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Ecology and Management of Annual Rangeland Series

Part 6: Vegetation Change and Ecosystem Services

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Publications in this series:

1 Mediterranean Climate (8540)
2 Ecological History (8541)
3 Soils (8542)
4 History of Range Livestock Production (8543)
5 Range Plant Growth and Development (8544)
6 Vegetation Change and Ecosystem Services (8545)
7 Livestock Production (8546)
8 Grazing Management (8547)
9 Vegetation Management (8548)

Vegetation types in the annual rangelands (fig. 1) include annual-dominated non-native grasslands, native-dominated grasslands, oak woodlands, chaparral, and coastal scrub. These vegetation types are relatively stable, but changes can occur in response to common disturbances such as the invasion of non-native species, fire, and grazing. The ecosystem services, or benefits, that humanity obtains from each vegetation type change as the vegetation type changes and need to be assessed accordingly. This publication describes the dominant and common species in each vegetation type, the vegetation changes and change agents that are commonly recognized, and an approach to evaluating ecosystem services.

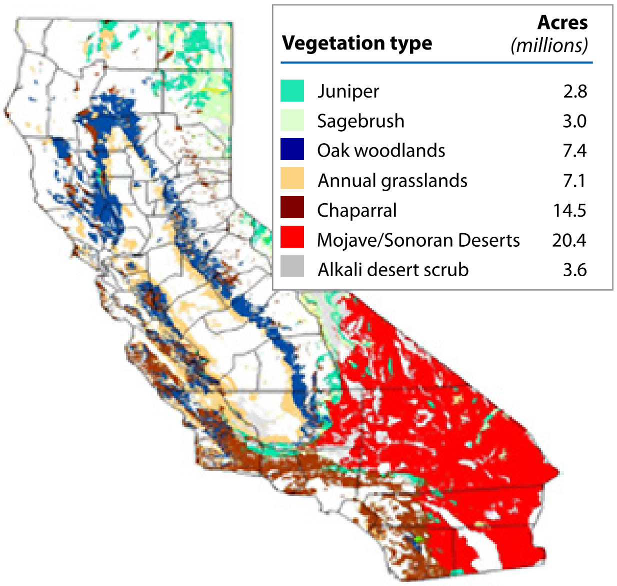

Figure 1. Location and area of annual rangelands (oak woodlands, annual grasslands, and chaparral) and other rangeland types in California.

Annual rangelands vegetation types are often adjacent to each other and sometimes mixed in a mosaic. There is considerable variation within the types, but each has botanical characteristics that separate it from the others. The vegetation types are in different states of change, and ecosystem services differ for each state. Ecosystem services are generally categorized into four kinds: provisioning, regulating, habitat, and cultural (TEEB 2010; MEA 2005). For example, chaparral vegetation regulates stormwater runoff and reduces erosion adjacent to urban areas; oak woodlands provide cultural value as open space; and annual grasslands are habitat for several endangered plant and animal species. Because our knowledge of ecosystem services is in its infancy, scientists and managers will need to evaluate ecosystem services as they develop models of vegetation change. At the conclusion of this publication, we present an approach to evaluating ecosystem services.

In the second publication in this series, “Ecological History,” the authors discussed the evolution of California grasslands, oak woodlands, chaparral, and coastal sage scrub. The purpose of this publication is to give the reader a broad overview of annual rangeland vegetation and an understanding of how it may change in response to common disturbances. Other publications in this series investigate grazing, livestock, and vegetation management practices.

