



TWENTY-NINE

Alpine Ecosystems

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Introduction

Alpine ecosystems comprise some of the most intriguing habitats of the world for the stark beauty of their landscapes and for the extremes of the physical environment that their resident biota must survive. These habitats lie above the upper limit of tree growth but seasonally present spectacular floral shows of low-growing herbaceous perennial plants. Globally, alpine ecosystems cover only about 3% of the world's land area (Körner 2003). Their biomass is low compared to shrublands and woodlands, giving these ecosystems only a minor role in global biogeochemical cycling. Moreover, species diversity and local endemism of alpine ecosystems is relatively low. However, alpine areas are critical regions for influencing hydrologic flow to lowland areas from snowmelt.

The alpine ecosystems of California present a special case among alpine regions of the world. Unlike most alpine regions, including the American Rocky Mountains and the European Alps (where most research on alpine ecology has been carried out), the California alpine region has a Mediterranean-type climate regime with winter precipitation and summer drought. This condition provides an added stress quite different from other alpine areas and has contributed to the unique biota of the Sierra Nevada alpine. John Muir, in

writing about the alpine meadows of the Sierra Nevada, felt his words were inadequate to describe “the exquisite beauty of these mountain carpets as they lie smoothly outspread in the savage wilderness” (Muir 1894).

Defining Alpine Ecosystems

Alpine ecosystems are classically defined as those communities occurring above the elevation of treeline. However, defining the characteristics that unambiguously characterize an alpine ecosystem is problematic. Defining alpine ecosystems based on presence of alpine-like communities of herbaceous perennials is common but subject to interpretation because such communities may occur well below treeline, while other areas well above treeline may support dense shrub or matted tree cover.

Defining alpine ecosystems on a floristic basis is also potentially flawed, as many plant species that dominate alpine communities well above treeline have ranges that extend down into subalpine or even montane forest communities (Rundel 2011; Figure 29.1). While we recognize that at the local scale

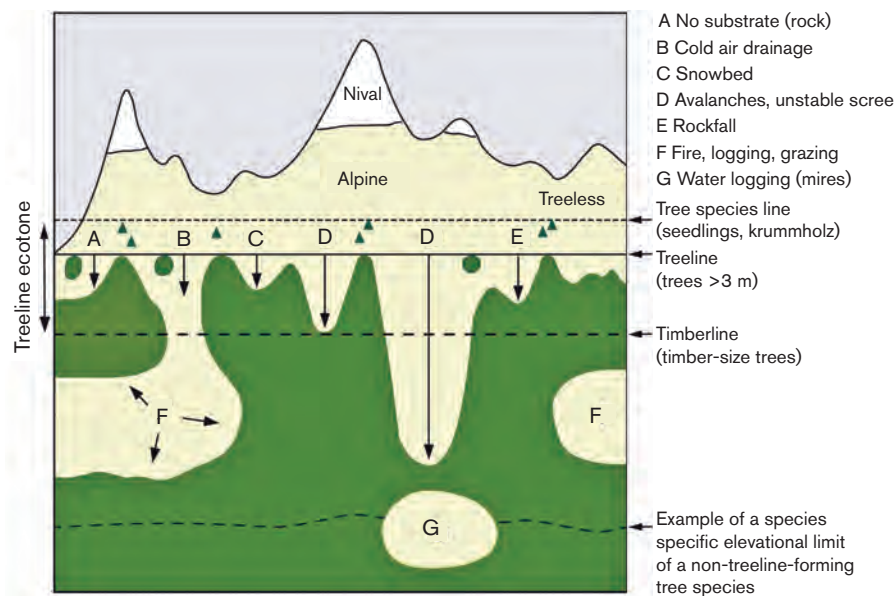


FIGURE 29.1 Schematic representation of the subalpine-alpine ecotone, showing various ways in which the thermal treeline can be displaced downslope by disturbance, snowbeds, or substrate. The alpine-nival ecotone is shown high on the peaks. Between these two ecotones is the alpine zone. Source: Modified from Körner 2012.

alpine ecosystems have excursions upward and downward for reasons including geology, geomorphology, and microclimate, to classify California alpine ecosystems at the regional scale, we adopt the global thermal limit for treeline as a convenient low-elevation baseline. Treeline has been defined as the zone on the landscape where average growing season temperature is 6.4°C or lower (Körner and Paulsen 2004). In this context, trees are defined as plants having upright stems that attain height ≥ 3 meters regardless of taxonomy, and the treeline community is characterized as more-or-less continuous patches of trees whose crowns form at least a loose canopy (Körner 2007).

Typically, the upper-elevational zones around treeline support mosaics of subalpine forest, dwarfed or *krummholz* trees, shrublands, and low alpine perennials, each responding to a complex mix of environmental conditions, soil, and disturbance history (Figure 29.2). Environmental stresses associated with temperate alpine ecosystems include extreme winter temperatures, short growing season, low nutrient availability, high winds, low partial pressures of CO₂, high UV irradiance, and limited water availability (Billings 2000, Bowman and Seastedt 2001, Körner 2003).

The California alpine ecosystem lies in regions colder, and usually above, this zone. For the purpose of this chapter, we allow alpine ecosystems to include also the small area of *Nival* regions that occurs in the state. The latter is defined by another globally occurring threshold: the zone where average growing season temperatures are $\leq 3^\circ\text{C}$, below which even plants shorter than 3 meters cannot endure freezing damage (Körner 2007). Only hardy lichens, isolated plants in protected micro-environments, snow algae, and other snow ice-dwelling invertebrates can survive these conditions. The definition of alpine

we adopt differs from what is often generically called tundra. Technically, “tundra” refers to specific vegetation formations as well as regions of permanently frozen soils and usually is applied to Arctic latitudes (Billings 1973). Alpine ecosystems extend beyond the typically envisioned high-elevation open slopes and summits of cold-adapted shrubs and herbs to also include lithic environments of cliffs, *Talus* fields, boulder fields and *Rock* areas; permanent and persistent snow and icefields, including glaciers; and various water bodies such as streams, *Tarns*, and large lakes.

Geographic Distribution of Alpine Ecosystems in California

The lower (warm) limit of the alpine ecosystem, or climatic treeline, varies with latitude across California, ranging from 3,500 meters in the southern California mountains, to 3,200 meters in the Yosemite region, to 3,000 meters near Donner Pass, to 2,800 meters with somewhat higher elevations in ranges of the western Great Basin east of the Sierra Nevada (Rundel 2011) (Figure 29.3). To the north, in the Cascade Range, climatic treeline begins at approximately 2,800 meters on Lassen Peak and 2,700 meters on Mount Shasta.

Moving from south to north, high elevations with alpine communities are first encountered in the Transverse and Peninsular Ranges of southern California. These ranges support local areas of weakly developed, alpine-like communities populated by a subset of Sierran alpine species (Hall 1902, Parish 1917, Horton 1960, Hanes 1976, Major and Taylor 1977, Meyers 1978, Gibson et al. 2008). Mount San Geronio in the San Bernardino Mountains reaches 3,506 meters and had local glacial activity in the Pleistocene (Sharp et al. 1959). Other high points are Mount San Jacinto in the San Jacinto Mountains at 3,302 meters and Mount Baldy (San Antonio) in the San Gabriel Mountains at 3,068 meters. Alpine species

Photo on previous page: Granitic cirque at head of Burt Canyon, Sierra Nevada, with wetlands along the creek and aster- and paintbrush-festooned upland slopes. Photo: Jeffrey Wyneken.



FIGURE 29.2 The forest-alpine ecotone at upper treeline is a zone on the landscape that can include krummholz whitebark pines, as here on the uplifted, metamorphic plateau of the Tamarack Crest, Sierra Nevada. Photo: Constance Millar.

are present in both xeric and mesic habitats at high elevations, but alpine communities in the form of extended areas dominated by assemblages of alpine species are only weakly developed.

The greatest area of alpine ecosystems in California occurs in the Sierra Nevada. The elevational contour of 3,500 meters, a limit that roughly corresponds to treeline in the southern Sierra Nevada, has been used as one simple parameter to delineate alpine ecosystems (Sharsmith 1940). This boundary defines a relatively continuous area from Kings Canyon and Sequoia National Parks along the crest of the central and southern Sierra Nevada extending to northern Tuolumne and Mono Counties. The alpine zone of the southern Sierra Nevada first appears on Olancha Peak (3,698 meters) on the Tulare-Inyo County line, the southernmost glaciated summit of the range (Howell 1951, Tatum 1979). Cirque Peak (3,932 meters) in Sequoia National Park forms the southern limit of an extensive and virtually contiguous alpine zone of glaciated peaks in the Sierra Nevada. Here occur extensive areas of alpine habitat and high peaks that reach above 4,000 meters, with Mount Whitney at 4,421 meters the highest point in the contiguous United States.

