath Mountains and southern Cascades, which can approach conditions of the Pacific Northwest, and lowest in the semiarid regimes of the southeastern Great Basin ranges (see Table 28.2). Despite their southerly latitude, precipitation in subalpine regions of southern California is similar to locations in the central Sierra Nevada, though far less than in the southern Cascades and Klamath Mountains. Precipitation also varies strongly across heterogeneous environments within mountain ranges, so some subalpine sites receive high precipitation despite their location in a generally dry region and vice versa.

More precipitation falls in summer in California's southern subalpine forests than in northern forests due to the Gulf of California monsoon influence (see Table 28.2). In the southeastern Great Basin ranges, for instance, summer monthly precipitation is about equal to the winter amount, although annual averages are an order of magnitude lower than in northern mountains. July tends to be the driest month in the subalpine zone, with increasing precipitation in August and September. This trend reflects the various influences of summer convective activity and monsoon, especially in the southern regions; and early snowfalls, especially in northern regions. Longitudinal trends also occur in precipitation across the subalpine regions of California, with mountains nearer the Pacific Ocean (e.g., Marble Mountains, Yolla Bolly Mountains) generally receiving more annual precipitation (including winter snowpack) than progressively inland ranges at the same latitudes. This results from California's regional rain shadow (see Chapter 2, "Climate"). Rainshadow effects are also common within mountain ranges and shape subalpine forest composition and structure at local and regional scales. These result from local OROGRAPH EFFE TS, where moisture-laden clouds condense as rain when clouds rise on west slopes of the mountains and evaporate on the east slopes. Orographic processes, even over short distances across range crests, can translate to large differences in annual precipitation for local subalpine forests.

Snowfall and snowpack data and models are lacking for most of the state's subalpine regions. In California,
sites (automated snow-measuring stations run by the U.S. Department of Agriculture Natural Resources Conservation Service) exist only in the Warner Mountains, central-eastern Sierra Nevada, the Carson Range, and the Sweetwater Mountains, and most stations are located in the upper montane forest zone rather than in the subalpine. The sufficiently high stations, however, provide a window into snowfall depth and interannual variation in subalpine forests across regions (Figure 28.3a). The trend of snowfall follows an expected geographic pattern, with latitude trumping orographic effects. One of the northernmost sites (Dismal Swamp), in the interior Warner Mountains, has the highest April 1 snow depth over the years of all sites. Snowpack generally decreases from north to south among the Sierra Nevada stations with the lowest depths at the southernmost station, Virginia Ridge just north of the Mono Basin. Snow depths also decrease eastward in the Great Basin, including the Carson Range (the Heavenly Valley station) and the Sweetwater Mountains (the Lobdell Lake station).

While it is common to define ecosystem envelopes by their temperature and precipitation parameters and to compare differences in these variables among regions, factors related to water availability and timing—not too much, not too little, when needed—are often more important in this region (Stephenson 1998). Temperature is important in controlling upper treeline, but evaporative stress, often measured through soil moisture interactions and MAT ATER DEF T (CWD), strongly influences subalpine distribution of species at lower elevations and interior dry margins. Intrinsic differences in evaporative demand and water supply regulate the ability of trees to survive and grow. Local topographic and substrate effects, interacting with rainfall and snowfall, determine the amount and retention of soil moisture and lead to differences in plant growth on soils of differing water-holding capacities, such as granitic versus metamorphic substrates. Similarly, differences in elevation of forests on different aspects reflect available growing-season soil moisture, which drives the presence of subalpine forests about 200 meters higher on steep, south-facing slopes than on steep, north-facing slopes (Fites-Kaufmann et al. 2007). In subalpine forests, CWD values are generally greater than 200 millimeters and are important in distinguishing the niche for this forest type from lower montane forests (Stephenson 1990, 1998). Variation in interannual CWD can be a key trigger, especially when combined with chronic warm summer temperatures, for subalpine forest insect outbreaks and forest mortality (Millar, Westfall et al. 2007; Millar et al. 2012).

While these summary patterns of temperature, precipitation, and available soil moisture define general boundary conditions, high interannual and interdecadal variation in California's weather exerts important controls on vegetation distribution and structure. The primary drivers of this vari-

TABLE 28.2
Climate data for subalpine forest zones in California by mountain range

| | | | | | Temperature °C | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | Jan | | July | | Annual | | | Precipitation (mm) | | | | |
| Location | Mountain range | Latitude (° W) | Longitude (° N) | Elevation (M) | max | min | max | min | max | min | mean | Jan | July | Aug | Sept | Annual |
| Kings Castle Pk | Marble Mtns | 41.616 | 123.222 | 2212 | 1.5 | -4.7 | 20.7 | 8.9 | 9.8 | 0.7 | 5.3 | 528 | 11 | 17 | 53 | 2902 |
| Warren Peak | Warner Mtns | 41.377 | 120.219 | 2820 | -2.1 | -10.5 | 18.7 | 3.0 | 6.9 | -4.7 | 1.1 | 162 | 14 | 21 | 39 | 1163 |
| Mt Shasta, Panther Mdws | S Cascades | 41.357 | 122.195 | 2454 | 1.0 | -6.5 | 19.9 | 6.5 | 8.8 | -1.1 | 3.9 | 332 | 10 | 16 | 38 | 2030 |
| High Lake, Russian Wild. | Salmon Mtns | 41.298 | 122.956 | 2209 | 2.2 | -4.8 | 20.6 | 9.5 | 9.8 | 1.0 | 5.4 | 249 | 16 | 23 | 43 | 1445 |
| Caribou Lake | Trinity Alps | 41.032 | 122.971 | 2133 | 1.9 | -5.2 | 20.2 | 8.6 | 9.6 | 0.4 | 5.0 | 510 | 4 | 51 | 30 | 2134 |
| Shadow Lake, Mt Lassen | S Cascades | 40.480 | 121.472 | 2332 | 3.1 | -6.3 | 21.9 | 6.9 | 11.2 | | 5.1 | 488 | 12 | 36 | 54 | 2838 |
| Lake Helen, Mt Lassen | S Cascades | 40.475 | 121.503 | 2608 | 1.8 | -7.2 | 19.9 | 5.9 | 9.4 | -2.1 | 3.7 | 519 | 12 | 39 | 58 | 2994 |
| S Yolly Bolly Peak | Yolla Bolly Mtns | 40.037 | 122.863 | 2320 | 3.5 | -4.6 | 22.1 | 10.0 | 11.5 | 1.5 | 6.5 | 364 | 6 | 10 | 25 | 1898 |
| Mt Rose Saddle | Sierra Nevada | 39.340 | 119.931 | 2970 | 0.4 | -10.0 | 18.7 | 4.6 | 7.8 | -4.3 | 1.8 | 229 | 21 | 24 | 44 | 1521 |
| Ebbetts Pass, Highland Pk | Sierra Nevada | 38.489 | 119.798 | 2754 | 2.5 | -8.3 | 19.4 | 6.3 | 9.8 | -2.3 | 3.8 | 234 | 27 | 40 | 38 | 1391 |

| | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Ellery Lake, Tioga Pass | Sierra Nevada | 37.934 | 119.238 | 2930 | 1.8 | -9.9 | 19.4 | 5.6 | 9.3 | -3.4 | 3.0 | 135 | 21 | 16 | 27 | 752 |
| Arrowhead Lk, Mammoth | Sierra Nevada | 37.581 | 118.981 | 3007 | 3.6 | -8.2 | 20.3 | 6.4 | 10.6 | -2.4 | 4.1 | 275 | 8 | 4 | 18 | 1348 |
| Crooked Creek | White Mtns | 37.506 | 118.170 | 3140 | 0.2 | -11.8 | 17.8 | 3.8 | 7.8 | -5.3 | 1.3 | 33 | 28 | 35 | 21 | 391 |
| First Lake, N Palisades | Sierra Nevada | 37.129 | 118.487 | 3073 | 1.7 | -10.3 | 18.4 | 4.4 | 8.8 | -4.0 | 2.4 | 132 | 10 | 13 | 39 | 836 |
| Wacoba Mtn | Inyo Mtns | 37.025 | 118.002 | 3105 | 2.4 | -8.3 | 19.0 | 6.5 | 9.4 | -2.4 | 3.5 | 33 | 25 | 29 | 19 | 346 |
| Cottonwood Basin | Sierra Nevada | 36.489 | 118.200 | 3262 | 1.0 | -10.7 | 16.8 | 3.4 | 7.7 | -5.0 | 1.4 | 87 | 7 | 8 | 18 | 511 |
| Telescope Peak | Panamint Range | 36.175 | 117.092 | 3150 | 1.9 | -8.9 | 21.0 | 6.0 | 10.8 | -2.5 | 4.2 | 39 | 20 | 39 | 34 | 362 |
| Cucamonga Peak | San Gabriel Mtns | 34.222 | 117.586 | 2700 | 6.7 | -2.9 | 23.3 | 10.3 | 12.8 | 1.8 | 7.3 | 231 | 6 | 15 | 31 | 1142 |
| San Gorgonio Mtn | San Bernardino Mtns | 34.103 | 116.822 | 3201 | 1.7 | -10.5 | 17.8 | 2.6 | 8.5 | -5.3 | 1.6 | 261 | 17 | 25 | 34 | 1306 |
| **Average** | | | | **2757** | **1.9** | **-7.9** | **19.8** | **6.3** | **9.5** | **-2.1** | **3.7** | **255** | **15** | **24** | **35** | **1437** |

SOURCE: Data excerpted from the PRISM climate model (Daly et al. 1994) for point locations selected as representative of the mid-upper subalpine zone for the region. PRISM data represent 1971-2000 normals, with 800 m grid.

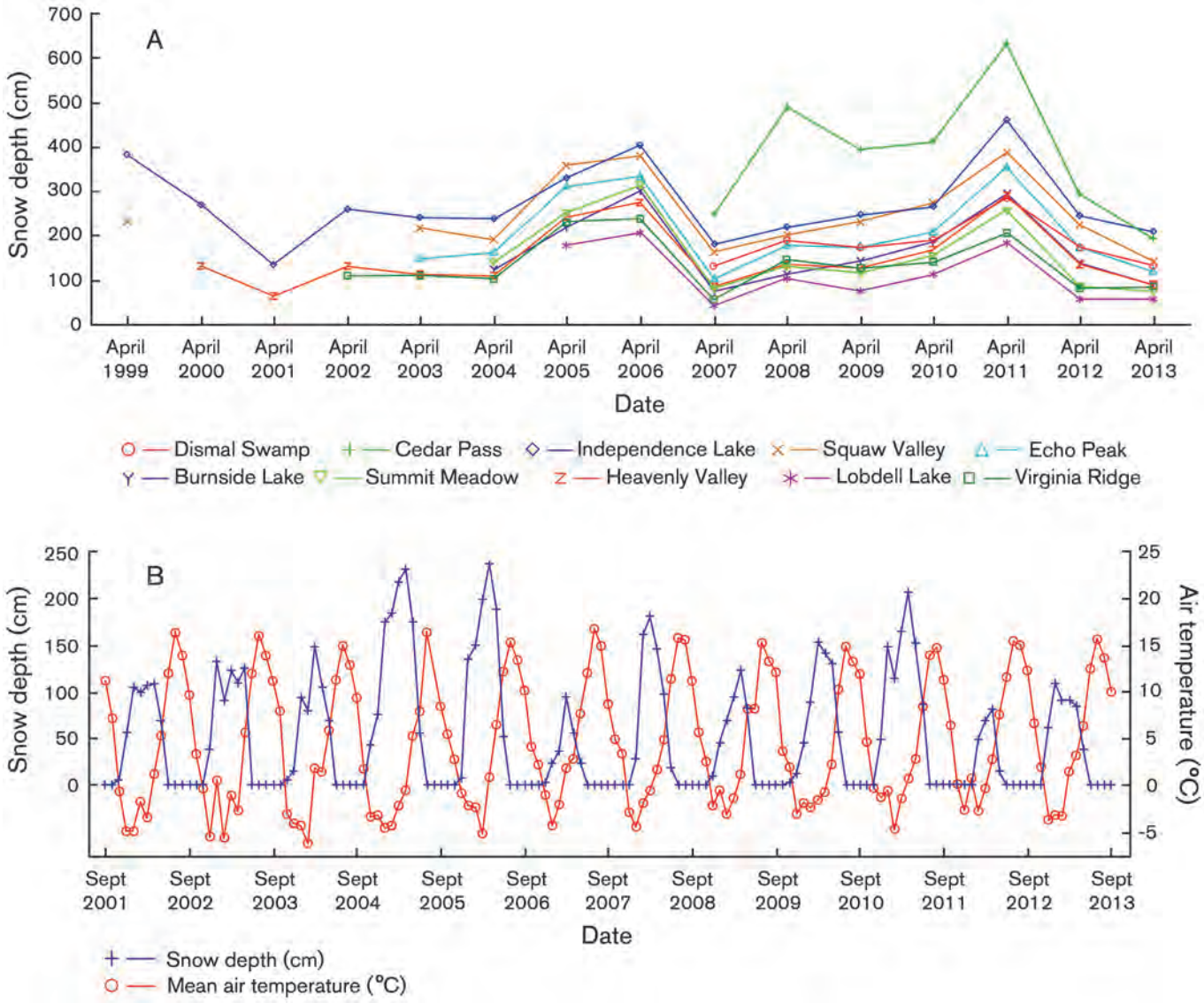


FIGURE 28.3 Snow depths from SNOTEL snow-monitoring stations in California subalpine zones. Source: Data extracted from NRCS SNOTEL station data, 2013.

A Snow-depth variation (April 1) across diverse subalpine locations in the Warner Mountains (Dismal Swamp, Cedar Pass), Sierra Nevada (Independence Lake, Squaw Valley, Echo Peak, Burnside Lake, Summit Meadow, Virginia Ridge), Carson Range (Heavenly Valley), and Sweetwater Mountains (Lobdell Lake), 1999–2013.