PLANT AND ANIMAL COMMUNITIES

Annual Grasslands

Historic Plant Communities

The presettlement composition of Mediterranean-type grasslands and the understories of associated shrublands and woodlands, now dominated by non-native annual species, are uncertain. The second publication in this series, "Ecological History," provides an in-depth review of how the grassland developed and changed over geologic time. Classical ecologist Fredrick Clements first proposed that the vegetation of the Central Valley, the central and southern Coast Ranges, and the valleys of southern California was perennial grassland (Clements 1920) and proposed that these were dominated by *Stipa* spp. Clements relied on observations of scattered patches of purple needlegrass *(Stipa pulchra*, or *Nassella pulchra)* along railroad rights-of-way (Keeley 1990; Hamilton 1998). It since has been suggested that several other perennial grasses (e.g., *Poa secunda, Leymus triticoides, Melica* spp., *Muhlenbergia rigens*) were historically more important constituents in some environments (Keeley 1990; Holland and Keil 1995; Holstein 2001; Schiffman 2007). Recent studies suggest that grasses were dominant only in coastal grasslands and along riparian corridors (Evett and Bartolome 2013). These studies also suggest that grasses were present in the other grasslands but that the dominant species may have been native annual forbs (Schiffman 2007; Minnich 2008).

The hypothesis that many of California's current grasslands were formerly dominated by woody vegetation and not "pristine" prairie (Cooper 1922) has been less popular, but it has received some scientific support (Hamilton 1998). Cooper noted numerous examples where repeated burning, often intentional, was sufficient to eliminate woody vegetation and replace it with weedy annuals. Some annual grassland sites may have previously been dominated by coastal scrub (Hopkinson and Huntsinger 2005) or native annuals (Solomeschch and Barbour 2006) and not perennial bunchgrasses. Keeley (1993) compared site characteristics of grasslands with significant native perennial grass stands and sites lacking native perennial grasses and concluded that, in the absence of disturbance by fire and livestock grazing, sites often were recolonized by shrubs.

While the presettlement grassland commonly included native perennial grasses, the composition (species and amounts) of the presettlement grassland is uncertain. Invasion of non-native annual species is well documented, beginning with European exploration and settlement as early as the late 1600s (Hendry 1931). The major period of invasion was in the 18th century, and many of these species were well established by the following century (Keeley 1990). Invasion and expansion continue today.

Current Plant Communities

California's annual grasslands are generally located below 3,000 feet, mostly in a ring around the Central Valley, which is dominated by crop production. Most of California's grasslands are dominated by non-native grasses and forbs of Mediterranean origin (Heady 1977; Baker 1989; Keeley 1990), although alien taxa in California come from all parts of the world (Hickman 1993).

Plant communities within this ecosystem have not been well defined beyond the classifications of Valley Grasslands and Coastal Prairie. Soft chess *(Bromus hordeaceus)* and broadleaf filaree *(Erodium botrys)* are common in areas with 65 to 100 centimeters of rainfall, and red brome *(B. madratensis)* and redstem filaree *(E. cicutarium)* are common on southern sites with less than 25 centimeters of precipitation (Bartolome et al. 1980). Native perennial grasses are more common on deep soils with high rainfall. Vernal pools, found in small depressions with a hardpan soil layer, support downingia (*Downingia* spp.), meadowfoam (*Limnanthes* spp.), and other species (Parker and Matyas 1981).

Annual grassland vegetation changes within and between years in response to prevailing weather conditions (see the first publication in this series, "Mediterranean Climate"). Long-term change in the annual grasslands and oak woodland understories is not explained by traditional equilibrium models of plant succession, which view succession as a series of seral