Alpine habitats in the central Sierra Nevada are well developed in the area of Leavitt Peak (3,527 meters) near Sonora Pass and south across Yosemite National Park, whose highest peak is Mount Lyell (3,999 meters). Further south, this belt of alpine habitat continues into Kings Canyon and Sequoia National Parks. Tioga Pass in Yosemite National Park (3,031 meters) and Mammoth Pass (Minaret Summit, 2,824 meters), which is the route for California Highway 203, provide two major breaks containing subalpine elevations but not true alpine habitats. North of the Tioga Pass area, the crest of the Sierra Nevada lies at lower elevations with only scattered areas of typical alpine habitat present. Fragmented communities of alpine species are present at elevations well below 3,500 meters, particularly along exposed ridgelines and on steep, north-facing slopes that were once heavily glaciated. Alpine habitats are weakly developed in Alpine County (Sonora Peak, 3,493 meters) and eastern El Dorado County (Freel Peak, 3,318 meters), extending to their northern limit on Mount Rose (3,285 meters) in the Carson Range east of Lake Tahoe along the California-Nevada border. Nevertheless, scattered com-

munities of alpine-like habitat exist at upper elevations in the northern Sierra Nevada, positioned above and around local, edaphically controlled treelines, and an alpine flora is well represented (Smiley 1915). The substrate north of Sonora Pass is largely volcanic and thus quite distinct from the granitic bedrock of the central and southern Sierra Nevada. Notable exceptions exist where granitic plutons are exposed in the Desolation Wilderness, Donner Pass region, and adjacent parts of the Tahoe Basin.

Several high mountain ranges lie to the east of the Sierra Nevada at the western margin of the Great Basin, and these support small but diverse areas of alpine ecosystems. The White Mountains have an extensive alpine area, with 106 square kilometers above 3,500 meters and the third highest peak in California, on White Mountain Peak, at 4,344 meters (Figure 29.4). To the south, Mount Waucoba forms the high point in the Inyo Mountains at 3,390 meters. The Panamint Mountains east of the Inyo Mountains reach a maximum elevation of 3,366 meters on Telescope Peak.

The Sweetwater Mountains, located 33 kilometers east of the north-central Sierra Nevada north of Bridgeport, reach 3,552 meters on Mount Patterson and contain a significant zone of diverse alpine ecosystems (Bell-Hunter and Johnson 1983; Figure 29.5). At the south end of the Mono Basin, volcanic Glass Mountain reaches 3,392 meters and supports a small, mostly edaphically controlled alpine zone.

To the north of the Sierra Nevada, the southern Cascade Mountains provide local areas of alpine habitat and were likely once stepping-stones for high-elevation plants and animals migrating into California with the late Neogene and Pleistocene tectonic dynamics of the Sierra Nevada (see Chapter 8, "Ecosystems Past: Vegetation Prehistory"). Mount Shasta reaches an elevation of 4,322 meters, while Lassen Peak extends to 3,187 meters (Gillett et al. 1995). Magee Peak (2,641 meters), located midway between Mounts Lassen and Shasta, supports limited areas of alpine vegetation in its north face (Major and Taylor 1977). In northeast California, the Warner Mountains, another fault-block range of the Great Basin province, run 140 kilometers from south to north and attain plateau heights near 3,000 meters. Alpine ecosystems are scattered along their crest, primarily in the South Warner section.



FIGURE 29.3 Distribution of alpine ecosystems in California. Source: Data from U.S. Geological Survey, Gap Analysis Program (GAP); and Cal Fire, Fire Resource and Assessment Program (FRAP). Map: Parker Welch, Center for Integrated Spatial Research (CISR).



FIGURE 29.4 Extensive alpine fellfields extend across the broad alpine plateaus of the White Mountains, interrupted occasionally by inselbergs, patterned ground, and other periglacial features. Photo: Constance Millar.



FIGURE 29.5 The diverse volcanic soils of the Sweetwater Mountains in the California Great Basin appear barren from a distance but support a great number of alpine herbs, including many endemics. Photo: Constance Millar.

In northwestern California the higher peaks of the Klamath Mountains, especially in the Trinity Alps, Marble Mountains, and Scott Mountains, support alpine ecosystems and contain areas of permanent or long-lasting snowfields on north-facing slopes (Howell 1944, Major and Taylor 1977). The highest peaks are Mount Eddy (2,750 meters) in Siskiyou County, Thompson Peak (2,744 meters) in Trinity County, and Mount Ashland (2,296 meters) in Jackson County, Oregon. Major and Taylor (1977) note that alpine species distributions dip as low as 2,000 meters or less on **ARST TOPOGRAPHY** associated with marble substrates in the Marble Mountains, and alpine-like communities also have lower-elevation excursions onto ultramafic (e.g., serpentine) soils (Kruckeberg 1984).

Climate Regimes and Abiotic Stress

At the regional or synoptic scale, the alpine zone of the Sierra Nevada experiences a Mediterranean-type climate regime with dry summers and with precipitation heavily centered on the winter months. This regime differs significantly from that

present in the more continental and monsoon-dominated regions of western and southwestern U.S. and in most of the continental alpine habitats of the world, where summer precipitation predominates. This seasonality is a significant element of the alpine environments of California and a strong factor in explaining the relatively high rate of endemism in the alpine flora. Much of the historic literature on plant and animal adaptations to high-elevation, alpine habitats has come from studies in the colder and more continental alpine ecosystems of the Rocky Mountains and the European Alps.

In alpine habitats at the upper treeline in the Sierra Nevada, about 95% of annual precipitation falls as winter snow. By contrast to the Pacific Northwest, where snowpacks accumulate during regular winter storms throughout the cold season, much snow in the California alpine zones falls during a very small number of storms separated by long, dry intervals. The absence of one or two of these storm episodes in a year can cause a dry snowpack year relative to average levels. By contrast, fortuitous landing of one or more **ATMOSPHER R ER** storms (“pineapple express”) on the California region can result in record wet years and deep snowpacks (Dettinger et al. 2011).

Deep snowpacks and cool temperatures at higher elevations mean that snowmelt extends into spring, but the length and magnitude of the summer drought period experienced by plants and animals is significant. Patterns of rainfall decline gradually from north to south in the main California cordillera, and summer drought decreases as elevation increases because of both increased levels of precipitation and cooler temperatures with lower evaporative demand at higher elevations (Stephenson 1998, Urban et al. 2000).

Very few climate stations are situated in the California alpine zone. In general, winter mean monthly low temperatures are moderate in the Sierra Nevada (Table 29.1) compared to the more continental climates of the interior Great Basin and Rocky Mountains, and in general soils rarely freeze beyond moderate depths. While the mean minimum temperature above treeline is generally below freezing for ten months of the year, nighttime lows typically reach only -3°C to -6°C , although temperature extremes can fall below -20°C on high, north slopes and in cold air sinks (Millar et

TABLE 29.1
Climate data for select alpine locations in California

Location	Mountain range	Latitude (° W)	Longitude (° N)	Elevation (M)	Temperature °C							Precipitation (mm)				
					Jan		July		Annual			Jan	July	Aug	Sept	Annual
					max	min	max	min	max	min	temp					
Mount Shasta	South Cascades	41.42997	122.19914	3261	-2.4	-10.9	15.2	0.8	4.9	-6.3	-0.7	275	17	15	43	1898
Thompson Peak	Trinity Alps	41.00065	123.04834	2717	0.9	-6.3	18.6	6.7	8.3	-1.0	3.7	436	9	56	35	1974
Mount Lassen	South Cascades	40.48916	121.50747	3130	-0.6	-9.1	18.0	3.0	7.5	-4.4	1.6	532	12	40	58	3064
Mount Rose	Sierra Nevada	39.34403	119.91807	3283	-0.4	-11.0	17.6	3.2	7.0	-5.5	0.8	229	21	23	47	1467
Barcroft Station	White Mountains	37.58281	118.23721	3790	-4.5	-12.4	12.6	2.7	2.7	-6.5	-1.9	36	23	30	22	450
Mammoth Crest	Sierra Nevada	37.55376	118.98012	3514	0.6	-10.1	16.9	4.5	7.3	-4.1	1.6	297	6	3	23	1473
Whitney N (Tulainyo Lake)	Sierra Nevada	36.60582	118.27619	3754	-1.7	-11.9	12.7	-0.5	4.1	-7.6	-1.8	114	8	10	19	697

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

al. 2014b, and unpublished data). A cooperative climate station on the summit of Mount Warren (3,757 meters, Western Regional Climate Center) operated for six years before high winds destroyed the major infrastructure in 2011. In 2009, when data were most complete for all months, average annual temperature was -1.3°C ; the lowest monthly minimum temperature (December) was -22.3°C and the highest monthly maximum temperature (August) was 20.1°C . Winds throughout 2009 were mainly westerly (cold seasons) and southwesterly (warm seasons), with gusts commonly over 54 m s^{-1} (120 mph). The maximum monthly wind gust (March) was 42 m s^{-1} (94 mph), and that month had two days with maximum gusts over 134 m s^{-1} (300 mph) including one at 171 m s^{-1} (382 mph)!

Climatic data to characterize the alpine environment of the White Mountains have been collected for many years at the Barcroft Station at 3,801 meters (Pace et al. 1974, Powell and Klieforth 1991). The mean monthly maximum temperatures at Barcroft vary from a high of 11.9°C in July to a low of -5.3°C in February. Record maximum temperatures of 22°C have been reached in July and August. Mean monthly maximum temperatures remain below freezing for six months of the year from November through April. Mean minimum temperatures range from a high of 2.4°C in July to a low of -14.0°C in March. Mean minimum temperatures drop below freezing for every month of the year except July and August (Rundel et al. 2008). Still, many winter days have midday temperatures that rise above freezing. Such temperatures, combined with soils that do not freeze below shallow surface layers, allow for diurnal water uptake by plant species.