B Monthly snow depth and temperature variation at the Virginia Ridge SNOTEL site in the subalpine forest of the Sierra Nevada (2879 meters), 2001–2013.

ability are forcing mechanisms related to ocean circulation. Precipitation especially varies in episodic, often quasi-cyclic manners, and in patterns that vary across California (Redmond and Koch 1991, Abatzoglou et al. 2009). In particular, the El Niño–Southern Oscillation (ENSO) (Cayan et al. 1999) and multidecadal modes, including the Pacific Decadal Oscillation (PDO) and Atlantic Multidecadal Oscillation (Mantua et al. 1997, Cayan et al. 1998, McCabe et al. 2004), drive large differences in precipitation delivered to California among years and among decades (see Chapter 2, "Climate"). An example of vegetation response to these variations is the episodic response of lodgepole pine recruitment into subalpine meadows during the twentieth century, which occurred during negative phases of the PDO (Millar et al. 2004). Particularly important for biota are recurring multiyear droughts that characterize the instrumental record (Cayan et al. 1999) as well as historical reconstructions (Biondi et al. 2001, Cook et al. 2007); these droughts often trigger forest insect and pathogen infestation (e.g., limber and whitebark pine; see Millar, Westfall et al. 2007; Millar et al. 2012). Recent research is also elucidating the importance of ATMOSPHER R ERS (Dettinger 2013) as a significant determinant of interannual variability in precipitation that, at elevations of subalpine forests, translates to large differences in snowpack (McCabe and Dettinger 1999) (see Figure 28.3b).

California's high wind speeds may occur anywhere within the state, with the greatest velocities at high elevations (WRCC 2013). An important controlling factor exerted by wind on subalpine forests is in combination with snowfall and topography, which together influence snowpack drifting

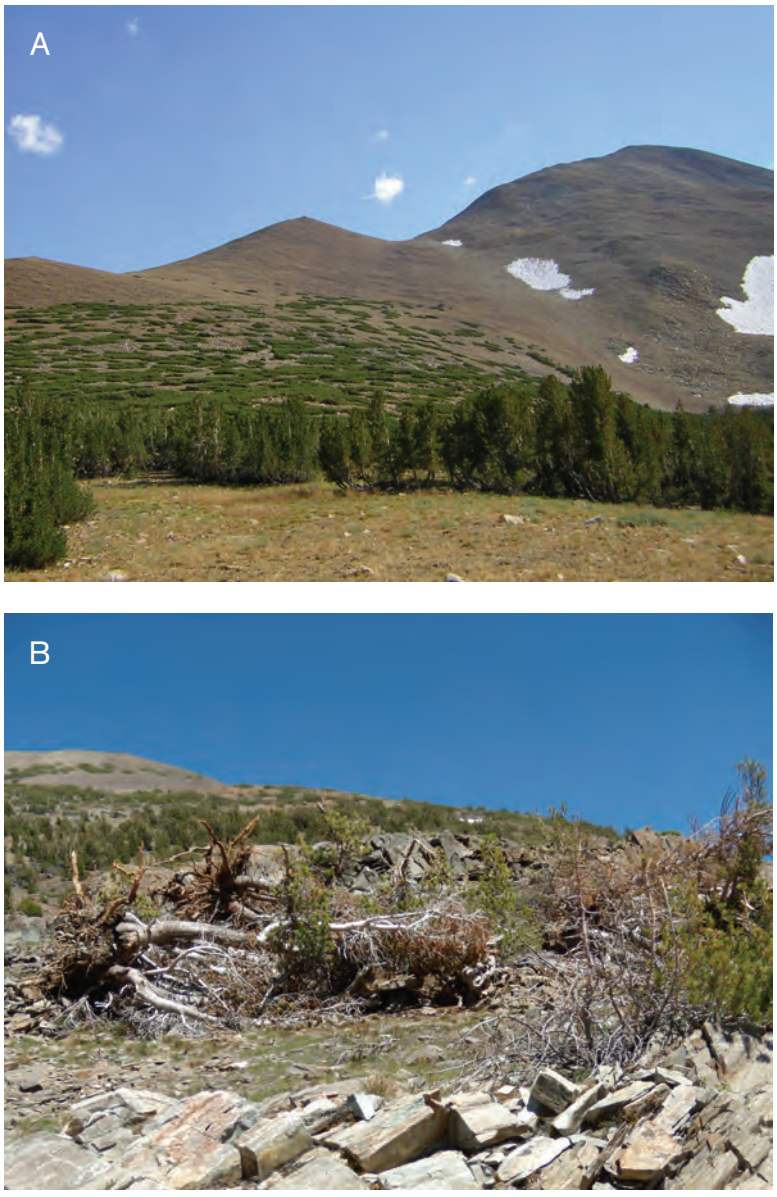


FIGURE 28.4 Wind-sculpted and wind-thrown whitebark pine forests near treeline. Photos: Constance Millar.

A Stunted trees and krummholz matts, Mount Dunderberg, Sierra Nevada.

B Windthrow in whitebark forests as a result of the autumn 2011 extreme downslope wind event, Tioga Crest, Sierra Nevada.

and variability in snow depth. Patches and zones of deeper, wind-influenced snowdrifts define areas that retain moisture late into the growing season (persistent snowfields) and have higher CWD. Many of these locations support subalpine forest but are surrounded by dry upland slopes with herbaceous or shrub cover. Scattered across the landscape, these support small to large "snowpocket forests," which tend to occur on north aspects and in slumps, along stepped terrain, or in depressions. In interaction with forest density, wind also influences the distribution of snow accumulation under the forest canopy. Low-moderate forest densities typical of many subalpine forests maintain the highest amount of snowpack relative to either higher or lower densities (Raleigh et al. 2013, Lundquist et al. 2014). Chronic winds in exposed areas, especially in winter when tree crowns are not protected by snow, affect crown growth and shape (e.g., krummholz and branch flagging; Figure 28.4a) and limit tree regeneration to wind-sheltered sites.

Windthrow is relatively rare in subalpine forests, given the inherent mechanical capacity of the species to accommodate and resist wind. Occasionally, however, the "perfect storm" of atmospheric conditions coincides to produce monstrous wind events. The most recent and potentially largest recorded of these was an extreme downslope wind event in the central Sierra Nevada on November 30 and December 1, 2011. This extreme event was unusual for its wind direction (north), duration (over twelve hours), and sustained high velocities, which exceeded 145 kilometers per hour for the duration of the event with gusts over 240 kilometers per hour (Hilimire et al. 2013). Montane forests on the high west slopes of Yosemite National Park and Devil's Postpile National Monument sustained massive, although localized, forest downfall, and subalpine whitebark pine forests of this region also experienced dramatic local areas of windthrow (see Figure 28.4b).

Avalanches occur throughout the snow zone of California's mountains but become more common with increasing elevation and steeper slopes. Avalanches exert locally important controls on subalpine forest ecosystems through effects on tree size, form, persistence, and species diversity. Severe avalanches uproot both mature and most young trees,

and recurring avalanches maintain slopes in treeless conditions, favoring sprouting shrubs such as alder (*Alnus* spp.). Avalanches also produce a variety of geomorphic effects on subalpine environments. These include scouring soils from hillslopes, maintenance of vertical troughs, accumulation of debris in the runout zone, and creation of impact and scour pits (Davis 1962). In some canyons avalanches are common enough (≥ one per decade) to give the slopes a striped appearance, where the tracks are treeless or with young tree cohorts and are separated by protected zones where mature forests can develop (Martinelli 1974, Mears 1992). Where avalanches are separated by intervals of several decades, conifers or aspen often regrow. A thick jumble of debris can remain in avalanche runout zones for decades if undisturbed and potentially influences other disturbances such as fire, insects, and disease. Along the edges of avalanche tracks, surviving trees are often broken and twisted with bark broken off—conditions that stress trees and favor entry of insects. During heavy snowpack years, such as the record wet winter of 1985–1986, avalanches occurred in unusually high numbers in the Sierra Nevada and toppled hundreds of hectares of subalpine forest (Wilson 1986, Kattleman 1996). A large proportion of trees were 125–150 years old. Some trees destroyed near Sonora Pass were 350 years old. The effect of avalanches in that season on forest throwdown can still be seen from many transmountain passes, such as along Tioga Pass in Yosemite National Park.

## Ecosystems of the Subalpine Forest Zone

Subalpine ecosystems in California are commonly dominated by open stands of conifer forest. Local areas of deciduous broadleaf trees can also occur along riparian corridors or other areas with available water. Scattered areas of wet and dry meadows, often with associated shrublands, are present; extensive montane chaparral communities dominate some regions. Through all of the subalpine forest communities in California is a general pattern of decreasing stand densities and basal areas with increasing elevation (Pinder et al. 1997). These declines are associated with a complex mix of environmental and climatic factors, including decreasing soil depth and development, lower temperature, shortening of the growing season, increased wind, and increased effects of snowmelt depth and topography on water availability. Models of site moisture availability and irradiance coupled with field measurements of stand characteristics and tree-ring records suggest strong correlations of microsite conditions with age class (Bunn et al. 2005). Finally, these declines have also been associated with lower nutrient inputs from aboveground litter (Fites-Kaufman et al. 2007).

### Subalpine Adaptations to Extreme Physical Conditions

Many species of subalpine ecosystems, like those in the alpine zone, have evolved specialized adaptations to endure extreme climates and environments including rocky substrates with thin, poorly developed and often nutritionally impoverished soils; steep, unstable slopes that experience avalanches and landslides; and subfreezing temperatures, high and desiccating winds, and intense solar radiation. A case in point is Great Basin bristlecone pine, which grows in the White-Inyo and Panamint Ranges of California and many more ranges in Nevada and Utah. Throughout its distribution, bristlecone pine forests occur at the highest elevations and extreme exposures under cold, arid climates.

Evolved adaptations to these conditions are many. One that contributes to the species capacity to persist in these environments is its needle retention, which is longer than other conifer species, reaching over fifty years (Barber 2013, Ewers and Schmid 1981). This unusual capacity enables trees to retain foliage and to photosynthesize (i.e., to survive) even during multiyear periods when weather conditions in the growing season are severe enough that new needles cannot develop. Waxiness and resin buildup on needles add to their durability as well. Another attribute contributing to the species' persistence and great longevity is the capacity to form stripbark growth. This occurs when portions of the main stem (secondary cambium) die back as the tree ages. This leaves increasingly smaller strips of live stem (cambium) and bark on one side of the tree. Such stripbark trees can continue to grow for centuries and millennia—a capacity shared with only a few other, and mostly subalpine, conifers.

The stripbark habit is assumed to be an adaptation to the extreme climate conditions of the species' range, enabling trees to "cast away" branches and stem as stress increases and remain alive with only part of the vasculature and crown functional. Many bristlecone pines, especially those that have developed stripbark, also have intensely spiral grain, known to be a highly heritable trait. This leads to a corkscrew form of the main stem, which has the effect of exposing more of the crown—especially when a narrow strip as a result of stripbark—to sunlight. High fecundity of bristlecone pine is known to persist throughout the life of individuals, and even trees more than three millennia in age produce many cones with fertile seed. Because replacement is very low for long-lived individuals, this high fecundity of stands of mixed ages provides high genetic diversity for seedling generations that can be important for natural selection as climates change over the course of time (decades to millennia).

Another example of adaptation to extreme conditions of the subalpine zone is the crown plasticity of several conifer species, especially the capacity to form krummholz. This ability to tolerate nonapical-dominance and to spread laterally allows species such as whitebark pine, limber pine, and mountain hemlock to remain below the sheltering influence of winter snowpacks, where temperatures are stable at freezing temperature and protected from desiccating winds.

### Whitebark Pine Forests

Whitebark pine is a wide-ranging treeline species that extends from central British Columbia east to Wyoming and south to the central Sierra Nevada (Weaver 2001). It forms the dominant treeline species in the southern Cascade Range and on the higher slopes in the Warner Mountains. Whitebark pine forests are scattered in the Klamath Mountains with populations on Mount Eddy, Thompson Peak, Russian Peak, and the Marble Mountains (Griffin and Critchfield 1976). At several locations in the Klamath Mountains, such as Crater Creek and Sugar Creek Research Natural Areas (RNAs), stands of exceptional subalpine diversity exist with high density, productivity, and basal area (Cheng 2004). In these areas, whitebark pine is one prominent subalpine forest type out of seven that commonly occur.

Whitebark pine is common in the bands of subalpine eco-

systems that ring the southern Cascade volcanoes, especially Mounts Shasta and Lassen. Whitebark pine forests occur mixed with mountain hemlock as low as 2,103 meters along ridgetops of the Antelope Creek RNA, forming one of the lowest subalpine whitebark pine occurrences in this region (Cheng 2004). In the Sierra Nevada, whitebark pine ecosystems occur abundantly from the Lake Tahoe Basin south to Mount Whitney. In the central Sierra, whitebark pine typically is present in mixed stands with lodgepole pine, mountain hemlock, and Sierra juniper; while in the southern Sierra it grows with limber pine and slightly overlaps in range with foxtail pine (see Figure 28.1). A watershed study in Eastern Brook Lakes on the eastern slope of the Sierra Nevada at 3,170 to 3,780 meters found mixed dominance of lodgepole pine and whitebark pine. The mean leaf area index for canopies of whitebark pine was 4.6 $m^2m^2$, compared to 4.1 $m^2m^{-2}$ for lodgepole pine (Peterson et al. 1989).