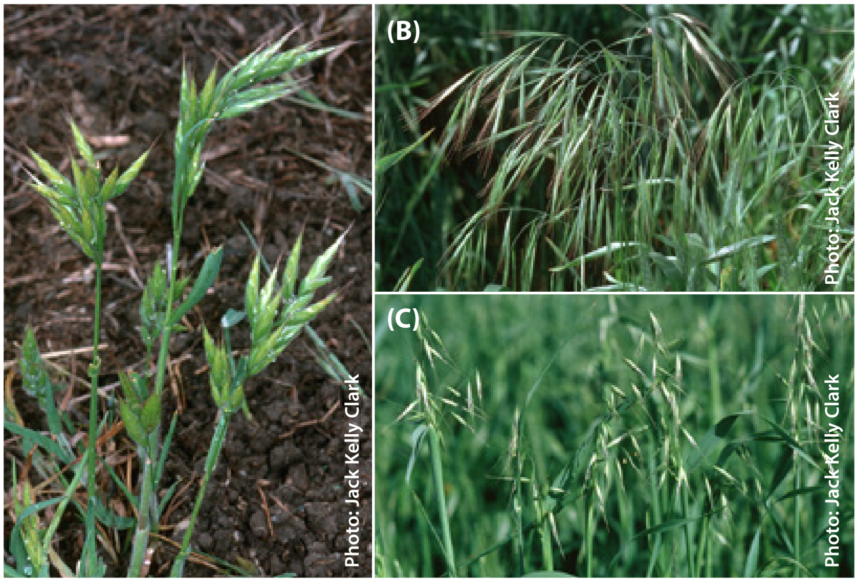

Photo: Jack Kelly Clark

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Figure 2. Soft chess (A), ripgut brome (B), and wild oats (C) are present in most annual grassland and oak woodland ecosystems in California.

Table 1. Frequency of the 20 most common annual grassland and oak woodland understory species in quadrats along 455 transects located from Mendocino and Shasta Counties to Kern and Ventura Counties

Common name	Scientific name	Frequency (%)
soft brome	*Bromus hordeaceus*	91.9
wild oats	*Avena* spp.	71.8
ripgut brome	*Bromus diandrus*	71.6
annual fescue	*Vulpia* spp.	64.9
filaree	*Erodium* spp.	43.7
barley	*Hordeum* spp.	37.1
red brome	*Bromus madritensis*	28.1
Italian thistle	*Carduus pycnocephalus*	26.6
rose clover	*Trifolium hirtum*	26.4
medusahead	*Taeniatherum caput-medusae*	20.4
tarweed	*Hemizonia* spp.	19.1
purple needlegrass	*Nassella pulchra* or *Stipa pulchra*	17.8
purple false brome	*Brachypodium distachyon*	17.4
bristly dogs tail grass	*Cynosurus echinatus*	17.4
bur clover	*Medicago polymorpha*	16.9
silver hair grass	*Aira caryophyllea*	13.2
spreading hedge parsley	*Torilis arvensis*	12.5
rat-tail fescue	*Vulpia myuros*	12.3
fiddleneck	*Amsinckia* spp.	11.4
big quaking grass	*Briza maxima*	10.8
lupine	*Lupinus*	10.3

Source: Alonso 2016.

stages leading to a stable climax community. Jackson and Bartolome (2002) developed a state and transition model for annual grasslands based on data from nine sites, ranging from 16 to 160 centimeters of average annual precipitation in the Coast Range. They concluded that vegetation change in the annual grasslands is largely controlled by interactions between site and weather. Residual dry matter was important at some sites. They proposed that nonequilibrium models of vegetation change were best for the annual grasslands.

Major Plants

Introduced annual grasses and forbs (fig. 2) dominate the annual grasslands. Soft chess *(Bromus hordeaceus*, formerly *B. mollis)*, ripgut brome *(B. diandrus*, formerly *B. rigidus)*, wild oats *(Avena fatua* and *A. barbata)*, red brome *(B. madritensis,* formerly *B. rubens)*, wild barley (*Hordeum* spp.), and foxtail fescue *(Vulpia myuros)* are common grasses (table 1). Common forbs include broadleaf filaree *(Erodium botrys)*, redstem filaree *(E. cicutarium)*, turkey mullein *(Croton setigerus)*, true clovers (*Trifolium* spp.), bur clover *(Medicago polymorpha)*, popcorn flower *(Plagiobothrys nothofulvus)*, and many others. California poppy *(Eschscholzia californica)*, the state flower, is found in the annual grasslands. Native grasses, such as purple needlegrass and blue wildrye *(Elymus glaucus)*, and native forbs can be found throughout the annual grasslands.