Because of their position in the rain shadow of the Sierra Nevada, precipitation in the White Mountains is only about a third of that in the Sierra Nevada at the same elevation (see Table 29.1). A Mediterranean-climate pattern remains of winter precipitation in the White Mountains, but a strong added influence of summer convective storms from the south and east brings scattered precipitation events throughout the growing season. Mean annual precipitation at Barcroft is 478 millimeters, with all of this precipitation falling as snow except in July through September. Mean monthly precipitation ranges from a high of 56 millimeters in December to a low of 18 millimeters in September, but year-to-year variation is high. The extremes in annual precipitation over the record period have ranged from 242 to 852 millimeters (Rundel et al. 2008).

California alpine ecosystems are influenced by interannual and interdecadal climate modes, such as the El Niño/La Niña system (ENSO) (Diaz and Markgraf 2000) and the Pacific Decadal Oscillation (PDO) (Mantua et al. 1997). These ocean-mediated climate modes have alternate states that bring to the California region years of wet, warm winters (El Niño) or cool, dry winters (La Niña). Decadal oscillators such as PDO amplify the effects of one or the other condition. While extreme conditions of ENSO usually occur about every two to seven years, in California more El Niño conditions occurred during the 1980s and 1990s, while La Niña conditions have had a stronghold in the 2000s. The latter tend to modify already dry winters to be record low precipitation years, even in alpine ecosystems. The ENSO system expresses itself in opposite patterns (wet-warm versus cold-dry) in the Pacific Northwest compared to the American Southwest, and northern California lies in the zone of transition between these patterns. Thus northern California alpine ecosystems as far south as the central Sierra Nevada can experience quite dif-

ferent winter temperatures and snowpacks than the southern parts of the range. Other, longer-term trends that affect the alpine zone include multiyear droughts. During the twentieth century in the central Sierra Nevada, these tended to recur every fifteen years or so and persist for five to seven years (Cayan et al. 1998, Millar et al. 2007).

Geologic and Geomorphic Setting

Historical Geology of Uplift and Erosion (Subsidence)

The geologic history of the Sierra Nevada has been discussed in more detail in previous chapters (see Chapters 4, “Geomorphology and Soils,” and 8, “Ecosystems Past: Vegetation Prehistory”), which have highlighted changing interpretations of the geomorphic development of the range. Traditional understanding held that the present-day Sierra Nevada was a young, uplifted mountain range resulting from Great Basin extensional forces and faulting. Although scientists have long recognized that mountains of volcanic origin existed in the late Mesozoic and early Tertiary at the site of the present-day Sierra Nevada, the prevailing view was that this ancient range had never gained elevation greater than approximately 2,000 meters and had eroded to lowlands during the early to mid-Tertiary. Fault-block tilting in the past 10–5 Ma was believed to have created the high elevation of the modern Sierra Nevada. New evidence suggests that the Sierra Nevada in fact reached heights of more than 2,800 meters in the early Tertiary and remained high through subsequent millennia (see Chapter 8, “Ecosystems Past: Vegetation Prehistory”). Nevertheless, the form, topography, and elevation of the modern Sierra Nevada were strongly influenced by effects of more recent extensional and faulting processes—processes that today continue through tectonic action along the Sierra Micro-Plate and Eastern California Shear Zones.

Glacial and Periglacial History

The major glacial activity present in California has been in the Sierra Nevada, and this history of multiple glacial advances and retreats has had a major impact on the distribution and fragmentation of the biota. During the last glacial maximum of the Pleistocene (approximately 20 ka; 1 ka = 1000 years), an ice cap 125 kilometers long and 65 kilometers wide spread over most of the high parts of the Sierra Nevada and reached downslope to an elevation of about 2,600 meters. Valley glaciers moving from the ice cap extended as far as 65 kilometers down canyons on the west slope of the range and 30 kilometers down canyons of the steeper eastern escarpment (Raub et al. 2006). Smaller areas of glaciers formed in the Trinity Alps, Salmon Mountains, Cascade Ranges (Mount Shasta, Mount Lassen, Medicine Lake), Warner Mountains, Sweetwater Range, White Mountains, and San Bernardino Mountains. Prior mountain glaciation events are evident most dramatically in the multiple MORA NES of the eastern Sierra Nevada, some of which reached greater extents than the last glacial maximum.

Evidence suggests that Pleistocene glaciers in the Sierra Nevada completely melted at the latest during the thermal optimum of the Holocene 4,000 to 6,000 years ago (Bowerman and Clark 2011). Neoglaciation began with a moderate advance, 3,200 years ago, followed by a possible glacier maxi-



FIGURE 29.6 Cirque, cliff, and valley slope environments of the eastern Sierra Nevada show erosional and depositional effects resulting from multiple Pleistocene glaciations. Small neoglacial icefields now occupy the highest of these cirque headwalls. Photo: Jeffrey Wyneken.

mum at ~2,800 years ago and four distinct glacier maxima at approximately 2,200 years, 1,600 years, 700 years, and 250 to 170 years ago, the most recent being the largest (Bowerman and Clark 2011). The advent of the global T T E E GE about 600 years ago (Grove 1988), brought on by shifts in the solar cycle and significant volcanic eruptions, resulted in a period with the coldest conditions of the past 4,000 years. The coldest part of the Little Ice Age in California occurred during the late 1800s and into the early decades of the twentieth century and left a legacy of rock ice formations and high-elevation microclimates that continue to have a significant impact.

Geomorphic Settings and Habitats

Community composition in alpine communities is strongly influenced by geomorphic structures and their relationship to erosion, snow accumulation, and snowmelt. Such features as soil accumulation and stability, water availability, and exposure to wind are strongly shaped by these settings.

Mountain Summits and Upland Alpine Plateaus

Mountain summits in the alpine zone of California are modifications of two primary shapes. One is the classic cone shape, most symmetric in volcanic cones such as Mount Lassen and Mount Shasta, while the other is the highly irregular result of fault-block tectonics. The latter, such as Mount Whitney, often have sheer cliffs on one side (the escarpment) while the other slopes often grade to broad, often surprisingly flat, alpine plateaus. These low-relief uplands, often terraces (treads) with steep cliffs (risers), have long been recognized as important features of the Sierra Nevada (Lawson 1904).

These plateaus are interpreted as former lowland erosion surfaces brought to their high-elevation locations during the late Tertiary and Quaternary through episodic tectonic uplift and fault action (Wahrhaftig 1965). The plateaus remain broad and flat, usually with a slight gradient and mostly not incised due to lack of opportunity for snowpack accumulation

and melt from higher elevations. The plateaus present a large habitat landscape for alpine communities at high elevations. Because of their elevations, the summits and high plateaus of the Sierra Nevada and White Mountains, Mount Shasta, and some regions of the Klamath Mountains experience repeated freeze-thaw action, which breaks what would in many cases be exposures of underlying plutons into extensive fields of shattered rock, known as FE SENMEER. The dynamic processes present in these habitats makes it difficult for plant communities to develop significant cover in them. Together summits and alpine plateaus experience rather unique climates for complex mountain regions. Given their extension upward to high altitudes and their relative isolation from adjacent barriers, these high points are strongly influenced by synoptic or regional climatology and more likely to “take the pulse” of changes in regional or hemispheric climate trends than are lower mountain elevations (Barry 2008).

Upland Slopes and Basins: Cirques, Cliffs, and Depositional Chutes

Below the highest mountain summits and upland plateaus of California’s alpine zone are cirque, cliff, and valley slope environments (Figure 29.6). Valleys in glaciated areas head in cirques, amphitheater-shaped basins with broad, flat floors and sloping walls, whereas unglaciated valleys head in slopes that often are narrow and can have very steep walls. Glaciated valley slopes, especially near the range crests and on escarpment direction, often have steep walls above U-shaped valley floors. The “trim line” represents the upper height of glacial activity. This is often visible as a change in slope and composition of the valley wall, with steep, ice-scoured rocks below the trim line and frost-shattered slopes rising to summits, ridgetops, and upland plateaus above. As a result of differences in substrate texture, vegetation is often quite different above and below trim lines. Glaciated and unglaciated valley walls support cliffs, talus slopes, and avalanche, debris, and landslide chutes that attract lithic-adapted flora and/or those adapted to unstable substrates. Shallower-gradient slopes support stable vegetation communities.



FIGURE 29.7 Rock glaciers, such as on the east slope of Mount Gibbs in the Sierra Nevada, are common periglacial features in many alpine canyons. Photo: Constance Millar.

Broken Rock Habitats: Rock Glaciers, Scree, Fellfield, and Talus Slopes

Rock glaciers and periglacial talus slopes are widespread geomorphic features associated with cirques and high valleys of the central and southern parts of the Sierra Nevada (Figure 29.7). Although widely overlooked as important features in the past, these now are understood to play an important role in mountain hydrology (Millar and Westfall 2008, 2010). Unlike typical ice glaciers and exposed areas of snowpack, the ice and groundwater contained within rock glaciers and talus slopes are insulated from the direct effects of solar radiation by blankets of rock debris (Clark et al. 1994). Amplifying the insulation effect of rock mantling are internal thermal regimes created by air circulation within the matrix of rock (Millar et al. 2013, 2014b).