Whitebark pine forests are considered EYSTONE E OSYS TEMS for the subalpine zone throughout the cordillera of western North America (Tomback and Achuff 2010). Whitebark pine is highly plastic in crown and growth form and varies readily in response to severity of growing conditions. On favorable sites it can form upright, small trees 10 to 15 meters in height that live to 350 years. At higher elevations above treeline or exposed slopes below, its crown becomes stunted, often exhibiting gnarled and twisted branches in response to desiccating winds. A lower ground layer of prostrate crown is often present in these stands. In the treeline ecotone and up to 500 meters above treeline, whitebark pines readily take on a multistemmed krummholz form of growth, and finally a low mat of growth less than 1 meter in height (Fites-Kaufman et al. 2007). At these locations whitebark pine stands commonly form monotypic communities that dominate the upper treeline ecotone and play important roles in snowpack retention. Krummholz plants often root as the crowns spread across the ground, and individuals can live up to 1,700 years old (King and Graumlich 1998). Krummholz mats are often thought to be ONA , deriving from a single seed, but genetic studies show this is not the case, at least for krummholz trees with crowns larger than about 3 meters in diameter (Rogers et al. 1999). A single krummholz mat can comprise 2 to 12 genets, with genetic variation and genetic distance among individuals within the krummholz increasing in the downwind direction. Krummholz crowns are very dense and provide important hiding cover for small mammals, especially the white-tailed hare (*Lepus townsendii*). A remarkable coadaptation exists between whitebark pine cones and seeds and Clark's nutcracker (*Nucifraga columbiana*), a midsized bird in the crow family (Tomback 2001). Increasing density in whitebark pine ecosystems in recent decades might relate to changes in behavior of Clark's nutcracker in response to changing climates as well as to direct response by the pine.

Whitebark pine forests exemplify a trend observed for other subalpine forests in California, with the exception of limber pine. Whereas there appears to be little significant advance of whitebark pine seedlings above the twentieth-century upper treeline, density in these zones has been steadily increasing throughout the century, with a net increase in the Sierra Nevada of 30%, including a 44–91% increase in small tree densities (Dolanc et al. 2013). Correspondingly, the density of large trees has declined. These increases in small tree density are accelerating, especially above 3,000 meter elevation.

## Western White Pine Forests

Western white pine (*Pinus monticola*) extends from British Columbia through the Cascade Range and Klamath Mountains, through the northern Great Basin ranges of California, and throughout the Sierra Nevada, where it reaches its limit in southern Tulare County. In the Sierra Nevada it is a minor component of upper montane forests but becomes increasingly important in subalpine habitats, although monotypic stands are rarely more than a few hectares. Most commonly, western white pine mixes with lodgepole pine, Jeffrey pine, mountain hemlock, red fir, and/or whitebark pine (Potter 1998). Although Sierran trees of this species may reach 40 meters in height and 2.5 meters in diameter, larger sizes are attained by the same species in the northern Rocky Mountains and Pacific Northwest (Van Pelt 2001). Western white pine generally maintains an upright tree form of growth nearly to treeline, where it is commonly replaced by whitebark pine or foxtail pine depending on geography. Seedlings are reported to be relatively few compared to other subalpine conifers (Parker 1988).

## Foxtail Pine Forests

Foxtail pine is the dominant subalpine and treeline pine of the southern Sierra Nevada and is locally important in subalpine forests of the Klamath Mountains. It has highly disjunct populations, with the Sierran and Klamath distributions separated by hundreds of kilometers. These two groups of populations are well differentiated, with the southern Sierra Nevada taxon, subspecies *austrina*, morphologically distinct in the foliage, bark, cones, and seeds from populations of subspecies *balfouriana* in the Klamath Mountains (Mastrogiuseppe and Mastrogiuseppe 1980). The disjunction of these two populations is thought to relate to the development of summer-dry Mediterranean climates during the late Tertiary (Millar 1996) further modified by effects of glacial/interglacial cycles of the Pleistocene and drought conditions of the mid-Holocene (Eckert et al. 2008).

Foxtail pine in the Sierra Nevada is restricted to higher elevations (2,600–3,660 meters) south of the Middle Fork of the Kings River. At its lower elevational limits it often occurs in open stands with lodgepole pine, Jeffrey pine, western white pine, and red fir. At higher elevations it forms relatively pure but low-density stands, although it often mixes with limber pine. Treeline stands of foxtail pine often show a preference for cooler, north-facing slopes (Rundel and Rabenold 2014), likely related to soil moisture availability (Bunn et al. 2005). Vankat and Major (1978) sampled stands of foxtail pine from elevations of 3,170 to 3,290 meters in Sequoia National Park and reported a relatively high mean density of 418 tree $ha^{-1}$ and a canopy cover of 26%, with a basal area of 31 $m^2ha^{-1}$. Tree densities and stand basal areas, however, decline with increasing elevation from foxtail pine woodlands to treeline (Lloyd 1997, 1998, Rundel and Rabenold 2014).

Foxtail pines can grow to be several thousand years old. Like bristlecone pine, foxtail pine has highly resinous wood that with the cold, arid climates in the southern Sierra Nevada can persist as remnant dead wood for millennia. Together the live and dead wood are important archives for paleoclimatic and paleoecological study. Foxtail pines have been documented to respond to warm and cold historical climate periods by, respectively, advancing upslope and retract-

FIGURE 28.5 Limber pine forests on the eastern escarpment of the Sierra Nevada, south of Mammoth Lakes. Photo: Constance Millar.

ing downslope (Scuderi 1993, Lloyd and Graumlich 1997). In the Klamath Mountains, foxtail pine plays a more diverse ecological role than in the Sierra Nevada. Habitat heterogeneity at multiple spatial scales has been found to favor persistence of foxtail pine populations in northwest California (Eckert 2010). At large spatial scales, the presence of ultramafic (low silica content, often basic) soils favors this species relative to other conifers and leads to greater ecological importance.

## Limber Pine Forests

Limber pine has a wide range extending from central Alberta and South Dakota south to New Mexico in the Rocky Mountains and across the higher ranges of the Great Basin. In California limber pine is most common along the eastern escarpment of the Sierra Nevada, where it extends from scattered and disjunct stands in Buckeye Canyon near Bridgeport, California, then southward with increasing importance (Figure 28.5). The transition at the north between limber pine and whitebark pine forests appears to reflect the latter's higher tolerance of high snowloads and long, dry summers. In Tulare County of the far southern Sierra, extensive limber pine forests occur on the west slope of the crest as well as on the east slope. In its Sierran belt, limber pine has a niche similar to whitebark pine as the upper-treeline dominant species, even forming ragged krummholz in the treeline ecotone. North of Mammoth Lakes, limber pine becomes restricted to steep, north slopes, usually of decomposed or fractured granitic rocks, whereas to the south and in other mountain ranges (with the exception of the White Mountains) it grows on diverse soil types and all aspects.

In the White and Inyo Mountains limber pine is common on granitic and other noncarbonate soils of the subalpine zone. At low and middle elevations limber pine forests are often monotypic, with virtually closed canopy conditions. At higher elevations, sparse stands comprise scattered gnarled giants that can live to two thousand years. Sharp delineations generally occur between limber pine stands on granitic soils and open stands of bristlecone pine on soils of dolomite parent material. While bristlecone pines occasionally mix with limber pine, few mature limber pine stands occur on dolomite soils in these mountains, and bristlecones have higher upper- and lower-range boundaries. Curiously, however, limber pine seedlings have been recruiting 300 meters upslope in the late twentieth and early twenty-first centuries, above living bristlecone pine forests. Further, these upslope expansions are occurring on dolomite soils, at least in the White Mountains above Patriarch Grove and in the northern Cottonwood Canyon, at elevations and locations where no live bristlecone pine seedlings have yet established. Similar recruitment by limber pine seedlings (only) above current upper treeline is under way in granitic soils in the northern White Mountains.

Limber pine forests also occur in Great Basin ranges north of the White Mountains, including the Sweetwater Mountains, Bodie Hills, and Glass Mountains. In the Sweetwaters, limber pine dominates the northern peaks, which have mafic soils of Tertiary volcanic origin, whereas whitebark pine forest is more common on the felsic (more silica-rich) soils of the southern peaks. In the Bodie Hills, limber pine is highly restricted and occurs as scattered individuals on Potato Peak and Bodie Mountain and small stands on the Brawley Peaks and Mount Hicks, just across the Nevada state line. Extensive stands occur in subalpine zones on the barren soils of Quaternary volcanic origin of the Glass Mountains and Mono-Inyo Craters.

Limber pine forests form the treeline community in the higher Transverse and Peninsular Ranges of southern California, with relict populations at relatively low elevations on the crests of Mount Pinos, Brush Mountain, and Frazier Mountain near the junction of the Transverse and Central Coast Ranges. These last populations occur as scattered trees at elevations of approximately 2,600 meters within an open forest dominated by Jeffrey pine. The presence of a relict alpine FE F E D (slope area with plant communities influenced by abiotic frost and freeze/thaw dynamics) community on the crest of Mount Pinos suggests that seasonal drought conditions and strong winds may allow the survival of limber pine (Gibson et al. 2008).

Although similar in general appearance, limber pine is not closely related to whitebark pine. Like whitebark pine, however, limber pine has convergently evolved large pine nuts that rely heavily on Clark's nutcrackers for seed dispersal (Tombach and Kramer 1980, Carsey and Tomback 1994).

FIGURE 28.6 Mountain hemlock forests favor cool, moist, often north-facing aspects, such as in Convict Canyon of the Sierra Nevada. Photo: Jeffrey Wyneken.

Unlike whitebark pine, limber pine cones open at maturity, and the seeds have a rudimentary wing. Some seeds are no doubt dispersed by wind and gravity, albeit at relatively short distances from the mother tree.

## Bristlecone Pine Forests

Great Basin bristlecone pine forms subalpine forests from Utah westward across the higher Great Basin ranges to the White Mountains, with scattered populations in the Inyo and Last Chance Mountains and on Telescope Peak in the Panamint Range. In the White Mountains bristlecone pine occurs largely on dolomite soils, although scattered trees may be present on sandstone and granitic soils with limber pine at elevations of 3,100 to 3,700 meters (Billings and Thompson 1957, Wright and Mooney 1965). It is a medium-size tree, typically 5–15 meters in height and trunk diameters up to 2.5–3.6 meters. Cones open at maturity, and the small seeds are winged and aerodynamic, although Clark's nutcrackers also disperse bristlecone pine. Some large-diameter trees have multiple stems, potentially resulting from seeds cached by Clark's nutcrackers (Carsey and Tombach 1994).

Bristlecone pines are a remarkable species in many respects. Their most well-known feature is the great age reached by individuals, making them the oldest known nonclonal organisms. In 2012 a tree in the White Mountains was found to be 5,062 years old, making it more than two centuries older than the famous Methuselah Tree, the former record holder. Tree ages vary with slope aspect in the White Mountains. North-facing slopes typically have the oldest trees, with an average of 2,000 years as compared to 1,000 years on south-facing slopes. The dry subalpine climate coupled with the durability of bristlecone wood can preserve them long after death, with dead trunks as old as 7,000 years scattered among living trees. The great longevity of trees and the long persistence of remnant dead wood combine to make bristlecone pine forests one of the most important scientific archives in the world for historical climate. Cross-dated tree-ring series, compiled from live and dead trees in overlapping fashion, have been developed for more than 9,000 continuous years of growth into the past. A short, several-century gap (no wood found) separates that archive from another well-resolved 2,000-year chronology. Climate reconstructions from this 11,000-year record provide continuous proxies for annual, interannual, decadal, and centennial climate variability over the entire Holocene.

Bristlecone pine stands on dolomite in the White Mountains are notable for their almost complete lack of woody understory plants—a striking contrast to the stands of limber pine, where a number of shrub species are present. Herbaceous perennials growing on dolomite also often differ substantially in community structure from fellfield communities a few meters away on granitic soils. Similarly sharp boundaries exist between dolomite soil communities and nearby sagebrush-dominated communities on shale substrate.

## Mountain Hemlock Forests

Mountain hemlock forests have a broad distribution that extends from the coastal ranges of Alaska south through British Columbia and the Pacific Northwest into the Sierra Nevada. In the northern Sierra Nevada this species can be found in upper montane forests of red fir and lodgepole pine (Potter 1998) but is more characteristic at higher elevations up to 3,500 meters, where it is frequently the dominant tree species in mixed stands with Sierra juniper and whitebark pine. Mountain hemlock is locally abundant in the Klamath Mountains and the subalpine zones of Mounts Shasta and Lassen in the southern Cascades. Most of the extent of mountain hemlock forests in the Sierra Nevada occurs from Sierra County south through Yosemite National Park, with a few isolated stands reaching Fresno and Tulare County.

Mountain hemlock in the Sierra Nevada is most characteristic of moist but well-drained mountain soils, often showing a preference for north-facing slopes (Figure 28.6; Fites-Kaufman et al. 2007). This contrasts with stands in the southern Cascade Range, where greater summer precipitation and warmer temperatures broaden topographic distribution (Parker 1994, 1995). Expansion of mountain hemlock in Lassen Volcanic National Park has been traced to warming temperatures as the Little Ice Age terminated in the early twentieth century, a response that might indicate the species' behavior to continued warming in the future (Taylor 1995).

FIGURE 28.7 Old-growth tree on Glass Mountain. Sierra juniper forests contain trees of often massive size and growing on exposed, rocky substrates. Photo: Constance Millar.

In the central Sierra of Yosemite National Park, mountain hemlock forests can be found in extensive groves with virtually closed canopies and individual trees reaching up to 30 meters in height and 2 meters in diameter. At higher elevations mountain hemlock is more scattered and often assumes a lower, shrubby growth form (Fites-Kaufman et al. 2007). Seedlings are relatively shade-tolerant compared to other subalpine conifers and grow well under this type of canopy. South of Yosemite, mountain hemlock becomes increasingly restricted to small stands in cold moist valleys and sheltered ravines, where snowbanks remain late into the summer. Unlike pure stands of the central and northern Sierra Nevada, these scattered trees in the southern portions of the range are commonly mixed with lodgepole pine, foxtail pine, western white pine, and red fir. The southernmost occurrence of mountain hemlock is below Silliman Lake in northern Tulare County, the site of a small grove of about sixty trees with heights up to 24 meters, diameters to nearly 90 centimeters, and healthy reproduction (Parsons 1972).