Animals

Of the 694 terrestrial vertebrates (amphibians, reptiles, birds, and mammals) native to California, over 285 species use annual grasslands for reproduction, feeding, and cover, including at least 97 species of mammals, 130 species of birds, and approximately 73 species of amphibians and reptiles (CDFG 2011). Some of these species are on state or federal threatened and endangered lists.

Many wildlife species use the annual grasslands for foraging, but some require special habitat features such as cliffs, caves, ponds, or habitats with woody plants for breeding, resting, and escape cover. Characteristic reptiles that breed in annual grassland habitats include the western fence lizard *(Sceloporus occidentalis)*, common garter snake *(Thamnophis* *sirtalis)*, and western rattlesnake *(Crotalus viridis oreganus)* (Basey and Sinclair 1980). Mammals typically found in this habitat include the black-tailed jackrabbit *(Lepus californicus)*, California ground squirrel *(Spermophilus beecheyi)*, Botta's pocket gopher *(Thomomys bottae mewa)*, western harvest mouse *(Reithrodontomys megalotis)*, California vole *(Microtus californicus)*, and coyote *(Canis latrans)* (White et al. 1980). The endangered San Joaquin kit fox *(Vulpes macrotis mutica)* is also found in and adjacent to the annual grasslands (U.S. Fish and Wildlife Service 1983). Common birds known to breed in annual grasslands include the burrowing owl *(Athene cunicularia)*, short-eared owl *(Asio flammeus)*, horned lark *(Eremophila alpestris)*, and western meadowlark *(Sturnella neglecta)* (Verner et al. 1980). This habitat also provides important foraging habitat for the turkey vulture *(Cathartes aura)*.

Native Grasslands

Not all Mediterranean grasslands in California are dominated by non-native plants. Vernal pools, serpentine grasslands, and coastal prairies, while threatened by alien annual grasses, are generally not dominated by them.

Vernal Pools

Vernal pools are seasonally dry depressions on annual rangelands that support and are typically dominated by native plants. Vernal pools provide habitat for diverse populations of crustaceans, grasses, and wildflowers (Solomeshch et al. 2007). Several plants and invertebrates are listed as threatened or endangered under the Federal Endangered Species Act. Vernal pools are threatened by urbanization, agricultural conversion, and flood control activities that change the pools' hydrology. The invasion of weedy annual species is promoted by hydrologic changes that shorten the period of inundation. Targeted grazing by domestic livestock has proven useful in slowing the invasion of alien annual grasses and maintaining the inundation period (Marty 2005). Trampling by grazing animals may also lengthen the inundation period.

Serpentine Grasslands

Serpentine grasslands occur on soils that develop on serpentine outcrops, mainly in the Franciscan formation of California's coastal range. Serpentine soils support vegetation that differs from surrounding nonserpentine soils in productivity, floristic composition, and often physiognomy. These unique characteristics are the result of low levels of major nutrients (nitrogen, phosphorus, and potassium), low levels of calcium combined with high levels of magnesium, and high concentrations of potentially toxic elements, such as nickel, chromium, and cobalt (Harrison and Viers 2007). Many or most plant species cannot tolerate these harsh conditions (serpentine avoiders), but others grow in and out of serpentine (serpentine tolerators). Some species grow only on serpentine. California is one of the world's hotspots of serpentine endemism. Researchers have identified over 200 species and subspecies that are strongly restricted to serpentine and many others that are weakly restricted.

Serpentine grasslands are best known not for their grasses but for their spring wildflower displays, including California goldfields *(Lasthenia californica)* mixed with many other native forbs in the genera *Layia, Gilia, Limnanthes, Microseris,* and *Eschscholzia.* Purple needlegrass and Sandberg bluegrass *(Poa secunda)* are often present but not abundant. Alien annual grasses such as wild oats *(Avena barbata)*, ripgut brome *(Bromus diandrus)*, and medusahead *(Taeniatherum caput-medusae)* often become dominant late in the growing season. Invasion of alien annual grasses threatens to displace some serpentine species. Nitrogen enrichment resulting from air pollution has been shown to increase the competitive ability of some annual grasses, thus magnifying their threat to this unique flora. Cattle grazing has been shown to reduce shading from the invasive annuals and is sometimes used to maintain the serpentine flora (Weiss 1999).