As a result, thaw of ice in rock glaciers lags behind thaw in typical ice glaciers. The former appear to be in disequilibrium with climate, especially when climates are changing rapidly such as at present. The unique thermal regimes of high and north-facing talus slopes and rock glaciers in the Sierra Nevada are cold enough to support persistent internal ice. Thus persistent cold conditions associated with rock glaciers can provide microclimates equivalent to alpine conditions 1,000 meters higher in elevation. Increasingly, these rocky environments are recognized as unique mountain ecosystems (Kubat 2000), with cold-displaced species such as the predatory rhagidiid mite (*Rhagidia gelida*) inhabiting internal matrices far below its usual elevation limits (Zacharda et al. 2005) and plant species adapted to unstable lithic environments growing on the rocky mantles (Burga et al. 2004). In California these alpine ecosystems are poorly described, but pilot studies indicate that distinct vegetation associations are found on the surfaces of talus slopes, and that the wetlands supported by talus and rock glacier springs also support distinct plant and arthropod communities (Millar, Westfall, Evenden et al. 2014). Meltwater from snow, internal ice, permafrost, and/or stable groundwater within and below these features appears to provide an important hydrologic reservoir through the summer months (Raub et al. 2006, Maurer 2007, Millar et al. 2013, Millar et al. 2014b), contribut-

ing to streamflow and downslope recharge. In this way, these features support abundant wetlands in high-elevation canyons and provide critical habitat for a host of alpine biota, of which some, like the American pika (*Ochotona princeps*), depend on wetland habitats supported by adjacent talus fields and rock glaciers (Millar and Westfall 2010). Moreover, wetlands act as sponges to retain water in upper-elevation basins in contrast to meltwaters from annual snowpacks and ice glaciers, which more typically flow out of the uplands in incised channels.

Patterned Ground

Patterned ground and related PERMAFROST features are common in arid, cold climates of the world, and permafrost dynamics can have a strong impact on the development of plant communities (Washburn 1980). However, these have been little-mentioned for the Sierra Nevada. This is because permafrost generally has not been assumed to exist in the range generally, although permafrost features now are known to exist in both rock glaciers and high, cold talus slopes (Millar et al. 2013, 2014b). Ample evidence of patterned ground, especially sorted circles and slope stripes from historical (likely Pleistocene) PERMAFROST action, exists in many alpine zones of the Sierra Nevada, especially upland plateaus. Some areas other than rocky slopes such as shallow edges of tarns (Figure 29.8) suggest that these processes are ongoing.

Intensive research in the adjacent White Mountains of California has demonstrated the presence of discontinuous, modern, patterned ground features and processes at 3,800 meters. Modern patterned ground processes with sorted circles, nets, and stripes become the dominant landscape phenomena above 4,150 meters (Wilkerson 1995). REE ETHERTONS throughout the year are common in some parts of the White Mountains, with over 220 cycles per year observed (LaMarche 1968). While the larger patterned ground features in the White Mountains have been assumed to be relict (Wilkerson 1995), the presence of active permafrost processes there suggests that similar active processes may exist in the Sierra Nevada, especially on exposed plateaus and ridgetops

where water collects yet wind sweeps away snow, maintaining exposure of the ground surface to freezing air (Millar and Westfall 2008, Millar et al. 2013).

Wetlands

Wetland environments, characterized by high groundwater moisture, are important generally in mountain regions of the world for the distinctive biodiversity they support. This is especially true in the California alpine zone, where Mediterranean-type and dry continental (Great Basin) climates and low latitudes combine to drive temperatures high and make water during the growing season scarce. Where wetlands occur, plant communities differ significantly from those occurring on uplands (Sawyer et al. 2009, Weixelman et al. 2011). Invertebrate assemblages also differ substantially between alpine upland and wetland habitats (Holmquist et al. 2011), with wetlands tending to be more speciose. In the California alpine zone, wetlands around springs and seeps and wet meadows derive their high soil moisture primarily from persistent subterranean groundwater sources that often are augmented by snowpack and snowmelt, especially where slope gradients are low (Figure 29.9). Snowbeds (small wetlands fed by late-lying snowfields that recur in specific locations) and glacial forefields (including rock glacier and talus slope forefields) are fed by closely adjacent water sources (melting snow and ice bodies). Riparian corridors tend to be very narrow and to track valley bottoms along streams as well as along creek drainages of valley slopes. The character of wetlands and thus the habitat they create for plants and animals varies depending on the substrate, which affects soil water-holding capacity and acidity. Some soils (e.g., volcanic) drain rapidly while others (e.g., granitic) can develop so-called Teflon basins that hold water near the surface.

Aquatic environments including the moving water of streams, creeks, and rivers and the still water of lakes, tarns, and ephemeral pools are also extremely important habitats in the otherwise relatively dry alpine zones of California (see Chapter 32, "Lakes"). In glaciated regions, TARNs, PATERNOSTER PONDS, and moraine-impounded lakes constitute the bulk of still waters, which number many in the Sierra Nevada (more than four thousand) (Knapp 1996) and Klamath Ranges and very few in the drier interior Great Basin ranges (Warner Mountains, Sweetwater Mountains, White Mountains). Snowmelt-derived streams flowing from high slopes and cirques are sources for important rivers of mid-montane and lowland reaches. Due to the presence of an extensive ice cap during the last glacial maximum in the Sierra Nevada, lakes and streams above 1,800 meters were fishless during the late Pleistocene and Holocene and prior to European settlement supported rich amphibian and invertebrate diversity (Jennings 1996, Erman 1996). Stocking of non-native fish starting in the early twentieth century, however, widely transformed these alpine waters; amphibian species have greatly declined in abundance and distribution, while aquatic invertebrate diversity has shifted drastically in response to predation by fish (Knapp 1996).

Glaciers and Permanent Snowfields

More than seventeen hundred permanent snow or ice bodies are located in California, with seventy of these larger than

0.1 square kilometers (Figure 29.10). Twenty of these glaciers have been named—seven on Mount Shasta and thirteen in the Sierra Nevada. Snow and ice bodies are also located in the Trinity Alps and near Mount Lassen. In total, permanent snow and ice bodies cover over 46 square kilometers of California (Fountain et al. 2007).

An inventory in 2006 identified 497 glaciers covering a total area of 50 square kilometers in the Sierra Nevada (Raub et al. 2006), while 421 rock glaciers and related features were inventoried from the central Sierra Nevada alone (Millar and Westfall 2008). Aside from the Sierra Nevada, the alpine zone of California supports glaciers primarily on Mount Shasta, where seven to ten glaciers were recognized as of 1987 (USGS 1986, Rhodes 1987). Despite regional warming over the past half century, the glaciers of Mount Shasta have shown a greater sensitivity to precipitation than to temperature and have continued to expand following a contraction during a prolonged drought in the early twentieth century (Howat et al. 2007). However, the strong warming trend predicted by regional climate models will be the dominant forcing with an expected near-total loss of glaciers on Mount Shasta and elsewhere in California by the end of the twenty-first century (Basagic 2008).

Processes and Ecosystem Dynamics

Alpine and subalpine watersheds in California play critical hydrologic roles for downstream agriculture and urban development in California, particularly with respect to the seasonality and amount of snowmelt (Bales et al. 2006). The hydrologic flow and biogeochemical processes of these high-mountain ecosystems are sensitive to small changes in growing-season temperature and water availability. The thin oligotrophic soils of alpine watersheds also have the potential to be significantly affected by atmospheric nitrogen deposition and acidification associated with the expanding urbanization of the San Joaquin Valley (Sickman et al. 2003). While there has been a long history of research on high-mountain hydrology and biogeochemistry of lakes and streams in the Sierra Nevada, these studies have largely focused on subalpine watersheds (see Chapters 28, "Subalpine Forests," and 32, "Lakes").

Hydrologic studies in high-elevation watersheds in the Sierra Nevada have modeled streamflows and water balance and the association of snowmelt and runoff with the solute chemistry of aquatic systems (Kattelman and Elder 1991, Williams and Melack 1991). Climate change is expected to affect hydrology by increasing snowmelt rates, promoting earlier runoff (Wolford and Bales 1996). Acid deposition has the potential to alter streamwater pH and increase sensitivity to acidification (Sickman et al. 2001). A key factor influencing nitrogen cycling is duration of snow cover, which influences plant uptake, mineralization, and mineral nitrogen export (Meixner and Bales 2003). Because of the extreme heterogeneity of soil depth and vegetation cover in alpine watersheds, soil mineralization rates for nitrogen are highly site-specific (Miller et al. 2009).

Although data on aboveground production are available for subalpine communities in the Sierra Nevada, very little attempt has been made to collect such data in alpine habitats above treeline. Studies from the central Rocky Mountains and the European Alps have generally found aboveground production rates of approximately 100 to 400 g m⁻² yr⁻¹, with



FIGURE 29.8 Sorted circles result from repeated freeze-thaw action when lake waters are shallow in alpine environments, as along the borders of the deep basin of Silverpine Lake, Sierra Nevada. Photo: Constance Millar.



FIGURE 29.9 Wetlands commonly surround alpine lakes, as at Greenstone Lake in the Sierra Nevada, where talus contributes persistent springs in addition to streamflow from upland glaciers. Photo: Constance Millar.