## Sierra Juniper

Sierra juniper is one of the most striking trees of subalpine Sierra Nevada ecosystems, with its short but massive trunk appearing to grow out of seemingly solid granite substrate (Figure 28.7). It ranges through the high Sierra Nevada from south of Susanville to Owens Peak in Kern County, with scattered trees in the Inyo, White, and Panamint Mountains (Griffin and Critchfield 1976). Disjunct populations also occur in the San Gabriel and San Bernardino Mountains. Sierra juniper typically grows on shallow soils from 2,100 to 3,000 meters elevation, often with Jeffrey pine, red fir, whitebark pine, mountain hemlock, and/or lodgepole pine. More than any other subalpine tree, Sierra juniper has a remarkable ability to colonize and become established in small fractures of granite domes that would not support other species.

Upper montane forests of lodgepole pine forest in the Tahoe Basin support mixed stands of Sierra juniper with red fir and Jeffrey pine, but these associated tree species are replaced by western white pine and mountain hemlock with increasing elevation (Fites-Kaufman et al. 2007). More typically, Sierra juniper occurs mixed in lodgepole pine stands up to treeline, where it may take on a krummholz growth form. Some Sierra junipers are reported to reach ages of over a thousand years (Graf 1999). The largest Sierra juniper—a tree 26 meters in height and 4 meters in diameter—is reported from the Stanislaus National Forest (Lanner 1999).

## Lodgepole Pine Forests

Open stands of lodgepole pine form a widespread forest belt that covers the upper montane zone and extends into the subalpine over much of California's high mountains (Figure 28.8). The most common lodgepole pine taxon in subalpine forests is *Pinus contorta* subsp. *murrayana*, as distinguished from the Rocky Mountain lodgepole pine (*P. contorta* subsp. *latifolia*), the beach pine of the coastal Pacific Northwest (*P. contorta* subsp. *contorta*), and the local endemic Bolander pine of the pygmy forest area of Mendocino County (*P. contorta* subsp. *bolanderi*). Lodgepole pine forests extend over a very broad geographic and elevational range, including subalpine inclusions in the Klamath Mountains (including an unnamed Del Norte County variant), through the southern Cascades with populations as low as about 1,000 meters on Mount Shasta, in the northern Sierra Nevada to elevations of about 1,830–2,400 meters, and up to 2,440–3,350 meters in the southern Sierra Nevada. Topography strongly influences elevational distribution; lodgepole pine forests reach much lower elevations with cold air drainage down glacial canyons (Potter 1998, Fites-Kaufman et al. 2007).

Lodgepole pine forests also commonly extend up into the subalpine zone in the northern and central Great Basin ranges, including the Warner Mountains, Carson Range, Sweetwater Mountains, Bodie Hills, and Glass Mountains. Disjunct colonies grow in the White Mountains, the largest of which is a nearly pure stand of approximately 100 hectares near Cabin Creek at 3,200 meters (Critchfield 1957). Larger populations appear on the San Gabriel, San Bernardino, and San Jacinto Mountains in southern California. Lodgepole pine has broad environmental tolerances, colonizing both shallow, rocky soils and semi-saturated meadow edges in an elevational belt from sea level to subalpine habitats. Only

FIGURE 28.8 Lodgepole pine forests often have narrow crowns and relatively closed canopies in the subalpine zone, as in Molybdenite Canyon, Sierra Nevada. Photo: Constance Millar.

rarely does it comprise true treeline forest ecosystems, as it is more typically replaced by whitebark pine, foxtail pine, or limber pine. The generally low stature and open stand structure of lodgepole pine subalpine forests are a function of the short growing season, associated severe climate conditions, and the thin, nutrient-poor soils that characterize the subalpine zone. These stands commonly contain few understory shrubs and little litter accumulation. Mature lodgepole pines in the subalpine zone are generally smaller than mature individuals of the dominant treeline pines and only rarely exceed 50 centimeters in diameter.

## Forests of Pacific Northwest Subalpine Tree Species

Three conifer species characteristic of subalpine communities of the Pacific Northwest and/or Rocky Mountains barely extend their range into California. Subalpine fir and Engelmann spruce (*Picea engelmannii*) are widespread in subalpine forests across western North America. The former has six known populations in the Klamath Ranges of western Siskiyou County at1,700 to 2,100 meters, while the latter is known from three populations in the lowest subalpine forests at 1,200 to 2,100 meters in the Klamath and Cascade Ranges. A third, wet-forest species from the Pacific Northwest, Alaska yellow-cedar, extends south from Alaska and barely reaches a few areas of the Klamath Mountains in Siskiyou and Del Norte Counties at elevations to 2,500 meters. While Alaska yellow-cedar is characteristically a species of cool, wet forests, its upper elevational limit extends into subalpine habitats.

## Deciduous Subalpine Forests

Several deciduous, broad-leaved tree species form dense local stands of subalpine forest in moist environments such as riparian corridors, meadow fringes, and upland slopes with abundant soil moisture. The most common is quaking aspen, which commonly occurs in pure groves fringing wet or moist meadows and on slopes watered by springs or seeps with subsurface water, including talus slopes (Figure 28.9; Potter 1998, Fites-Kaufman et al. 2007). Aspen is widespread in appropriate habitats throughout subalpine areas of the Klamath Mountains, southern Cascade Range, Warner Mountains, Sierra Nevada, and the high mountains of southern California. Aspen is shade-intolerant and requires high light conditions to regenerate. It sprouts vigorously from suckers arising on an extensive lateral root system following fire, which plays an important role in perpetuating aspen stands by reducing competition for light from conifers. This sprouting results in a dense stand of trunks formerly assumed to be wholly clonal. More recent genetic studies reveal that some aspen groves comprise multiple genotypes (Tuskan et al. 1996). Health threats to aspen forests throughout the species range from native insects, pathogens, and incursions from conifer recruitment have heightened attention to this broadleaf ecosystem. Californian populations, however, have so far mostly been unaffected; areas of concern are concentrated in northeastern California and some parts of the northern Sierra Nevada. Notably, rapid mortality caused by sudden aspen decline (Shepperd 2008), first observed and studied in Rocky Mountain and intermountain populations, has not been reported in California (Morelli and Carr 2011).

Water birch (*Betula occidentalis*), a widespread multistemmed small tree 6–9 meters in height, occurs over a wide range of elevations across the western United States and Canada. In California, water birch ecosystems are common at 1,500 to 2,750 meters and grow mostly along stream corridors draining the east side of the central and southern Sierra Nevada into the Owens Valley, White Mountains, and in disjunct populations in the Klamath ranges. The species is absent from the northern Sierra Nevada and northern California. A third deciduous broadleaf tree that occasionally reaches subalpine habitats is black cottonwood (*Populus trichocarpa*). This tree is widespread on alluvial flats and streamsides across California up to 3,000 meters.

Curl-leaf mountain mahogany, a tall evergreen shrub or small tree in the rose family, extends into the subalpine zone of California, where it can form extensive and dense canopies on dry, rocky, and exposed slopes (Brayton and Mooney 1966). Mountain mahogany has a wide distribution in subalpine zones throughout California, including the Klamath Mountains, southern Cascades, Sierra Nevada, Great Basin ranges, and high ranges of southern California. It has

FIGURE 28.9 Quaking aspen stands are common along watercourses, such as in Parker Canyon of the eastern Sierra Nevada, along meadow edges, or on slopes with high soil moisture. Photo: Constance Millar.

extremely hard wood and can attain ages of least 1,350 years (Schultz et al. 1990). Mountain mahogany provides browse for deer and bighorn sheep and important hiding cover from predators for these and other midsize to large mammals. Mountain mahogany ecosystems influence subalpine conifers by fixing nitrogen through associated root nodules, thereby increasing available nitrogen in otherwise nutrient-limited high-elevation soils (Lepper and Fleschner 1977).

## Subalpine Meadows

Meadows are scattered throughout the subalpine and montane forest zones of the Klamath Mountains, Cascade Range, Sierra Nevada, and high southern California mountains.

The single most important factor explaining the distribution of meadows is the presence of a shallow water table that provides high soil moisture and excludes establishment by woody plants (Wood 1975). Although the total area of meadows is small, herbaceous plant species in meadows make up a large part of the floral diversity of subalpine zones. Meadow community composition, productivity, and biomass vary widely depending on a suite of factors. Subalpine meadows can be classified into four broad types based on vegetation composition and water table depth. These broad meadow types have been further classified based on vegetation, elevation, water table, landform, hydrology, and soil characteristics (Bennett 1965, Benedict and Major 1982, Ratliffe 1985, Allen-Diaz 1991, Sawyer et al. 2009, Stevenson 2004, Rundel et al. 2009, Weixelman et al. 2001).

Wet meadows are composed predominately of perennial sedges, rushes, and grasses. Dominant species generally spread by rhizomes and often form dense sod over large areas. Soils in this type are saturated in the rooting zone for most of the growing season and are generally dark loams due to large amounts of organic material (Weixelman et al. 2001). In contrast, dry meadows are dominated by herbaceous species adapted to drier conditions, including grasses, sedges, and herbaceous dicots. Soils are not saturated within the rooting zone during the growing season, with saturation typically much deeper than the rooting zone (Allen-Diaz 1991, Weixelman et al. 2001). In shrub meadows, open areas are interspersed with clumps of shrubs, often willow (*Salix* spp.) but sometimes evergreen, ericaceous shrubs such as *Rhododendron columbianum* (formerly *Ledum glandulosum*), *Kalmia polifolia*, and *Vaccinium cespitosum* (Rundel et al. 2009). Willow stands can include any of a diverse set of *Salix* species as dominants and occur on sites with periodic flooding during the growing season. Floods allow the ongoing establishment of willow from seed. Drier shrub meadows can have scattered but significant cover of red heather (*Phyllodoce breweri*), pinemat manzanita (*Arctostaphylos nevadensis*), the winter deciduous Utah serviceberry (*Amelanchier utahensis*), bitter cherry (*Prunus emarginata*), and California mountain ash (*Sorbus californica*).

Woodland meadows are the fourth community type, typified by scattered sedges, grasses, and broadleaf herbs in open stands of lodgepole pine and/or aspen. Great diversity of herbaceous species occurs within this type, varying with elevation, water table, and geographic region, (Fites-Kaufman et al. 2007). The causes and dynamics of lodgepole pine establishment and survival in Sierra meadows appear to be a function of both existing water tables and climate cycles. Fluctuations in water table with interannual and interdecadal climate variability can result in cyclical lodgepole establishment, survival, and mortality (Bartolome et al. 1990, Millar et al. 2004).

## Wildlife Diversity of Subalpine Forest Ecosystems

Fifty native mammal species commonly use California subalpine forest ecosystems as seasonal or permanent habitat (Table 28.3; Ingles 1965, Jameson and Peeters 2004). These include a range of orders and families, including shrews, bats, rabbits, many rodents, carnivores, and ungulates. Iconic species of the upper subalpine and alpine zones include yellow-bellied marmot (*Marmota flaviventris*), alpine chipmunk (*Neotamias alpinus*), Belding's ground squirrel (*Urocitellus beldingi*), American pika (*Ochotona princeps*), and both Sierra Nevada and desert bighorn sheep (*Ovis canadensis*), each of which depends on specific environments for shelter and forage. Unfortunately, all these species are challenged or thought to be at

TABLE 28.3

Mammal species that use California subalpine ecosystems as habitat (Ingles 1965; Jameson and Peeters 2004)

| Order | Family | Species | |
|---|---|---|---|
| Insectivora | Soricidae | *Sorex* | *palustris* |
| | | | *lyelli* |
| | | | *monticolus* |
| Chiroptera | Vespertilionidae | *Myotis* | *lucifugus* |
| Lagomorpha | Ochotonidae | *Ochotona* | *princeps* |
| | Leporidae | *Lepus* | *americanus* |
| | | | *californicus* |
| | | | *townsendii* |
| Rodentia | Aplodontidae | *Aplodontia* | *rufa* |
| | Sciuridae | *Marmota* | *flaviventris* |
| | | *Tamias* | *alpinus* |
| | | | *amoenus* |
| | | | *minimus* |
| | | | *quadrimaculatus* |
| | | | *speciosus* |
| | | | *umbrinus* |
| | | *Callospermophilus* | *lateralis* |
| | | *Otospermophilus* | *beecheyi* |
| | | *Urocitellus* | *beldingii* |
| | | *Tamiasciurus* | *douglasii* |
| | Geomyidae | *Thomomys* | *bottae* |
| | | | *mazama* |
| | | | *monticola* |
| | Cricetidae | *Reithrodontomys* | *megalotis* |
| | subf Cricetinae | *Neotoma* | *cinerea* |
| | | *Peromyscus* | *maniculatus* |
| | subf Microtonae | *Clethrionomys* | *californicus* |
| | | *Microtus* | *longicaudus* |
| | | | *montanus* |
| | | | *oregoni* |
| | | *Phenacomys* | *intermedius* |
| | Zapodidae | *Zapus* | *princeps* |
| | | | *trinotatus* |
| | Erethizontidae | *Erethizon* | *dorsatum* |
| Carnivora | Canidae | *Canis* | *latrans* |
| | | *Vulpes* | *vulpes* |
| | Felidae | *Felis* | *rufus* |
| | | *Puma* | *concolor* |

*(continued)*

TABLE 28.3 *(continued)*

| Order | Family | Species | |
|---|---|---|---|
| | Mustelidae | *Gulo* | *gulo* |
| | | *Martes* | *americana* |
| | | | *pennanti* |
| | | *Mephitis* | *mephitis* |
| | | *Mustela* | *erminea* |
| | | | *frenata* |
| | | *Taxidea* | *taxus* |
| | Procyonidae | *Bassariscus* | *astutus* |
| | | *Procyon* | *lotor* |
| | Ursidae | *Ursus* | *americanus* |
| Artiodactyla | Cervidae | *Odocoileus* | *hemionus* |
| | | *Ovis* | *canadensis* |

risk from various human stressors. Most common are declines or impacts associated with contemporary climate change (Moritz et al. 2008). Marmot, alpine chipmunk (Rubidge et al. 2012), bushy-tailed packrat (*Neotoma cinerea*; Moritz et al. 2008), and Belding's ground squirrel (Morelli et al. 2012) have experienced changes in distribution and population dynamics from warming temperatures and changing snowpacks. American pika has long been considered at risk from changing climate and appears threatened in the central Great Basin. California populations, however, appear to be more buffered against change (CDFW 2013).

Sierra Nevada bighorn sheep, a distinct subspecies in the central and southern Sierra Nevada, suffered drastic population declines over the twentieth century. The species was placed on the federal Endangered Species list in 2000 when its numbers declined to near one hundred. Implementation of formal recovery plans has led to recovery toward the goal of five hundred adults distributed throughout historical herd units (Stephenson et al. 2011).

Avian species that depend on subalpine forests include mountain bluebird (*Sialia currucoides*), red crossbill (*Loxia curvirostra*), pine grosbeak (*Pinicola enucleator*), Cassin's finch (*Carpodacus cassinii*), Williamson's sapsucker (*Sphyrapicus thyroideus*), black-backed woodpecker (*Picoides arcticus*) (Mayer and Laudenslayer 1988), and Clark's nutcracker (Meyer 2013). The dependence of whitebark pine on Clark's nutcracker for reproduction is a remarkable example of coadaptation among species in subalpine forests. Seed cones of whitebark pine are unique among the pines in having indehiscent bracts—that is, the cones do not break apart on their own when mature (Figure 28.10). Further, cones remain closed and tightly adhered to the stem even at seed maturity. Cones can only be broken open and seed released by Clark's nutcrackers, which in turn depend on whitebark pine seeds for food (Tomback 1982, 1986). The birds open the cones while on the tree, carry batches of seeds in specialized pouches under their bills, and plant seeds in caches, usually in protected locations. A single Clark's Nutcracker caches as many as ninety-eight thousand seeds per season (Hutchins and Lanner 1982). The birds have uncanny ability to relocate their caches, even under a meter of snow, and they utilize these caches to feed young birds through early growth and development. Sufficient seeds are left unrecovered by Clark's nutcrackers that whitebark pine seedlings can germinate (Lanner 1996). Clark's nutcrackers also use limber, foxtail, bristlecone, and western white pine. During migrations to lower altitudes, the birds also extensively harvest the seeds of pinyon pines.

Like Clark's nutcracker, several other bird species and small mammals serve important ecological roles for subalpine tree species. Douglas's squirrel (*Tamiasciurus douglasii*), lodgepole chipmunk (*Neotamias speciosus*), and other seed-caching wildlife species are important seed dispersers and predators of subalpine tree species in subalpine ecosystems (Tomback 1982, Van Der Wall 2008).

## Origins of Subalpine Forest Species and Ecosystems

The biogeographic origins of California's present-day subalpine forest species and forest communities are highly complex given the geologic uplift and subsidence history, diversity of historical climates, and influences on vegetation of multiple periods of dramatic climate change that characterize the region (see Chapter 8, "Ecosystems Past: Vegetation Prehistory"; Millar 1996, 2012). The biogeography of most present-day species extends back more than twenty million years. However, species' locations, environmental contexts, elevations, climates, and vegetation associations have varied drastically over time. Many cool-temperate species, including subalpine conifers and other mountain-adapted plant species still in the region, found refugial habitat in the expansive Nevadaplano uplands during a long period when temperate zone climates elsewhere throughout North America were subtropical. The pre–Sierra Nevada ranges did not form a hydrologic divide as the Sierra Nevada do now, nor were they the

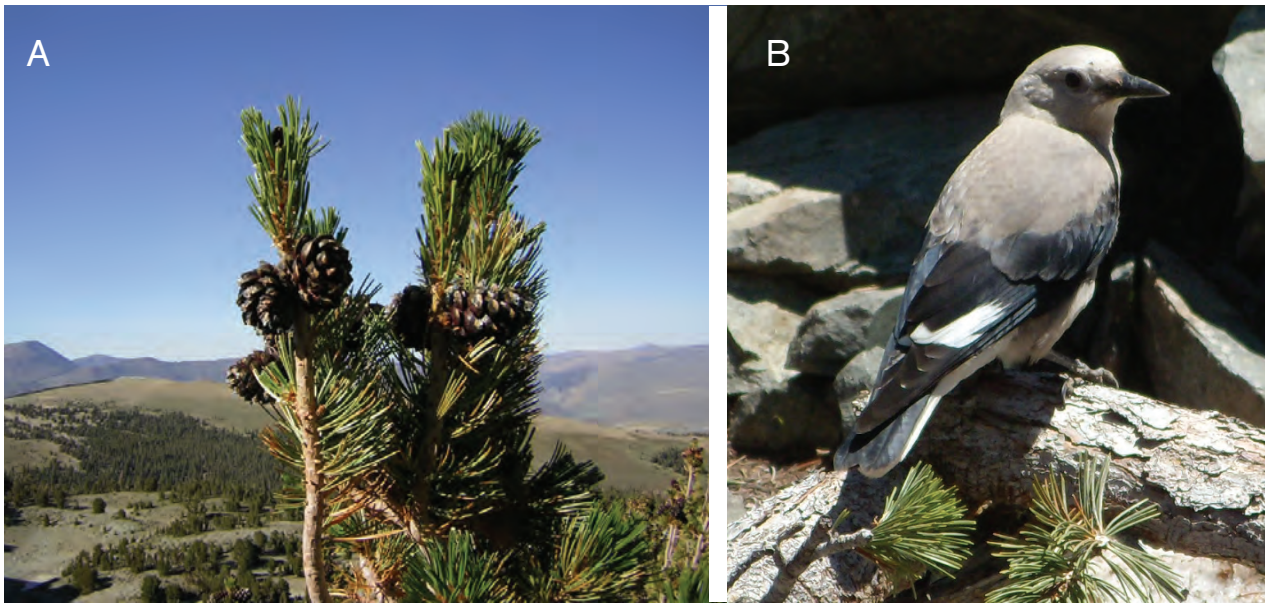


FIGURE 28.10 Coadaptations between (A) whitebark pine cone and (B) Clark's nutcracker ensure that the birds have sustenance and that pines are planted. Photos: Constance Millar.

highest summits of this expansive upland region. The elevations of many ranges within this Nevadaplano, including the pre-Sierran mountains, had summits estimated to extend more than 3,000 meters.

Fossil flora that date to the middle Tertiary from this region, now located mostly in Nevada but indicative of California, include a great diversity of gymnosperm and angiosperm taxa, including subalpine species with affiliations to bristlecone pine, foxtail pine, lodgepole pine, western white pine, Alaska yellow-cedar, and mountain hemlock (Millar 1996). These floras, however, do not reflect ecological stratification as do present upland communities, as they included in single associations a mix of diverse montane-adapted species as well as conifer taxa now occurring only in lower montane and coastal types. In addition, many summer/wet-adapted angiosperm species that grow now in southeast North America and even in subtropical climates co-occurred in these upland sites. The diversity and lack of zonation of these Tertiary floras is interpreted to indicate, despite the high elevations, that climates were relatively warm and wet with precipitation distributed year-round.

Subsequent changing dynamics of plate boundaries and new tectonic activity associated with the development of the San Andreas, Southern California Shear, and Walker Lane fault zones initiated massive changes to the topography and climate of the region. These in turn triggered drastic changes in the vegetation of the mountains of California and Nevada. By about ten million years ago, extensional forces led to the development of the Great Basin, with its more than three hundred fault-blocked mountains and basins and internal drainage, as well as to development of the present-day Sierra Nevada with its increasing significance as a major hydrologic divide. These tectonic changes catalyzed orographic rainshadow effects leading to vegetation zonation both in elevation, introducing modern subalpine ecosystems, and from the Pacific coast inland (i.e., longitudinally). The California Mediterranean-climate regime grew in dominance, exerting strong selection pressures for traits enhancing survival of increasingly long, dry summers. Truly arid environments (desert) and alpine ecosystems began to emerge for the first this time in the California/Nevada region as well. These changes triggered major extirpations of summer/wet-adapted species. Many montane conifers and cool/mesic-adapted plant species that had lived for millennia on the Nevadaplano persisted in the present-day Sierra Nevada and in northwest California while disappearing from inland Great Basin regions as climates dried.

The present-day diversity of subalpine conifers was in place in the California high mountain regions at the onset of the Quaternary, two million years ago (Millar and Woolfenden 1999). The roller-coaster climate changes that ensued brought as many as forty cycles of cold glacial and warm interglacial conditions to North America, with maximum temperature differences in the western mountains of as much as 8°C to 10°C (Millar 2012). Abrupt and gradual changes in climates catalyzed significant movements of subalpine conifers—downslope to 2,600 meters in the Sierra Nevada during glacials when ice caps covered the mountains and upslope during interglacials such as the present Holocene.

The maximum altitudinal response of subalpine species to glacial-interglacial cycles was approximately 1,000 meters. During the warmest intervals within interglacials, such as the mid-Holocene interval (four thousand to eight thousand years ago), treeline ascended about 100 meters higher than at present in the Sierra Nevada (Anderson 1990, Hallett and Anderson 2010) and as much as 150 meters in the White Mountains (LaMarche 1973). Compositions and associations of subalpine communities also changed between glacials and interglacials with changing taxonomic diversities, species abundances, population expansion and contractions (into important refugial areas), and changes in disturbance regimes (e.g., Mohr et al. 2000, Anderson 1990, Hallett and Anderson 2010) but with no apparent extirpations or extinctions (Millar and Woolfenden 1999). During the latter period of the last glacial period, 13,000 to 11,500 years ago, giant sequoia (*Sequiadendron giganteum*) moved far

above its current range in the Sierra Nevada as recorded in a sediment core at 2,863 meters from East Lake. Its floristic associates included subalpine taxa and indicated that giant sequoia was part of the subalpine ecosystem at the time (Power 1998).

Changes in the fire regimes of mountain ecosystems across fluctuating glacials and interglacials mirrored changes in mountain climate and vegetation composition and structure (Skinner and Chang 1996). Where fire history studies have been done in the subalpine zones of California, they show increasing fire severity and extent when climate was wet enough to support dense forest growth, and reduced fire effects during dry intervals—both cold and warm—when subalpine forests became sparser. In the central Sierra Nevada near Mammoth Lakes during the end of the last glacial period, when climates were cold and dry and subalpine pine and mountain chaparral species remained sparse as they shifted upslope into deglaciated areas, fires were few and low severity (Hallett and Anderson 2010). After eight thousand years ago, as mountain hemlock moved into the region and dense forests formed, fire became more frequent and intense. During the warm and dry mid-Holocene, subalpine forests again became sparser and fire was less important. During the neoglacial dry periods starting approximately four thousand years ago, fire was also of minor importance in the subalpine forests. After about twelve hundred years ago, fires in the subalpine forests became increasingly synchronized with inferred drought, and fire activity in the high Sierra is interpreted to have been highly sensitive to dynamics of the El Niño–Southern Oscillation (Hallett and Anderson 2010).

In the Klamath Mountains fire history reconstructed over the past 15,500 years shows a slightly different pattern of changes in forest composition and density and fire relationships (Mohr et al. 2000). Before the end of the last glacial period, subalpine forests were open and parklike, dominated by scattered pines and firs and marked by low fire frequencies. Forest density increased in the latest Pleistocene and shifted to western white pine, lodgepole, and firs, yet fire frequency remained low during a period interpreted as cold and wet. During the middle Holocene, conditions became warm and dry with increasing fire frequencies. Similar, high frequencies were inferred at the onset of the neoglacial period four thousand years ago as hemlock increased in abundance, displacing pines and oaks. Elsewhere in the Klamath region, fire-scar records of the last four hundred years in the Scott Mountains show that fire return intervals ranged from one to seventy-six years with averages of about seven years (Skinner 2003). Most fires, however, scarred only one sampled tree, suggesting that although fires were frequent in subalpine forests, most were probably small and low-intensity.

In the southern Cascades, Bekker and Taylor (2001) found long fire return intervals over the past 350 years in subalpine forests of the Thousand Lake Wilderness. Fire regimes varied with forest composition, elevation, and inferred soil moisture, and fire return intervals ranged from twenty to thirty-seven years for lodgepole pine forests and twenty to forty-seven years for mountain hemlock types. Fires occurred mostly in the late growing season and dormant season (Bekker and Taylor 2001). Similar patterns marked historical western white pine subalpine forests over the last 350 years at Mount Lassen (Taylor 2001). In both regions of the southern Cascades, marked declines in fire frequency took place in the twentieth century.

## Ecosystem Dynamics

### Wildfire

By and large, fire is less important in subalpine forests than in forests at lower elevations. Landscape-scale fires are rare because high-elevation landscapes form a mosaic of individual trees; tree stands; upland shrub and herbaceous communities including meadows, wetlands, and riparian corridors; rock outcrops; talus; avalanche tracks; creeks; and lakes. Fuel buildup is usually slight in these extreme conditions with short growing seasons, limiting opportunities for fire to spread. In open whitebark pine woodlands and even krummholz communities, lightning ignitions can cause single trees to explode and burn, but fires that do start from these points tend to smolder at ground level and extend only to the edges of patches of fuel accumulation.