FIGURE 29.10 North Palisade Glacier, Sierra Nevada. Glaciers in the California alpine zone are remnants from the Little Ice Age, 1450–1920 CE and, except for glaciers on Mount Shasta, exist only in highest headwall cirques. Photo: Constance Millar.

typical values closer to $200 \text{ g m}^{-2} \text{ yr}^{-1}$ (see Bowman and Seastedt 2001, Körner 2003). However, these mean values mask the high spatial heterogeneity in rates of aboveground net primary productivity, with plot-level values ranging from as low as $50 \text{ g m}^{-2} \text{ yr}^{-1}$ to as much as $500 \text{ g m}^{-2} \text{ yr}^{-1}$ or more (Bowman et al. 1993, Walker et al. 1994). This heterogeneity is strongly influenced by topographic controls on microclimate conditions as well as biotic impacts from grazers and burrowing animals (Scott and Billings 1964). Interannual variation in productivity is also typical, with summer temperatures, patterns of snowmelt, and levels of summer drought strongly influencing the length of growing season. On an ecosystem level, much of the biomass accumulation and net primary productivity of alpine communities occurs belowground. Ratios of belowground to aboveground biomass range from approximately 2.5 to 8.8 in studies carried out in alpine systems in the Rocky Mountains and European Alps (see Bowman and Seastedt 2001, Körner 2003). Studies of alpine meadows at Niwot Ridge in the Rocky Mountains have reported ratios of belowground to aboveground productivity that vary from approximately 1.0 in moist alpine meadows to 1.6 in wet meadows and 2.3 in dry meadows (Fisk et al. 1998).

Vegetation and Flora

Local distribution of individual plant habitats is determined strongly by features of the physical environment including topographic position, wind exposure, snow accumulation, and soil depth and drainage (Taylor 1977, Sawyer and Keeler-Wolf 2007). These diverse habitats include windswept ridges, snowbeds, dry meadows, basins and gentle slopes, and shrub-dominated drainage channels. The most severe conditions for plant growth occur on windswept summits and ridges. These communities may be snow-free through much of winter and typically consist of well-drained, coarse soils. Under extreme conditions, patterned soils can occur in these settings from frost heaving. *E F E D* communities fall into this category and often exhibit a dominance of cold- and drought-tolerant mats and cushions along with low-growing herbaceous perennials.

Areas with late-lying snowbeds are characterized by a short growing season with limited water stress and typically support communities dominated by grasses and sedges. Dry meadows occur in areas with shallow soils and with little access to soil moisture once drought conditions extend into the summer. These communities are dominated by a mix of low-growing herbaceous perennials and *GRAM NO DS* and typically are more limited in growth by water availability than by the length of the growing season. Broad alpine valleys and meandering streams exhibit a mix of herbaceous communities dominated by a mix of graminoids and forbs on shallower soils and shrub cover on areas with water availability and some shelter from wind exposure. Willow (*Salix*) species often form dense, low-growing stands or mats, and a diversity of low, ericaceous shrubs are often present. More arid areas of glaciated bedrock with shallow and rapidly draining sandy soils may support stands of *Artemisia*, particularly east of the Sierra crest.

A number of studies have developed relatively detailed classifications of flora and plant community alliances and associations for major habitats (Howell 1951, Klikoff 1965, Pemble 1970, Taylor 1976a, Taylor 1976b, Major and Taylor 1977, Tatum 1979, Burke 1982, Porter 1983, Constantine-Shull

2000). Alpine herbaceous and shrub alliances are described comprehensively by Sawyer et al. (2009) in the broader context of California vegetation types, although these types are often difficult to reconcile with specific stands of alpine vegetation. Ecological habitat descriptions for the alpine zone of the White Mountains have been made by Morefield (1988, 1992) with a somewhat simpler system of seven categories proposed by Rundel et al. (2008). Along a rough gradient from mesic to xeric these ecological habitats comprise aquatic sites, wet sites (areas with saturated soils and riparian habitats), moist sites (wet meadows and areas with snowmelt accumulation), fellfields with seasonal moisture availability, talus slopes, open slopes, and dry rocky slopes. Howell (1944) commented on the elements of boreal flora in the Klamath Mountains.

Plant Functional Groups and Adaptive Traits

Regardless of specific growth form, alpine plants are typically small and grow close to the ground. Spacing between plants is often wide with intervening areas of soil or rock. Such patterns illustrate the role of the physical environment in finely influencing microclimate to create favorable or nonfavorable microsites for plant establishment and growth. A few centimeters' difference in microtopography can have significant influence on air and soil temperatures, wind desiccation, and snow accumulation.

While plant life forms are commonly discussed in modern treatments of alpine vegetation (Billings 2000, Bowman and Seastedt 2001, Körner 2003), only limited attention has been given to quantifying these as plant functional groups. Herbaceous perennials of a variety of forms and architectures (i.e., broad-leaved herbaceous perennials, mats and cushions, graminoids, and more rarely geophytes) form the dominant community cover in temperate alpine ecosystems. Also present with lower species richness are shrubs, as subshrubs (chamaephytes) with a low form of woody growth. Other plant life forms such as taller woody shrubs (phanerophytes) and annuals (therophytes) are rare in most alpine habitats.

Life forms of the Sierra Nevada alpine flora, as in other temperate alpine floras, are heavily dominated by broad-leaved herbaceous perennials (48% of species) followed by graminoid perennials (22%) and mats and cushions (12%). Annuals and woody shrubs account for 6% each of the flora. Life forms are similar in the alpine flora of the White Mountains with broad-leaved herbaceous perennials dominant (53%) followed by graminoid perennials (22%), mats and cushions (11%), annuals (8%), and woody shrubs including low subshrubs less than 50 centimeters in height (6%). The proportion of annual species is relatively high in the Sierra Nevada and White Mountains compared to other continental alpine regions. Annual plants face a strong disadvantage in alpine ecosystems because of the short, cool growing season during which they must complete their entire life cycle. The relatively warm growing season temperatures of alpine habitats in California likely explains this greater success. Clear differences in root morphology exist between growth forms, suggesting functional differences in adaptive strategies. Cushion plants and subshrubs exhibit characteristic tap roots, while mat-forming cushions also have shallow, spreading, adventitious roots arising along stems to take advantage of temporary surface soil moisture (Billings and Mooney 1968). Perennial graminoids have spreading, fibrous roots. A consistent

pattern across growth forms exists wherein most alpine species have stomates on both their upper and lower leaf surfaces, reflecting the high light environments in which they grow (Rundel et al. 2005). Studies of seed germination and seedling establishment across a gradient of changing soil substrate in the Sierra Nevada have shown that water might be the limiting factor for species germination and that differential nutrient availability across soil types strongly influences early seedling growth (Wenk and Dawson 2007).

Ecophysiological traits of alpine plants have been broadly reviewed (Billings and Mooney 1968, Billings 1974, Bowman and Seastedt 2001, Körner 2003) but are not well studied in California alpine plants. Rundel et al. (2005) compared ecophysiological traits of leaf structure, midday leaf temperature, mean maximum photosynthetic rate, and predawn and midday water potentials among four perennial life forms in an alpine fellfield in the White Mountains without finding consistent patterns associated with plant functional types. However, plant growth form may significantly influence diurnal leaf temperatures. The ability of some canopy architectures to promote high leaf temperatures helps explain the ability of the C_4 grass *Muhlenbergia richardsonis* to grow successfully at elevations up to nearly 4,000 meters in the White Mountains (Sage and Sage 2002). In adjacent communities the leaf temperatures of two upright species (*Chrysothamnus viscidiflorus* and *Linanthus nuttallii* subsp. *pubescens*) track ambient air temperature, while the mat-forming *Penstemon heterodoxus* has leaves that are heated significantly compared to air temperatures at midday (Rundel et al. 2005).

Floristics Diversity and Phylogenetic Breadth and Depth

The alpine zone of the Sierra Nevada, if defined as nonforested areas at or above 3,500 meters, includes 385 species of native vascular plants (Rundel 2011). If the alpine boundary were defined as at or above 3,300 meters, the alpine flora would grow to 536 species. Ninety-seven species reach elevations of 4,000 meters, and 27 species reach to 4,200 meters. Only a relatively small number of species are high-elevation specialists; 9 species have ranges restricted to elevations above 3,500 meters, and an additional 67 species (17% of the flora) are restricted to subalpine and alpine habitats. These high-elevation specialists are spread across multiple families but as a group share the feature of relatively high endemism compared to the overall Sierra Nevada flora. More than a quarter of the species in the Sierran alpine flora have elevational ranges that extend as low as foothill habitats below 1,200 meters (Rundel 2011).

Over half of the Sierran alpine species occur in just six families, led by the Asteraceae (55 species), Poaceae (39 species), Brassicaceae (34 species), and Cyperaceae (39 species). The largest genus present is *Carex* with 29 species, and 18 more species would be added by lowering the alpine boundary to 3,300 meters. Next in size are *Draba* (14 species) and *Lupinus* (11 species). The level of endemism in the Sierra Nevada alpine flora is moderate to high depending on how the geographic unit for endemism is defined. The 36 Sierran endemics present in the alpine flora compare with 205 endemic taxa for the montane areas of the range and thus compose 18% of the endemic flora of the higher Sierra Nevada (Rundel 2011). The unique Californian component of the alpine flora of the Sierra Nevada is considerably greater if one con-

siders 31 species present in the alpine flora that are not limited to the Sierra Nevada but occur elsewhere in California or in ranges adjacent to the Sierra Nevada. Under this definition, 66 endemic taxa represent 16% of the Sierran alpine flora. This is high compared to other alpine ranges in continental North America and Europe and reflects both the environmental stress associated with the summer-dry, Mediterranean-type climate of the Sierra Nevada and the relative isolation of the range.