Where stand densities increase to the point of canopy closure, however, crown fires and fires of high intensity can occur in subalpine ecosystems. Even in these forests, such as lodgepole pine and mountain hemlock types, deep snowpacks and saturated soils from spring snowmelt usually restrict fires to the late growing season or dormant season (Skinner et al. 2006). On some shallow substrates with poor fertility, as in the Klamath Mountains and southern Cascade Range, fire behavior influences the persistence and dominance of montane shrub communities (e.g., *Arctostaphylos nevadensis*, *Chrysolepis sempervirens, Quercus vaccinifolia,* and *Ceanothus* spp.). Once trees are removed by crown fire and shrub species regenerate into burns, they can claim dominance over time because their resinous, highly flammable canopies increase fire frequencies and they sprout or seed into burned areas more successfully and rapidly than conifers (Pinder et al. 1997).

Where investigated, fire regimes in the denser subalpine forest types were characterized by long return intervals in the presettlement period (1700–1800s) (van de Water and Safford 2011). The longest fire interval reported, 133 years, is for typical subalpine forest types that include whitebark, bristlecone, limber and/or foxtail pine, and mixed stands containing those species plus western white pine, lodgepole pine, and mountain hemlock. Fire return interval for Sierra juniper forests, which almost always occur as sparse stands on rocky substrates, was eighty-three years. Western white pine and curl-leaf mountain mahogany forest fire return intervals were about fifty years, and lodgepole pine forest intervals were thirty-seven years. Somewhat unexpectedly given their high soil moistures, fire return intervals for aspen were shortest of all subalpine types at nineteen years (van de Water and Safford 2011).

Presettlement spatial patterns of fires in subalpine environments are difficult to assess and, except at the lower ecosystem border or in special conditions, mostly influence local structure and composition (Caprio and Graber 2000, Meyer 2013). Mean fire size in the southern Cascade subalpine elevations was estimated as 405 hectares for lodgepole pine forests and 140 hectares for red-fir/mountain hemlock, with mean size at Mount Lassen of 176 hectares. Studies in the Tahoe Basin indicate mostly small and patchy presettlement fires, with evidence that some areas burned severely enough to produce even-aged cohorts (Scholl and Taylor 2006). During the later twentieth and twenty-first century, observations of uncontrolled wildfires in subalpine forests of California indicate much smaller spatial extent than these presettlement estimates, with most less than 4 hectares (Meyer 2013). Even with a slight increase in fire size observed during the first

decade of the twenty-first century (Miller et al. 2009), the small sizes and long return intervals of fire in subalpine forests underscore the minor and local effects that fires have on controlling ecosystem structure and function.

## Insects and Pathogens

Cold temperatures, low humidities, rocky environments, and wide spacing of trees limit insects and disease-causing organisms to minor roles in subalpine forests. Although insects that damage or kill trees (e.g., defoliators and bark beetles) occur in forests at those elevations, they rarely reach outbreak conditions (but see Brunelle et al. 2008 for the Rocky Mountains). Their effects, as observed over the past century, have been to influence background mortality. In the latest twentieth and early twenty-first century, however, tree mortality related to insect and disease outbreaks appears to have vastly increased in subalpine forests of western North America. Investigation of these changes in bark beetle activities point to warming temperatures, which allow the insects to overwinter and in some locations to complete two generations each year (Logan and Powell 2001, 2007). In association with periodic drought, and in conditions where soil moisture stress is high, bark beetle outbreaks, primarily mountain pine beetle (*Dendroctonus ponderosae*) on whitebark pine, have been at record high levels.

California's subalpine forests have so far resisted landscape-scale mortality from bark beetles (Millar et al. 2012). They have experienced, however, population-scale outbreaks and mortality events in the late twentieth century and early twenty-first century on limber pine (*Pinus flexilis*) and whitebark pine (Millar, Westfall et al. 2007; Millar et al. 2012). Increasing background temperatures, multiyear drought, and low soil moisture (low CWD) are implicated in both cases. In both outbreaks only stands at low elevations for each species' range, northerly aspects, and young, dense, fast-growing stands were affected. Further, the degree of forest mortality increased latitudinally, from the southern Sierra Nevada to the Warner Mountains, reflecting improved conditions for insects as precipitation and stand densities increased (Millar et al. 2012).

Limitations to spread of beetle outbreak in California are likely related to endogenous factors (insect competitor and prey relations) but also to environmental context of the forests. California's historically warm and dry Mediterranean climate both preadapts forests to arid conditions and influences bark beetle behavior in ways quite different from situations in the Pacific Northwest and Rocky Mountains (Bentz et al. 2014). In Californian beetle populations, due to historic adaptation to warm, dry climates, the trend toward O T N SM (two generations per year) is less common, and will require greater temperature increases to evolve, than elsewhere.

The major disease-causing species in current subalpine forests of western North America is the invasive white pine blister rust (WPBR), caused by the fungus *Cronartium ribicola*. This fungus was introduced on nursery stock more than one hundred years ago and has since been spreading on five-needled pines (subgenus *Strobus*) throughout North American forests (Smith 1996). The high-elevation pine species are highly susceptible, but remote locations and unfavorable climate conditions have until recently limited effects on subalpine forests. In recent decades, WPBR has invaded subalpine forests in the Cascade Range, inland mountains, and Rocky Mountains. The rust has caused extensive mortality on whitebark pine, and in 2011 the U.S. Fish and Wildlife Service granted the species protection under the Endangered Species Act (USFWS 2011). California subalpine forests have so far experienced only localized mortality from WPBR (Maloney and Dunlap 2007, Dunlap 2012) in some parts of the western Sierra Nevada, Mount Rose, and at scattered, low levels elsewhere. WPBR has caused extensive damage to lower-elevation white pine species, especially sugar pine and western white pine.

A suite of other insects and pathogens cause minor damage and localized mortality on subalpine forests. Dwarf mistletoes (*Arceuthobium* spp.), a group of vascular plants that live aerially on conifer branches and stems, cause branch death and brooming on the subalpine pines and many other species (Hawksworth et al. 1996). Dwarf mistletoe is not common in subalpine forests but does occur on limber pine forests of the eastern Sierra Nevada (Millar, Westfall et al. 2007) and whitebark pine forests in northern California, where it appears to exacerbate outbreaks of mountain pine beetle.

In the first decade of the 2000s, occasional individual or clumps of bristlecone pine trees in the subalpine forests of the White Mountains were observed dying or experiencing branch dieback. These sporadic effects seem most likely to be caused by black stain fungus (*Leptographium wageneri*), a native species not known or expected to cause widespread damage to the bristlecone pine forests (B. Bulaon, U.S. Forest Service, pers. comm.). No mountain pine beetle incidences have been known in bristlecone pine forests of California to date. Native red turpentine beetle (*Dendroctonus valens*) has been found on bristlecone pine in the White Mountains but is mostly a secondary invader that forages on dying trees and dead wood.

## Biogeochemical Cycling and Hydrology

The biologically rich subalpine and alpine basins of the Sierra Nevada have had a long history of descriptive study, with much of what is known about the hydrology and biogeochemical cycling coming from long-term studies of the subalpine Emerald Lake basin in Sequoia National Park (see Chapter 32, "Lakes"). Many of the hydrologic studies in the Sierra Nevada centered on assessing and monitoring patterns of seasonal and interannual change across large elevation gradients from subalpine and alpine watersheds to the San Joaquin Valley. Recent studies have shown that the fluctuations of selected rivers draining the Sierra Nevada and Rocky Mountains are highly correlated each spring, indicating an organized, regional-scale signal of snowmelt initiation and runoff (Cayan et al. 2001). These basins integrate the effects of broad ranges of aspect and elevation. Hydrologic studies in subalpine watersheds have focused on understanding streamflows, water balance, and the association of snowmelt and runoff with solute chemistry (Kattelmann and Elder 1991, Williams and Melack 1991 Meixner and Bales 2003, Meixner et al. 2004). Other studies have quantified the components of old water stored in the watershed from the previous year (10–20%) compared to new water from current snowmelt (80–100%) (Huth et al. 2004).

The Emerald Lake watershed provides a case study of biogeochemical cycles of nitrogen in a subalpine watershed (Tonnessen 2001). The soil pool of organic nitrogen was about ten times nitrogen storage in litter and biomass, and assimilation by vegetation was balanced by the release of nitrogen from litter decay, soil mineralization, and nitrification (Williams et al.

TABLE 28.4
Biomass of plant material in the 120 hectare Emerald Lake watershed, Sequoia National Park

| Community type | Basin coverage (ha) | Aboveground biomass (kg ha-1) | Belowground biomass | Litter biomass |
|---|---|---|---|---|
| Willow | 8.55 | 965 | 567 | 439 |
| Mesic shrub | 0.73 | 26.5 | 42.4 | 29.5 |
| Mesic crevice | 15.15 | 36.9 | 58.8 | 40.0 |
| Wet meadow | 4.14 | 130 | 999 | 47.3 |
| Xeric crevice | 13.40 | 6.0 | 33 | 48.7 |
| Dry meadow | 7.73 | 62.9 | 361 | 49.7 |
| Fellfield | 0.84 | 0.4 | 2.1 | 0.3 |
| Colluvium | 3.44 | 1.5 | 8.5 | 1.2 |
| Trees | ND | 16,000 | 5,630 | 37.7 |
| TOTAL | | **17,200** | **7710** | **694** |

SOURCE: Adapted from Rundel et al. 1989. See Rundel et al. 2009 for a description of communities.

1995, Wolford et al. 1996, Wolford and Bales 1996, Meixner and Bales 2003, Sickman et al. 2001, 2003). Trees make up about 90% of the aboveground biomass and nitrogen in plant tissue in the watershed, but only about three-fourths of belowground biomass and half of belowground nitrogen (Table 28.4). As much as 90% of annual wet deposition of nitrogen was stored in the seasonal snowpack, and both nitrate and ammonium ions were released in a strong ionic pulse with the first fraction of spring snowmelt. This nitrate release was evident in a small but significant pulse in streamwater concentration with early snowmelt. However, almost all of the ammonium input from both wet and dry deposition was retained in the watershed by biological assimilation (Williams et al. 1995).

## Ecosystem Services

### Snowpack and Water Supply

By far the greatest ecosystem service provided by high mountain watersheds is their capacity for storage and delivery of critical water supply for downstream agricultural, industrial, urban use. Subalpine hydrologic reserves, stored primarily as winter snowpack, provide water both to the west in California and to the increasingly urbanized eastern front of the Sierra Nevada/Carson Ranges. Snowpack retention is an extremely important function of subalpine forests given the long Mediterranean summer drought regime of the California climate. Density of trees and canopy cover are important determinants in the amount of snow that develops on the forest floor and also on the retention into spring (Raleigh et al. 2013, Lundquist et al. 2014). Although many subalpine forests are sparse, those with moderate density provide the greatest snowpack retention of all forest types.

In addition to forest canopy and density, many factors affect the stability and hydrology of high-elevation environments. Subalpine ecosystems are sensitive to small changes in growing season conditions of temperature and water availability, and their stability impacts hydrological conditions of lowland ecosystems (Bales et al. 2006, Trujillo et al. 2012). Given the high interannual variability of precipitation in the California region, and corollary differences in snowpack depth, water supplies in the critical spring forecast season vary drastically (Figure 28.11). In that precipitation and snowpack vary greatly from year to year as a result of natural forcing (McCabe and Dettinger 1999), further impacts on these sensitive functions have large cascading impacts. The most significant effect on snowpack and water supply is from warming temperatures as a result of anthropogenic forcing on climate (Bonfils et al. 2008). With snowpack amount declining and snowmelt advancing, the ability to provide water to increasingly hot and arid urban users during a prolonging summer drought will be severely challenged (Stewart et al. 2005). The many skeletal and oligotrophic subalpine watersheds of the Sierra Nevada also have the potential to be strongly affected by atmospheric nitrogen deposition and acidification associated with the expanding urbanization of the San Joaquin Valley (Sickman, Leydecker et al. 2003).