The alpine zone of the White Mountains, defined as nonforested areas above 3,500 meters, includes 163 native species of vascular plants. Seven families account for nearly two-thirds of the flora, led by the Asteraceae (30 species), followed by the Brassicaceae (18 species), Poaceae (17 species), Cyperaceae (15 species), Rosaceae (9 species), Caryophyllaceae (9 species), and Polygonaceae (7 species). While 31% of the alpine flora are restricted to alpine habitats, more than two-thirds of this flora extend to lower-elevation communities in the White Mountains of montane forest, pinyon-juniper woodland, or cold desert. Fellfields form the characteristic habitat for 41% of the flora, while moist meadows and open-slope habitats contain 24% and 22% of the flora, respectively. Endemism is low in the alpine zone of the White Mountains, with just three endemic species, although three more come close to being endemic. Two of these have small populations on the east slope of the Sierra Nevada, and one has a disjunct population in the Klamath Mountains.

The Sweetwater Mountains, 33 kilometers east of the Sierra Nevada, support an alpine flora of 173 species in 16 square kilometers of alpine habitat and share 94% of this flora with the Sierra Nevada (Bell-Hunter and Johnson 1983). The small alpine zone on Mount Grant to the north of the Sweetwater Mountains in western Nevada supports a flora of 70 species dominated by Sierra Nevada elements in just 2.6 square kilometers (Bell and Johnson 1980).

Evolution of the Flora

The evolution of the alpine flora of the Sierra Nevada has involved a variety of factors including geologic history, climate history, modes of colonization, and factors promoting regional speciation (Stebbins 1982). On a biogeographic basis, there are strong indications of a north-to-south route of colonization of high mountain areas of the Sierra Nevada during the late Pliocene and Pleistocene. This evidence comes from a pattern of decreasing presence of Rocky Mountain floristic elements and an increased number of endemic alpine species as one moves from the northern to southern crest of the range where elevations are higher (Chabot and Billings 1972, Raven and Axelrod 1978, Rundel 2011). This gradient is shaped not just by geographic distance but also by steadily decreasing levels of precipitation moving to the south. Floristic elements of subalpine, subalpine wet meadows, and other moist sites typically have broad geographic ranges but become increasingly restricted to the most mesic sites as precipitation decreases southward in the Sierra Nevada (Kimball et al. 2004). Species growing in xeric rocky habitats show higher levels of endemism and smaller range sizes due to isolation and divergence from ancestral populations distributed in wetter habitats to the north. Endemism also increases in the Sierra Nevada with increasing elevation. Of species obligately occurring above 3,000 meters, fully one-third are California endemics, double the level of endemism for the entire mountain range.

A number of alpine species reach their southern occurrence limit on Mount Lassen, suggesting that some of these and other Cascade Range species might have been present in the Sierra Nevada in the late Pliocene or early Pleistocene. Although the species compositions of lower- and middle-elevation conifer forests of Lassen National Park are strongly related to those of the Sierra Nevada, the summits of the highest peaks in Lassen support an alpine flora with stronger floristic links to Mount Shasta and the Cascade Range to the north (Gillett et al. 1995). The Klamath Mountains also mark the southern distribution limit for a number of high-elevation species that do not occur in the Sierra Nevada (Howell 1944). The relative isolation of the Sierra Nevada from northern ranges and the summer drought have acted as a filter to exclude some widespread, circumpolar, arctic-alpine species such as *Dryas integrifolia* and *Silene acaulis*, which do not occur in California.

More controversy exists about the possible migration of significant components of the Sierran alpine flora from the Rocky Mountains across the Great Basin. Both geological and paleobotanical evidence exist to suggest that the mean elevation of the Great Basin was up to 1,500 meters higher in the Miocene and that the current basin and range topography is the result of subsidence rather than uplift (Wernicke et al. 1988, Wolfe et al. 1997). The presence of higher elevations in the Great Basin during the Pleistocene could have provided stepping-stones for the dispersal of alpine organisms from the east. Several notable examples exist of disjunct Rocky Mountain species with restricted distributions in the central and southern Sierra Nevada, often growing in azonal soil conditions (Major and Bamberg 1967, Taylor 1976a). Molecular evidence has shown that at least one lineage of butterflies entered the Sierra Nevada by this route (Nice and Shapiro 2001). However, other authors feel that the majority of these disjunct plant species reached the Sierra Nevada by the same dominant route via the Cascade Range (Chabot and Billings 1972). Only a preliminary understanding exists of the origins of the endemic alpine flora of the Sierra Nevada and White Mountains, and modes of speciation are clearly complex (Rundel 2011). Factors promoting endemism in the alpine flora include the recent uplift of the mountains, the relative isolation of the Sierra Nevada from other ranges, glacial restrictions on migrations, Holocene climate variability, the mixing of desert and mountain floras, and the unusual conditions of summer drought (Chabot and Billings 1972).

There are many examples of genera in the alpine flora where apomixis (emergence of asexual reproduction) has been important in speciation. These include *Boechea* (Schranz et al. 2005, Dobeš et al. 2007) and *Draba* (Jordon-Thaden and Koch 2008) (Brassicaceae), *Antennaria* (Bayer and Stebbins 1987) and *Arnica* and *Crepis* (Noyes 2007) (Asteraceae), *Poa* and *Calamagrostis* (Poaceae), and *Potentilla* (Rosaceae) (Asker and Jerling 1992). Diploid lineages of polyploid complexes often occupy unglaciated areas and resist introgression, hypothetically due to a significantly higher seed set. However, asexual apomictic populations are often more widespread than their sexually reproducing relatives in glaciated areas. The advantages of apomixis include reproductive isolation and stability of vegetative lineages in their area of distribution. Other modes of alpine speciation include population disjunction, reproductive isolation (Chase and Raven 1975), and upslope migration and colonization by arid-adapted lowland taxa at the end of the Pleistocene (Went 1948, 1953).

The White Mountains present a particularly interesting area for study of evolutionary history of the flora and fauna given their position at the interface between two major geomorphic provinces, the Sierra-Cascade Province and the arid Basin and Range Province. Despite this interface, the White range is isolated from direct contact with high elevations of these provinces. Moreover, warmer and more xeric climatic conditions of the middle Holocene climatic optimum allowed an upward movement of subalpine conifers, restricting the area available for growth of alpine communities (Jennings and Elliot-Fisk 1991, 1993). Thus the White Mountains present an example where both climate history and geographic isolation have played significant roles in the evolution of the biota.

Fauna

The alpine zone of California harbors relatively low mammal diversity. Few species are restricted to alpine habitats, while many more use the alpine environment transiently or seasonally (Table 29.2). Large herbivores such as mule deer (*Odocoileus hemionus*) (Anderson and Wallmo 1984) and desert and Sierra Nevada bighorn sheep (*Ovis canadensis nelsoni* and *O. c. sierrae*, respectively) (Wehausen et al. 2007) use the alpine zone in summers both for foraging and as retreat and escape from predators. The prime predator of these ungulates, mountain lion (*Puma concolor*), occasionally follows them to the alpine regions.

Sierra Nevada bighorn sheep (*Ovis canadensis sierrae*) makes major use of alpine areas of the Sierra Nevada during summer. Individuals range over a broad elevational distribution, with winter range as low as 1,450 meters. Individuals near the Mono Basin also migrate far to the east. Sierra Nevada bighorn sheep favor open areas where predators can be seen at a distance and steep rocky slopes can serve as refuge from attacks by mountain lions. There once were as many as a thousand bighorn sheep in the Sierra Nevada, but this number had declined to about 125 adults at the time of their listing as endangered in 1999 (Wehausen et al. 2007). By 2007 they had recovered to more than 400 individuals distributed in a metapopulation of eight subpopulations. They are approaching the target population size of 500, thanks to concerted efforts both to augment herd units and to reduce predator pressure. Threats to Sierra Nevada bighorn sheep survival include disease transfer from domestic sheep, mountain lion predation, and extreme climate conditions.

Many more small and meso-mammals occur in the alpine zone than large animals, and a few are highly restricted to that zone. Among the more charismatic of small mammals is the American pika (*Ochotona princeps*), a small rabbit relative highly restricted to talus slopes and similar broken-rock landforms (Smith and Weston 1990) (Figure 29.11). Pikas range throughout the mountains of western North America. In California they are found throughout the Sierra Nevada, White Mountains, Bodie Mountains, Sweetwater Mountains, southern Cascades, and Warner Mountains (USFWS 2010, Millar and Westfall 2010.) Like other lagomorphs, pikas do not hibernate and collect a diverse range of herbaceous and shrubby vegetation during the warm season, which they cache in stacks (referred to as “haypiles”) within the talus and consume during the winter. Pikas are poor thermoregulators, tolerant of cold yet sensitive to heat, and are often assumed to be alpine-restricted and at risk from global warming. In