### Biodiversity

Subalpine ecosystems in California support important and distinct biodiversity. In addition to the tree diversity of subalpine forest ecosystems, many thousands of vascular and nonvascular plant species grow in the diverse habitats of California's high elevations. The Jepson eFlora lists taxa by floristic subprovinces, from which estimates for the number of plant taxa in several subalpine regions can be derived. Of more than 6,500 plant taxa in California as a whole, these include 1,710 species in the high North Coast Ranges, 1,860 species in the high Cascades, and 2,740 species in the Sierra Nevada (Jepson eFlora 2014). Although these numbers are only rough estimation of actual subalpine zone diversity, they

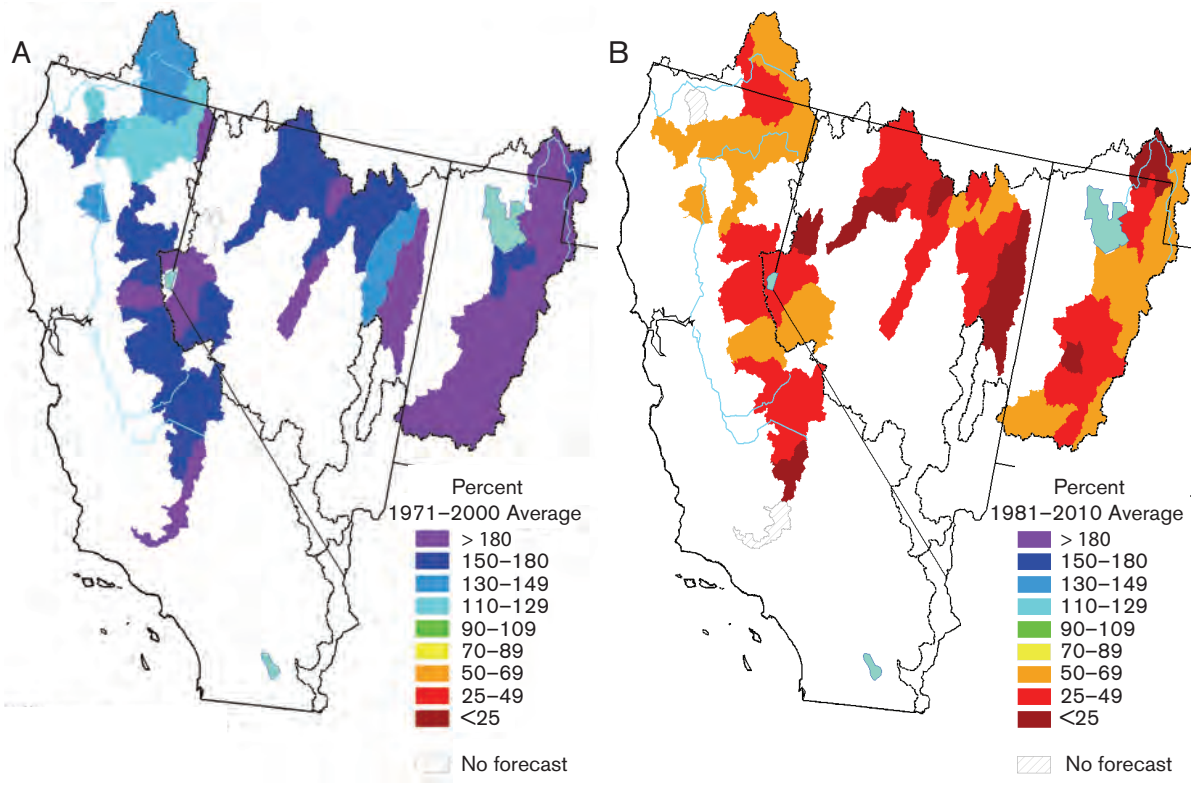


FIGURE 28.11 Great Basin and major water supply basins in California showing contrasting water years of wet (A, 2010–2011) and dry (B, 2012–2013). Source: From spring and summer streamflow forecasts by the U.S. Department of Agriculture Natural Resources Conservation Service (NRCS), National Water and Climate Center.

exemplify the high overall diversity and trend of increasing diversity southward. Wetlands and wet meadows support the highest plant biodiversity of all subalpine communities (see Chapter 31, "Wetlands"; Weixelman et al. 2011), including taxa with adaptations to high-elevation extreme temperatures, freeze-thaw conditions, extreme soil moisture variability, and heavy snow cover.

Meadows, riparian habitats, and other wetlands are especially important in the dry mountains of California's Great Basin, southern Sierra Nevada, and southern California, where harsh and arid upland environments limit plant diversity and wetlands become important hot spots for vegetation. Wetlands are critical habitat for the mammal species that use subalpine habitats. Bird diversity (Beedy and Pandolfino 2013) and arthropod diversity (Holmquist et al. 2011) of subalpine elevations also depend on and concentrate in wetlands. With diminishing snowpacks and increasingly earlier snowmelt, wet environments are likely to dry earlier, and many will convert to nonwetland types. An important exception are wetlands associated with springs resistant to warming, such as those in the forefields of rock glaciers and many talus fields (Millar, Westfall, Evenden et al. 2014).

## Cool Refugia under Warming Climates

Generalized projections for future subalpine ecosystems under global warming conclude that subalpine taxa will shift continuously upslope until they run out of area at mountain summits and mostly disappear (e.g., Hayhoe et al. 2004). While this is possible in many decades to centuries, mountain environments are highly heterogeneous and present great physical diversity across small distances. This patchiness creates escape avenues other than upslope. Patchiness occurs across slope, aspect, substrate, elevation, and microclimate heterogeneity (Lundquist and Cayan 2007). Paleoecological research in mountain regions worldwide indicates that mountain environments, when and where not covered by ice caps or valley glaciers, provide refugial habitats where species persist during unfavorable climates (e.g., Ravazzi 2001, Bennett and Provan 2008, Mitton et al. 2000). As climates ameliorate, refugia become highly important sources of diversity for emigration and reestablishment of former as well as new habitats (Dobrowski 2011). Coupled environments, such as talus fields and their wetland forefields, that already support high diversities of cool-adapted plant, mammal, and arthropod species could become increasingly important in the future as refugia in California's mountains (Millar, Westfall, Evenden et al. 2014).

## Recreation, Scientific, and Commodity Services

Subalpine forests throughout California are widely cherished for developed (e.g., ski areas) as well as dispersed uses (e.g., hiking, camping, hunting, fishing). Much of the subalpine forest landscape is contained in wilderness designation, which provides long-term protection of little-disturbed ecosystems for societal enjoyment. As California's population becomes increasingly urbanized (Duane 1996a), demand for access to both rustic and wild landscapes in California's mountains as retreat for personal refreshment, recreation,

and exercise similarly heightens (Duane 1996b). Expansion of the urban front of the eastern Sierra Nevada and Carson Range in Nevada heightens demand for recreation in the subalpine forest ecosystems of that region.

Protected subalpine environments also provide important services as ecological archives for scientific research. In that much of California's landscapes elsewhere are highly modified by direct human development and use, subalpine ecosystems afford opportunity to study natural composition, structure, and function. The rich archives stored in long-lived trees and preserved deadwood, such as bristlecone pine, have served the international science community. Finally, with much of the subalpine zone in wilderness or other limited-use designations, little extractive and commodity services are available under present policy. Whereas mining of gold, silver, and tungsten, for example, have been important historically in many high elevations of California, and in some regions continuing into the mid-twentieth century, only limited commercial requests for mining access occur at present.

## Agents of Anthropogenic Change

### Climate Change

Because many lineages of subalpine forest species evolved more than thirty million years ago, taxa that live now in the California mountains have been shaped by forces of climate variation and change throughout their evolution. Mechanisms for adapting to climate change include natural selection (changes in genetic composition), migration (shifts in geography), and ecological accommodation (reassembly of abundances and species diversities) (Millar and Brubaker 2006). Subalpine forests in California over the past twenty million years have experienced drastic changes in species diversity and distribution (Millar 1996, 2012). Over the past two million years (the Quaternary period), however, the diversity of conifer species of the subalpine zone has mostly remained constant within respective mountain regions, with only one extirpation known from the early to mid-Quaternary (a species of spruce [*Picea* sp.], from Tahoe Basin and Owens Valley) (Adam 1973, Litwin et al. 1997). By contrast, the distribution and extent of subalpine species have changed drastically in response to past changes in climate (Millar and Woolfenden 1999).

Added to the list of factors that create changes in climate are anthropogenic forces—most significantly, emissions of greenhouse gases. While human controls on the climate system began millennia ago with the rise of land-clearing, forest burning, and agriculture (Ruddiman 2003), the rate of emissions has accelerated drastically in the industrial era. The impact of anthropogenic forcing is increasingly a primary control on climate; the degree to which it will interact in the future with natural forcing remains poorly understood.

In California, as elsewhere, major changes in climate have been recorded over the past hundred years. Recent climate trends indicate that the mean annual and monthly temperatures have increased in the higher elevations (more than 2,200 meters) of the Sierra Nevada, with as much about 1°C increase over the past century (Moritz et al. 2008) and accelerating rises within the past thirty years (Edwards and Redmond 2011, Moser et al. 2009). Changes in late twentieth-century temperatures in mountain regions of the western United States are attributed primarily to anthropogenic forces rather than natural climate variability (Bonfils et al. 2008). Further, the annual number of days with below-freezing temperatures at higher elevations has declined, resulting in a 40–80% decrease in spring snowpack over the last fifty years in the northern and central Sierra Nevada and onset of spring advancing by two to four days per decade (Cayan et al. 2001, Lundquist et al. 2004, Moser et al. 2009). Snowpack in the southern Sierra Nevada has increased 30–100% over the same period, due partly to the higher-elevation terrain of the region. Precipitation has remained stable or steadily increased over the past several decades in the higher elevations of the California cordillera (Edwards and Redmond 2011, Safford et al. 2012).

Significant effects on subalpine forests are anticipated as a result of future changes in climate (Hayhoe et al. 2004). Most projections anticipate upslope movements of plants with warming temperatures. For subalpine forests where diminishing land area exists at increasing elevation, these projections translate to up to 90% losses of the ecosystem under extreme scenarios (Hayhoe et a. 2004). Early observations, however, are not (yet) revealing significant upslope movement. Rather, twentieth-century changes in subalpine forests have been characterized by increases in forest density (Dolanc et al. 2013), changes in subalpine tree growth and form (Millar et al. 2004), type conversions within the subalpine zone (Millar et al. 2004), changes in forest insect outbreaks and mortality (Millar, Westfall et al. 2007, Millar et al. 2012), and even downslope movement (Crimmins 2011).

### Regional Environmental Changes

Remoteness, federal ownership, and management designation limit anthropogenic effects on subalpine forest ecosystems in California. Much subalpine forest is designated as federal Wilderness Areas, which enforces roadless conditions and minimal human impact in general. Outside of federal Wilderness Areas, subalpine forests occur primarily within National Forests and National Parks, where management commonly emphasizes primitive and undeveloped uses with only localized development.

Aside from the effects of greenhouse gas emissions, the most widespread anthropogenic stressor on subalpine forests is atmospheric contamination (Burley and Bytnerowicz 2011, Bytnerowicz et al. 2013; see Chapter 7, "Atmospheric Chemistry"). In California, ozone ($O_3$) is the main phytotoxic air pollutant for plants at ambient levels and derives from transportation and industrial sources. While usually found near urban centers, elevated levels of ozone have been recorded in remote locations, with concentration increasing above 2,000 meters. These include subalpine ecosystem elevations in the central Sierra Nevada, from Lake Tahoe to the Mammoth Lakes area, and in the White Mountains (Burley and Bytnerowicz 2011, Bytnerowicz et al. 2013). Ozone induces a mottled condition on foliage and, more importantly, contributes to tree stress.

Although timber harvest occurred prior to current protections in a few of California's subalpine forests, logging is mostly limited now to hazard tree removal, trail or road construction and maintenance, management of recreation facilities, and fire suppression and control. Highways traverse subalpine forests in limited areas, and some dirt roads also have been built in areas outside federal Wilderness Areas. Both affect only adjacent tree stands, although in some locations where salt is used for de-icing, roadside trees are damaged or killed. Of greater impact are sediment effects to subalpine

watersheds where roads occur, including impacts on aquatic biota, erosion, and downstream water quality and supply. Historical mining impacts are highly localized and mostly occur in the Great Basin ranges, although mining exploration was a widespread catalyst for road building in the early twentieth century, and many existing roads trace to mining origins.

Livestock grazing historically was a widespread and dominant agent of change in high-elevation regions of California. By the mid-1800s, millions of sheep were grazed without regulation in the high Sierra Nevada, White Mountains, and other ranges of the state. The heavy summer grazing of high Sierran meadows began when the record precipitation of 1861–1862 was followed by major droughts in 1862–1863 and 1863–1864, forcing herders to seek higher-elevation meadows. This led to the annual practice of summer grazing in the mountains, with associated overstocking and overgrazing of high mountain meadows. All of the major montane and subalpine meadows in the Sierra Nevada were heavily grazed each summer by flocks in search of pasture with significant overstocking (Ratliff 1985), and the abundance of sheep is reflected in John Muir's reference to them as "hoofed locusts." Many graphic accounts describe the damage caused by sheep herding in this era (Odion et al. 1988, Dilsaver and Tweed 1990, McKelvey and Johnston 1992, Kinney 1996). Most heavily impacted were the alpine zone and subalpine meadows, but effects on subalpine forests were likely significant as well because sheep were trailed through these forests to reach pastures. Impacts include changes in meadow and upland biodiversity, introduction of invasive species, soil compaction and resulting changes in erosion, water-table depth, and runoff. Because sheep grazing was so widespread, leaving few known ungrazed areas (i.e., control areas), legacy impacts from the early era are difficult to assess.

Sheep and cattle grazing were eliminated from the National Parks in the early to mid- twentieth century, and high-elevation livestock allotments on other federal land (primarily U.S. Forest Service) increasingly are being closed. Closures are intended to reduce disease transmission to Sierra Nevada bighorn sheep (in the case of domestic sheep allotments) and for protection of fragile upland ecosystems generally. Allotments still occur, however, in many subalpine forest ecosystems of eastern California. Damage, including plant trampling and soil disruption, is often considerable in meadows and riparian forests in areas such as the northern White Mountains (Holmquist et al. 2013).

Exotic invasive plant species exert significant local but limited landscape effects in subalpine forests. In California, as elsewhere, abundance of invasive plant species tend to decline as elevations increase (Alexander et al. 2011, Rundel and Keeley 2014). At high elevations, impacts from invasive species occur within meadows and wetlands, riparian areas, and aquatic ecosystems associated with subalpine forests. Wet meadows, for instance, have a relatively large list of high-impact invasive species (Stillwater Sciences 2012). Despite a long history of grazing, relatively few non-native species have established in subalpine forests of California, indicating that environmental stress rather than propagule dispersal has been the major limiting factor. However, species invasions are a dynamic process, and new, non-native introductions from other high mountain regions of the world present a possible future concern. On dry uplands but in limited regions cheat grass (*Bromus tectorum*) can invade the subalpine zone. This widespread Mediterranean-origin invasive grass mainly invades lower elevations in Great Basin ecosystems following grazing and fire. Once established, it is virtually impossible to control and causes significant changes in ecosystem composition, structure, and function. Regeneration of native subalpine conifers, especially lodgepole pine, into meadows is often considered an invasion, although at high elevations this appears to be primarily a response to climate change (Millar et al. 2004). In lake ecosystems of the subalpine zone, invasive species are a significant factor controlling native biodiversity and ecological functioning (see also Chapter 32, "Lakes").