TABLE 29.2
Mammal species known to occur in alpine ecosystems of California

Common name	Scientific name	Elevation (m)	Citation for species' elevation
Large mammals			
Desert bighorn sheep	<i>Ovis canadensis nelson</i>	4300	California Department of Fish and Wildlife
Sierra Nevada bighorn sheep	<i>Ovis canadensis sierra</i>	1500–4270	California Department of Fish and Wildlife
Mule deer	<i>Odocoileus hemionus</i>	< timberline	Anderson and Wallmo 1984
Black bear	<i>Ursus americanus</i>	100–3000+	California Department of Fish and Wildlife
Sierra Nevada red fox	<i>Vulpes vulpes necator</i>	1200–3600	Perrine et al. 2010
*Mountain lion	<i>Puma concolor</i>	< 4000	California Department of Fish and Wildlife
Mesocarnivores and small predatory mammals			
*Sierra Nevada marten	<i>Martes americana sierra</i>	2300–3150	Kucera et al. 1996, Storer et al. 2004
Long-tailed weasel	<i>Mustela frenata</i>	< 3500?	Storer et al. 2004
Small mammals			
White-tailed jackrabbit	<i>Lepus townsendii</i>	< 3650	Storer et al. 2004
Bushy-tailed woodrat	<i>Neotoma cinerea</i>	1500–4000	Grayson and Livingstone 1989; Storer et al. 2004
Golden-mantled squirrel	<i>Callospermophilus lateralis</i>	1646–3200	Moritz et al. 2008
Mount Lyell shrew	<i>Sorex lyelli</i>	2100–3630	Epanchin and Engilis 2009
Water shrew	<i>Sorex palustris</i>	1658–3535	Epanchin and Engilis 2009
	<i>Sorex monticolus</i>	3400	Epanchin and Engilis 2009
	<i>Sorex vagrans</i>	3400	Epanchin and Engilis 2009
	<i>Sorex tenellus</i>	4267	Epanchin and Engilis 2009
Belding ground squirrel	<i>Urocitellus beldingi</i>	2286–3287	Moritz et al. 2008
Alpine chipmunk	<i>Tamias alpinus</i>	2307–3353	Moritz et al. 2008
American pika	<i>Ochotona princeps</i>	2377–3871	Moritz et al. 2008
Deer mouse	<i>Peromyscus maniculatus</i>	57–3287	Moritz et al. 2008
Yellow-bellied marmot	<i>Marmota flaviventris</i>	2469–3353	Moritz et al. 2008

SOURCE: * indicates occasional use in the alpine zone.

fact, pikas range from sagebrush-steppe ecosystems through the montane zones to the highest summit reaches and find their optimal elevation range from the mid-subalpine to mid-alpine zone (Millar and Westfall 2010; Millar et al. 2014a). The capacity of pikas to tolerate warm ambient temperatures despite their thermal sensitivity relates both to the unique microclimates of talus and related landforms (Millar et al. 2014b) and to their behavioral adaptations. Talus thermal regimes are highly buffered from external air, remaining cool in summer and warm in winter. Pikas adapt behaviorally by using this “air-conditioned” habitat for refuge as needed in response to external air temperatures (Smith 1974).

Yellow-bellied marmots (*Marmota flaviventris*) are another important mammal species for alpine ecosystems in the White Mountains, Sierra Nevada, and higher mountain ranges to the north. Yellow-bellied marmots have a harem-

polygynous social system whereby a male defends and mates with one or more females. Female daughters often do not disperse and settle around their mothers. Sons invariably disperse as yearlings and try to find and defend one or more females. Females tend to breed as two-year olds. Litter sizes average a bit over four pups, of which about half survive their first year. Yellow-bellied marmots chuck, whistle, and trill when alarmed by predators. They breed in alpine and subalpine meadows.

A number of other small mammal species have ranges extending up to elevations with alpine conditions but are more characteristic of upper montane and subalpine habitats. These include the bushy-tailed woodrat (*Neotoma cinerea*) (Grayson and Livingstone 1989), Belding's ground squirrel (*Urocitellus beldingi*), golden-mantled squirrel (*Callospermophilus lateralis*), alpine chipmunk (*Tamias alpinus*), deer mouse



FIGURE 29.11 The American pika, a typical small mammal of the alpine zone. Photo: Andrey Shcherbina.

(*Peromyscus maniculatus*), and Mount Lyell shrew (*Sorex lyelli*) (Epanchin and Engilis 2009). Recent studies resampling century-old plots in Yosemite National Park have shown that all of these species as well as pikas (although the sample size for pikas was low and the patterns not strongly significant) and yellow-bellied marmots have increased their lower elevational limit of occurrence, likely reflecting warming climatic conditions (Moritz et al. 2008, Tingley et al. 2009).

Several species of small to medium-sized carnivores have ranges that extend beyond the conifer zone into open rocky alpine areas of the Sierra Nevada and Cascade Range. These include the rare wolverine (*Gulo gulo*), which may prey on marmots, and the rare Sierra Nevada red fox (*Vulpes vulpes necator*) (Perrine et al. 2010). American martens (*Martes americana*) feed on a variety of vertebrates including chipmunks and ground squirrels and occasionally prey on pikas (Kucera et al. 1996, Jameson and Peeters 2004). While bird use of alpine habitats is largely seasonal and transitory, a notable exception is the gray-crowned rosy finch (*Leucosticte tephrocotis*), which is a common winter resident of the high Sierra Nevada, Mount Shasta, Mount Lassen, and the Sweetwater and White Mountains at elevations up to 4,000 meters. It forages on the ground, in dwarf shrub habitat, and in alpine barrens above timberline for seeds and insects. The finch breeds in talus slopes and in rock-face crevices. In their California range, these birds are nomadic rather than migratory.

Another common member of the alpine avifauna that breeds and summers in California is the water pipit (*Anthus spinoletta alticola*), which ranges from the central to southern Sierra Nevada and occasionally uses high elevations of the San Geronio Mountains of southern California (Miller and Green 1987). Water pipits prefer wet meadow habitat but also frequent open rocky plateaus and slopes. Sage grouse (*Centrocercus urophasianus*) inhabit high-elevation sagebrush and grassland habitat across the Great Basin and occur as high as 3,700 meters in the White Mountains. Resident birds in subalpine forests such as pine siskin (*Carduelis pinus*), dark-eyed junco (*Junco hyemalis*), mountain quail (*Oreortyx pictus*), Clark's nutcracker (*Nucifraga columbiana*), and others may extend their foraging above timberline but are not regular residents. Red-tailed hawks (*Buteo jamaicensis*), peregrine falcons (*Falco peregrinus*), and golden eagles (*Aquila chrysaetos*)

are occasionally observed flying over alpine habitats but are not regular residents and breed at lower elevations (Charlet and Rust 1991).

The Sierra Nevada yellow-legged frog (*Rana muscosa*), native to high subalpine and alpine lakes in the mountains, was once the most common frog species over broad areas. Over the past century, however, this species has dramatically declined in abundance (Drost and Fellers 1996, Vredenburg et al. 2005). Although this decline was largely attributed for many years to the introduction of non-native trout and/or to pesticides, recent declines have continued even in apparently unpolluted lakes without fish. Studies have now identified pathogenic chytrid fungi (*Batrachochytrium dendrobatidis*) as an additional cause of population loss (Briggs et al. 2005). It has been suggested that the former abundance of this species made them a keystone predator and prey and a crucial agent of nutrient and energy cycling in Sierra Nevada aquatic and terrestrial ecosystems (Drost and Fellers 1996).

A second species of once-common amphibian in wet subalpine and alpine meadows that has experienced sharp drops in population numbers in recent decades is the Yosemite toad (*Anaxyrus canorus*). The species epithet references the melodic call of the male toads. A notable feature of this species is the sharp differentiation in color patterns of males and females, arguably the greatest sexual dimorphism of any anuran in North America. These are long-lived toads with upper age limits estimated from fifteen to twenty years—a life span thought to be an adaptation to their seasonal, high-elevation environment.

Human Interactions

Despite their high elevation, abundant evidence indicates that Native Americans made at least limited use of alpine ecosystems in both the Sierra Nevada and White Mountains. Early use of alpine zones in California included transient use by male hunters to track and procure large game, likely with significant impacts on desert and Sierra Nevada bighorn sheep populations (Wehausen et al. 2007). After about two thousand years, family groups started to move to alpine zones for the warm season, where they established village sites in the high White Mountains as well as in two alpine ranges of Nevada (Bettinger 1991, David Hurst Thomas, pers. comm. 2012). With entire family units residing in alpine regions, much wider use of mammal species occurred for consumption, clothing, and shelter materials, and small mammals (rodents and lagomorphs) were hunted regularly (Grayson and Livingstone 1989). It is clear also that prehistoric humans influenced the abundance and distribution of deadwood in alpine landscapes, complicating interpretations of paleotree lines (Grayson and Millar 2008).

The heavy summer grazing of high Sierran meadows by sheep was widespread up into alpine meadows in the last four decades of the nineteenth century. Several accounts describe how overstocking and overgrazing altered vegetation composition in high-elevation Sierran meadows (Ratcliff 1985; see Chapter 31, "Wetlands"). A permit process to limit grazing in national park lands began in 1905, and much recovery has occurred, although cattle grazing is still permitted in some high-mountain meadows on national forest land. Grazing in high-elevation meadows of the White Mountains was halted in 1988, and recovery has been taking place (Ababneh and Woolfenden 2010).

Invasive Species

Alpine plant communities in California have remained free of any significant invasion by non-native plant species, likely due to the extreme conditions presented by the physical environment. A small number of non-native species have been collected around areas of human activity in the alpine zone of the White Mountains, but none of these appear to have become permanently established (Rundel et al. 2008). Information is lacking on significant establishment of non-native plant species in the high Sierra Nevada. Past disturbance by grazing and other human activities suggests that an absence of propagule dispersal is not the limiting factor in the rarity of non-native species. Nevertheless, aggressive species from other global regions of high-elevation habitat could become widely established in the future if introduced.

Subalpine and alpine lakes in the Sierra Nevada originally lacked fish, but the widespread introduction of non-native trout species began in the mid- to late nineteenth century and populated all watersheds. Fish stocking was completely halted in the Sierran national parks in 1991 but continues on national forest lands. Studies in high-elevation Sierran lakes and streams have shown significant impacts of introduced trout on native trout, amphibians, zooplankton, and benthic macroinvertebrates (Knapp 1996; see Chapter 32, "Lakes"). White-tailed ptarmigan (*Lagopus leucurus*) were introduced to the high Sierra Nevada in 1971–1972 by the California Fish and Wildlife Service and have become well established locally in alpine grassland and fellfield habitats. No studies to date have assessed possible impacts of this introduction.

Conservation

Alpine ecosystems in California today remain largely free of major human impacts due to their isolated locations and positions within protected areas and national parks. Some high-elevation degradation still takes place on national forest lands, but the major effects today are the scattered impacts of summer cattle grazing and recreational activities including pack trains and mountain biking. These activities are much more common in subalpine meadows rather than alpine meadows. Alpine watersheds with pack animal presence and summer cattle grazing have increased periphytic algal biomass, attached heterotrophic bacteria, and *E. coli* compared with nongrazed areas. Thus pollution from cattle grazing might be a significant cause of deteriorating water quality within some watersheds (Derlet and Carlson 2006, Derlet et al. 2012, Myers and Whited 2012).

Invasive plants have not yet become a conservation issue, but this could change in the future. Introduced trout in alpine streams and lakes have certainly had an impact on native amphibian populations. Possible impacts of introduced white-tailed ptarmigan have not been studied. Overall, the collective impacts from all of these invasions are relatively small. Of much greater concern, as described earlier, is the potential impact of climate change on alpine ecosystems.

Climate Adaptation

The significant roles of climatic variables in shaping alpine ecosystem productivity suggest that climate change impacts on alpine plant communities could be more pronounced than

on lower-elevation communities (Grabherr et al. 2000). Moreover, alpine ecosystems are predicted to experience some of the highest levels of warming globally and are expected to exhibit signs of change before other terrestrial ecosystems because of their high sensitivity to disturbance. Alpine ecosystems likely also will be affected by other attendant factors such as declining snowpack, earlier spring runoff, and earlier phenology (Cayan et al. 2001, Duffy et al. 2007, Mote et al. 2005, Stewart et al. 2005).

The international program for monitoring response of alpine plants to climate change, GLORIA (Global Observation Research Initiative in Alpine Environments; see Grabherr et al. 2000, Malanson and Fagre 2013), promotes stations on mountain summits worldwide. For each "target region," standardized monitoring designs are installed on four mountain summits that span the elevational extent from upper treeline to the highest peak in the local region. Seven target regions have been established in California: the Panamint Range; the White Mountains; the Sierra Nevada; and the Sweetwater Mountains (see the North American GLORIA website at <http://www.fs.fed.us/psw/cirmount/gloria/>). The earliest were established in 2004, and several will undergo the second round of five-year remeasurements in 2014. Early results show no striking or significant changes in vegetation or floristics; the most obvious changes are increases in soil temperature. Data from the California GLORIA target regions document local floristic diversity of the summits and provide an excellent reference for local conditions. In addition to these standard target regions, the White Mountain Research Center (at the University of California) operates as one of two GLORIA master sites (the other is in Austria) where interdisciplinary alpine studies are conducted in addition to the multisummit protocol to monitor the impacts from and adaptation to climate change of alpine biota and ecosystems (see <http://www.fs.fed.us/psw/cirmount/gloria/>).

At the broad scale of environmental modeling and climate change, global change models (GCMs) predict that alpine areas will experience higher levels of temperature increase than global averages (Theurillat and Guisan 2001, Beniston 2005). Concerns about the potential impacts of higher temperatures on high-elevation communities have led to a variety of studies, including experimental warming manipulations to look at impacts of increased temperatures on alpine and subalpine plant phenology and community structure (Harte et al. 1995, Price and Waser 2000, Klein et al. 2005). As useful as GCMs can be, they operate on grid scales of kilometers along horizontal axes and tens of meters along the vertical. Thus they are most effective at heights well above the soil, excluding the plant canopy levels where alpine microclimate affects biological and local ecosystem processes. For alpine ecosystems a range of factors complicate the straightforward interpolation from macroclimate to microclimate (Wundram et al. 2010). Boundary layer dynamics at the ground surface complicate predictions because the complexity of interactive factors such as wind shear, pressure gradients, and energy balance cause the environment to become decoupled from free-air conditions above the ground surface.

The topographic heterogeneity of alpine habitats creates a fine pattern of thermal microhabitat conditions at a scale of centimeters. The magnitude of these temperature differences is greater than the range of warming scenarios over the next century in IPCC projections (Graham et al. 2012). If short dispersal and establishment is possible for alpine plants, then fellfield habitats may offer significant buffering from global

warming because of the mosaic of thermal microclimates present. However, we know very little about the significance of moisture availability for plant distributions or its interactions of temperature and soil moisture (Winkler 2013). GCM models are able to make temperature predictions with far more confidence than precipitation ones, leaving open the question of moisture availability. The roles of microclimate in alpine habitats suggest that models predicting upslope movements of species under increasing temperatures might not be entirely realistic and that sufficient microclimate heterogeneity might exist to slow species range shifts.

Summary

Alpine ecosystems are typically defined as those areas occurring above treeline, but alpine ecosystems at a local scale can be found below this boundary for reasons including geology, geomorphology, and microclimate. The lower limit of alpine ecosystems, the climatic treeline, varies with latitude across California, ranging from about 3,500 meters in the southern California mountains and southern Sierra Nevada to 3,200 meters in the Yosemite region, 3,000 meters near Donner Pass, 2,800 meters at Lassen Peak, and finally 2,700 meters on Mount Shasta. Alpine ecosystems extend beyond the typically envisioned high-elevation open slopes and summits of cold-adapted shrubs and herbs to include as well lithic environments of cliffs, talus fields, boulder fields and rock glaciers; permanent and persistent snow and icefields, including glaciers; and various water bodies such as streams, tarns, and large lakes. Alpine ecosystems provide severe physiological stresses for both animal and plant populations. These environmental stresses in California include low winter temperatures, short growing season, low nutrient availability, high winds, low partial pressures of CO₂, high UV irradiance, and limited water availability under summer drought.

The alpine regions of California typically experience a Mediterranean-type climate regime with dry summers and precipitation heavily centered on the winter months. This regime differs significantly from that present in most of the continental alpine habitats of the world, where summer precipitation predominates. At the upper treeline in the Sierra Nevada about 95% of annual precipitation falls as winter snow, with much of this accumulating during regular winter during a very small number of storms separated by long, dry intervals. This pattern produces extreme interannual variability in precipitation and water availability. Alpine plant communities are dominated by herbaceous perennials (broad-leaved herbaceous perennials, mats and cushions, graminoids, and geophytes) that form the dominant community cover. Also present with lower species richness are low shrubs and semi-woody subshrubs. Other plant life forms such as taller woody shrubs and annuals are rare. Alpine ecosystems support a low diversity of resident mammal species, but many others use the alpine environment occasionally or seasonally. Notable are large herbivores such as mule deer and desert and Sierra Nevada bighorn sheep that forage in the alpine zone in summer. Many more small and mid-sized mammals occur in the alpine zone, with yellow-bellied marmots and pikas commonly seen in such habitats. Alpine ecosystems are predicted to experience strong levels of temperature increase from global warming globally but will likely be most impacted by indirect effects such as declining snowpack, earlier spring runoff, and earlier growth and flowering phenology.

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Glossary

- ATMOSPHERIC RIVER** A narrow atmospheric band of concentrated moisture that can cause extreme precipitation events at midlatitudes. Atmospheric rivers affecting the coast of western North America are informally referred to as “pineapple express” phenomena.
- CIRQUE** An amphitheater-shaped basin below a mountain peak carved by glacial action.
- FELLFIELD** Alpine habitat with shallow, stony, and poorly developed stony soils.
- FELSENMEER** Exposed rock surface that has been broken up by frost action so that much rock is buried under a cover of angular, shattered boulders.
- FREEZE-THAW CYCLE** A weathering cycle in which water seeps into cracks and then freezes and expands, promoting breakdown of the rock.
- GRAMINOID** Having a grasslike form of growth, as in the Poaceae, Cyperaceae, and Juncaceae.
- KARST TOPOGRAPHY** A region where the terrain has been impacted by the physical and chemical weathering of carbonate rocks such as dolomite and limestone.
- KRUMMHOLZ** A stunted and often deformed growth of trees at the treeline limit.
- LITTLE ICE AGE** A global period of cooling, extending from about 1550 or earlier to about 1850, marked by a significant expansion of glaciers.
- MORaine** An accumulation of unconsolidated glacial debris.
- NIVAL** Growing with or under snow; also used to connote an upper alpine region continuously under snow or ice throughout the year.
- PATERNOSTER POND** A glacial pond or lake connected to multiple others in a string by a single stream or a system of linked streams.

PERIGLACIAL Describes any place where geomorphic processes related to freeze-thaw cycles of water occur.

PERMAFROST Permanently frozen subsurface layers of soil.

ROCK GLACIER Geomorphological landforms consisting of angular rock debris frozen in interstitial ice.

TALUS FIELD, TALUS SLOPE Describes a landform of jumbled rock debris lying with an inclination up to the maximum angle of repose.

TARN A small lake at the base of a cirque formed by past glacial action.

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