Another common species, until recently considered exotic in the high elevations of California with status still uncertain, is the North American beaver (*Castor canadensis*). Known to have occurred in historical times at low elevations of the Central Valley and Owens Valley, beavers were not observed as native by the early naturalists, including the intrepid George Grinnell, above 300 meters through the early 1900s (Tappe 1942, Hensley 1946, Busher 1987). Beavers were widely introduced for fur trapping to lakes and streams of high elevations in California, where they have established and spread. Recent evidence from an excavated dam in the North Fork Feather River Watershed—60 miles north of Truckee, California, at 1,637 meters—showed radiocarbon dates prior to the historical regulation time, namely 580 CE and 1730 CE (James and Lanman 2012). Subsequent documentation from historical records and ethnography argues that beavers were native to other parts of the high Sierra as well (Lanman et al. 2012), although physical evidence has not been recovered elsewhere and their status in high elevations of the central and southern Sierra Nevada remains controversial. As environmental engineers, beavers vastly transform watersheds, damming streams, altering streamflows and water quality, creating ponds, submerging riparian and valley forests, and harvesting aspens and other hardwoods. Beavers and their effects are widespread in the high valleys of the eastern Sierra Nevada, where they episodically expand to new canyon territories. In other regions where beavers are known to be native, such as the Utah mountains, engineering capacities of beavers have been harnessed through resource management projects to maintain, restore, and augment water in increasingly dry upland watersheds (GCT 2013).

Recreation is a common use of subalpine forests in California, although it is generally limited to regions along trails, lakes, and campsites. As such, effects on forests are generally localized, and include soil trampling, fuelwood cutting, and introduction of invasive species via cars, boots, and improper hygiene. This might include the introduction to high-elevation waters of giardia bacteria (*Giardia intestinalis*), which causes intestinal disorders for humans and other mammals. Localized effects on subalpine forests occur around developed ski areas, which are almost exclusively located in the subalpine zone. At those locations tree harvest, snow-making, de-icing, road-building, groundwater pumping, and other infrastructure developments can alter both forest structure and function and also affect watershed conditions. Many ski resorts increasingly promote all-season recreation, expanding impacts on the local forests and watersheds. One Sierran ski resort, June Mountain Ski Area, was strongly affected by the 2006–2012 drought and bark beetle outbreak. The event caused high mortality in whitebark pine forests throughout the resort, decreasing snowpack retention, wind buffering, visual quality, and safety of recreationists. Dead trees are being harvested for safety and resource management.

The most widespread effect of recreation in and near California subalpine forests is as an ignition source. Wildfires left unattended and ignitions along highways cause fires in both

subalpine forest and at lower elevations. The Rim Fire of 2013, for instance, was the third largest wildfire in California history and the largest recorded in the Sierra Nevada. Ignited by an illegal hunter's campfire near the south-central border of Yosemite National Park, the fire eventually spread over 1,041.31 square kilometers and consumed large areas of subalpine forest on the west slope of the Sierra Nevada.

## Management Issues and Climate Adaptation

In much of the subalpine forest landscape, resource management primarily aims to minimize impacts from human use and restore and maintain natural conditions. As recreation increased in subalpine ecosystems over the twentieth century, restrictions were put in place to protect natural features (Duane 1996b). In lands with limited-use designation, these included restrictions on group sizes, type of uses, road decommissioning, trail improvement to protect resources, campsite restrictions, regulations to protect water quality and watershed conditions, and restoration of degraded habitats such as overused camps along lakeshores and streamsides. Around developments such as ski resorts, federal special-use permit conditions focus on protection of impacts from resort development and maintenance of ecosystem health on the surrounding lands. Similarly, recent evaluations of high-elevation watersheds in canyons containing reservoirs have been conducted throughout California's mountain in response to updating FERC (Federal Energy Regulatory Commission) permit conditions. Renewal of these permits included much stronger environmental protection clauses for subalpine forests than defined in the original permits, often issued early in the twentieth century, and focused on comprehensive watershed health and ecosystem restoration and sustainability.

Fire management is less of a resource focus than in lower montane forests. Fire policy in federal Wilderness Areas and similar designations aims primarily to maintain natural process and protect human lives and infrastructure. In many cases naturally ignited fires that do not threaten wilderness values are allowed to burn with minimal control or management. As mountain hemlock and lodgepole pine forests are the types most likely to burn at large scales in California's subalpine zone, fire suppression efforts most often are directed toward those forest ecosystems.

Control of invasive species has been a major focus of resource management in high-elevation habitats. Efforts have primarily addressed invasive species in aquatic environments, where projects to remove exotic fish and restore native aquatic fauna and riparian vegetation have been under way for several decades, especially in the Sierra Nevada (see Chapter 13, "Biological Invasions"). Early progress was hopeful for widespread restoration, but in recent years the spread and devastation caused by chytrid fungus on amphibian species has imposed formidable challenges (Bradford et al. 1994, Fellers et al. 2001). In subalpine meadows, restoration of meadow hydrology and biodiversity has been the focus of aggressive resource management (e.g., "plug and pond"), especially in the Tahoe Basin of the Sierra Nevada. Applying these techniques widely through high-elevation meadows, with a focus on removing invasives and restoring wetland functions, is the goal of current projects (e.g., CIPC 2014). Many of these efforts are increasingly urgent given the pressure exerted by changing climates. Innovative new approaches to increase resilience of subalpine meadows to warming climates are being developed to retain wetland condition rather than allow meadows to convert to dry or nonmeadow types (AR 2014, WCS 2014). Finally, management of pack animals in high-elevation wetlands is an ongoing concern. Federal Wilderness plans limit domestic packstock use in subalpine and alpine environments; these limits have recently been revised to better protect fragile ecosystems.

### Climate Adaptation

Climate-adaptation efforts for subalpine forest ecosystems have focused to date on conducting vulnerability assessments, evaluating risks, developing priorities, and outlining climate-adaptation strategies for the near future (e.g., Morelli et al. 2012) or midterm horizon (e.g., USDA 2013). For federally administered lands, these planning efforts follow newly developed guidance for climate adaptation (Peterson et al. 2011, USDA 2008, USDI 2010) that include the following steps: (1) review basic climate change science and integrate that understanding with knowledge of local resource conditions and issues, (2) evaluate and rank sensitivity of natural resources to climate change, (3) resolve, develop, and implement options for adapting resources to climate change, and (4) observe and monitor the effectiveness of on-the-ground management and adjust as needed.

In the third step, climate-adaptation practices encompass four management strategies—resistance, resilience, response, and realignment—that encourage consideration of a wide range of possible options (Millar, Stephenson et al. 2007). Resistance includes actions that enhance the ability of species, ecosystems, or environments (including social) to resist forces of climate change and maintain values and ecosystem services in their present or desired states. A resilience strategy enhances the capacity of ecosystems to withstand or absorb increasing effects without irreversible changes in important processes and functionality. The response strategy assists transitions to future states by mitigating and minimizing undesired and disruptive outcomes. Finally, the realignment strategy uses restoration techniques to enable ecosystem processes and functions to persist through a changing climate. Processes and tools used to accomplish adaptation differ among subalpine forest types, depending on local resource conditions, management objectives, and organizational preferences. As of 2014, new resource-management plans are in process for many of the California public lands at high elevations and, when complete, these will include direction for climate adaptation and mitigation in the subalpine forest zones.

## Future Climate Scenarios

Quantitative models evaluated from hemispheric to regional scales project warming of approximately 1°C to 6°C in annual temperature in California by the end of the twenty-first century (Hayhoe et al. 2004, CCCC 2006, Moser et al. 2009). Growing yet inconclusive evidence indicates rates of warming are elevation dependent and that higher elevations are changing faster than lower (i.e., are more sensitive to forcing factors) (Diaz and Bradley 1997, Rangwala and Miller 2012). To the extent this is the case—and exceptional growth rates from subalpine species such as bristlecone pine in the highest White Mountains hint that it is (Salzer et al. 2009)—subalpine forests might face rates of warming higher and/or sooner than projected for the California lowlands. Coupled

with these increases are less certain projected changes in precipitation, though current models are converging on drier futures. Together these projections portend decreased snowpack in the subalpine zones, drier soils with greater climatic water deficits, earlier snowmelt, and lower streamflow volumes. Increasing variability, with extreme years of high and contrasting amplitude are also projected, with both drought and heavy precipitation years more likely (Dettinger 2013). Although some parts of the highest Sierra Nevada and other high peaks of the state such as Mount Shasta, might maintain snow depths at high elevations, recent research on changes in Pacific-origin storms counter this projection. Modeling westerly winds that normally bring rain and snow to the cordillera of western North America, Luce et al. (2013) show that declines in mountain precipitation are resulting from climate change–induced slowdown of winds.

A second general caveat regarding the subalpine zone and climate projections for the future at state and regional scales relates to the mesoscale and microscale variability that characterizes mountain environments. Mountains have enormous heterogeneity in slope, aspect, topography, relative context, landform, and other factors (Daly et al. 2007, Lundquist and Cayan 2007), affording dependent plants and animals escape opportunities more diverse than merely upslope. For instance, cold air drainage creates positive lapse rate conditions (i.e., decreasing temperature with declining elevation) widely in mountain environments. This process might actually increase in the future under forcing factors of anthropogenic climate change (Pepin and Lundquist 2008), with the net effect that canyon bottoms, basins, and swales become cooler than slopes and summits. Another example of mountain landforms at least partially decoupled from synoptic climatology are rocky environments such as talus slopes and rock glaciers. These features develop internal thermal regimes buffered from extremes and potentially resistant to rates of temperature exchange in free air above them (Millar, Westfall, and Delany 2014).

These generalities about high mountain environments and their climates lead to considerable uncertainty about future effects on subalpine forest ecosystems in California. On the one hand, models based on regional warming and assumptions that ecological habitats will shift upslope over the twenty-first century project and that 50% to 90% (depending on the model) of subalpine forest habitat in California will be lost (Hayhoe et al. 2004). On the other hand, high heterogeneity of mountain microclimates might provide refugial environments for long-term persistence of subalpine biota (e.g., Millar, Westfall, Evenden et al. 2014). Projections of plant species distributions in the White Mountains under forecasted warming climates showed near-total losses of habitat by the end of the twenty-first century for many subalpine species, including bristlecone pine (van de Ven et al. 2007). Subsequent observational studies of thermal regimes in the White Mountains, however, indicated patterns of microclimate variability and strong cold air drainage trends even on shallow slopes and basins (van de Ven and Weiss 2009). Refugial environments might therefore exist for plant species that were projected by regional models to disappear upslope of the summit of the range.

## Summary

The subalpine forests of California comprise the highest-elevation ecosystems dominated by upright trees. They are influenced primarily by abiotic controls, including persistent snowpack, desiccating winds, acute and chronic extreme temperatures, soil moisture and evapotranspirative stresses, and short growing seasons. Bounded at the upper elevation by treeline, these forests persist under conditions of deep snows, exposure to severe winds, and high solar radiation. Biotic interactions and disturbances like fire are less important than in lower-elevation montane forests. Most subalpine forests in California are sparse woodlands, with short-statured individuals and wide spacing of young as well as old trees, commonly interrupted by areas of exposed rock, dry upland slopes, meadows, and lakes. Subalpine forest ecosystems extend across California in the highest mountains. In the subalpine, conifer forest types are diverse and characterized by iconic and charismatic species such as bristlecone pine, whitebark pine, mountain hemlock, foxtail pine, limber pine, western white pine, and Sierra juniper. Broadleaf subalpine ecosystems include those associated with high soil moisture, such as quaking aspen and water birch, as well as evergreen species on dry uplands such as mountain mahogany.

Subalpine forests have existed in California for more than twenty million years, although species diversity, ecosystem function, and mountain climates have changed drastically during that time. Unique adaptations have evolved among subalpine forests species to cope with extreme climates. These include individual longevity, long needle retention, strip-bark growth habit, and high fecundity. A remarkable coadaptation for seed dispersal and planting is exemplified by the mutual dependence of Clark's nutcracker and whitebark pine, whereby the indehiscent seed cones of the pine must be opened by birds, and birds in turn depend on seeds for food. By caching pine nuts for later harvest, the birds ensure pine regeneration in the thin and desiccating soils of the subalpine zone. Much of the area of these forests lies in remote locations under federal administration with limited recreational and grazing uses. However, subalpine forests in California face an uncertain future under changing climates. Some projections show very high losses if species move upslope and off mountain summits with warming, while others suggest that environmental heterogeneity could afford adequate refugia for long-term species persistence.

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## Glossary

ATMOSPHERIC RIVERS Giant, episodic storms that funnel large amounts of precipitation, orographically scaled, to regions of southwestern North America and particularly California. Bivoltinism The capacity of insects—in particular, bark beetles—to successfully brood two generations per year.

CLIMATIC WATER DEFICIT Evaporative demand not met by available water—a measure of how much more water could have been evaporated or transpired from a site covered by a standard plant, had that water been available. Climatic water deficit is a meaningful measure of absolute drought that is independent of the actual vegetation of the site.

CLONAL A single individual consisting of multiple stems yet all the same genotype.

ECOTONE The transition area between two communities or biomes—for instance, the alpine treeline ecotone is the zone where forest and herbaceous or shrubby vegetation meet.

FELLFIELD Alpine habitat with shallow, stony, and poorly developed stony soils.

KEYSTONE SPECIES/ECOSYSTEMS Species, plant communities, and biomes that serve critical functions to many other species.

KRUMMHOLZ A stunted growth form, matt-like or shrub-like, developed by several subalpine conifers in response to desiccating winds and subfreezing temperatures.

OROGRAPHIC EFFECT The enhancement of precipitation in mountain regions that results as water-laden clouds rise along upwind slopes, cooling, condensing, and falling as rain as they encounter higher altitudes. Due to orographically enhanced precipitation on the windward side, the lee side of mountains are often correspondingly dry, called a rainshadow effect.

SNOTEL The automated snow-measuring stations administered by the U.S. Department of Agriculture's Natural Resources Conservation Service.

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