Coastal Prairie

Coastal prairie communities grow in discontinuous patches in a thin band near the coast. The prairie is often adjacent to and mixed in a mosaic with coastal scrub communities. The coastal prairie has been separated from the annual-dominated valley grassland because of different species composition, as well as different temperature and precipitation regimes. Keeler-Wolf (2007) described the north coastal grassland that extends from the Oregon border southward to the San Francisco Bay area (or farther, to the central coast, depending on the ecological investigator).

While the coastal prairie has been invaded by non-native annual grasses and forbs, it still is a perennial-dominated grassland in most cases. According to Keeler-Wolf (2007), California oatgrass *(Danthonia californica)* is the most important native grass in the coastal prairie, with three common types described. The most common type includes native perennial species such as California brome *(Bromus carinatus)*, purple needlegrass, and annual species such as English plantain *(Plantago lanceolata)*, sheep sorrel *(Rumex acetosella)*, subterranean clover *(Trifolium subterraneum)*, and bur clover *(Medicago polymorpha)*. A second type includes tufted hairgrass *(Deschampsia caespitosa)* and coyote bush *(Baccharis pilularis)* and a variety of native perennial and exotic annual species. A third type, described as exotic perennial grassland, includes hairy oatgrass *(Danthonia pilosa)* and various rushes (*Carex* spp.) on moist, sometimes acidic soils. Exotic perennial grasses, including Kentucky bluegrass *(Poa pratensis)*, velvet grass *(Holcus lanatus)*, sweet vernal grass *(Anthoxanthum odoratum)*, tall fescue *(Festuca arundinacea)*, and Harding grass *(Phalaris aquatica)*, are common in this type.

The coastal prairie is an herbaceous community that has been greatly altered by urbanization and conversion to agriculture. Where these communities remain, they have been subjected to invasion of alien annual grasses and forbs similar to those described in the annual grassland section. Livestock grazing, short fire intervals, and drought tend to maintain these grassland communities and limit succession to coastal scrub. Shrubs such as coyote bush, often adjacent to coastal scrub communities, may invade as a result of long fire intervals and reduced grazing pressure. Ford and Hayes (2007) described coyote bush succession in a state and transition model that included prairie, coyote bush, and chaparral and woodland states. Fire intensity and frequency, along with grazing, are the primary disturbances in this state and transition model. Conversion of coastal grassland to shrublands dominated by coyote bush has been documented by McBride and Heady (1968) and Russell and McBride (2002).

Oak Woodlands

Historic Plant Communities

The oak woodlands range in structure from a blue oak *(Quercus douglasii)* savanna with few or no shrubs to a woodland with a shrub layer as well as a tree and understory layer. In a ring around the Central Valley, the blue oak savanna commonly lies between the annual grasslands (lower elevation) and the oak woodlands (higher elevation).

Most native tree and shrub species are still present in oak woodland communities but probably in different amounts due to changes in fire frequency, grazing pressure, harvesting, and other disturbances. The boundary of the oak savanna and annual grassland may be higher than in the past (see the second publication in this series, “Ecological History”). The species composition of herbaceous vegetation in the oak woodlands prior to European contact is unknown. It is commonly held that native perennial grasses such as purple needlegrass were widespread (Clements 1934; Heady 1977). However, others have made the case that native forbs were once dominant, especially in drier parts of the woodland (Hamilton 1998). With the introduction of domestic livestock grazing and invasion of alien species during the Spanish colonization, herbaceous cover has changed from perennial to annual and from native to exotic (Holmes 1990). Fire interval and intensity have increased (McClaren and Bartolome 1989). Overstory cover has generally increased (Holzman and Allen-Diaz 1991). Soil moisture late in the growing season has decreased, and soil bulk density has increased due to compaction from large herbivore numbers grazing during the rainy season (Gordon et al. 1989).

Current Plant Communities

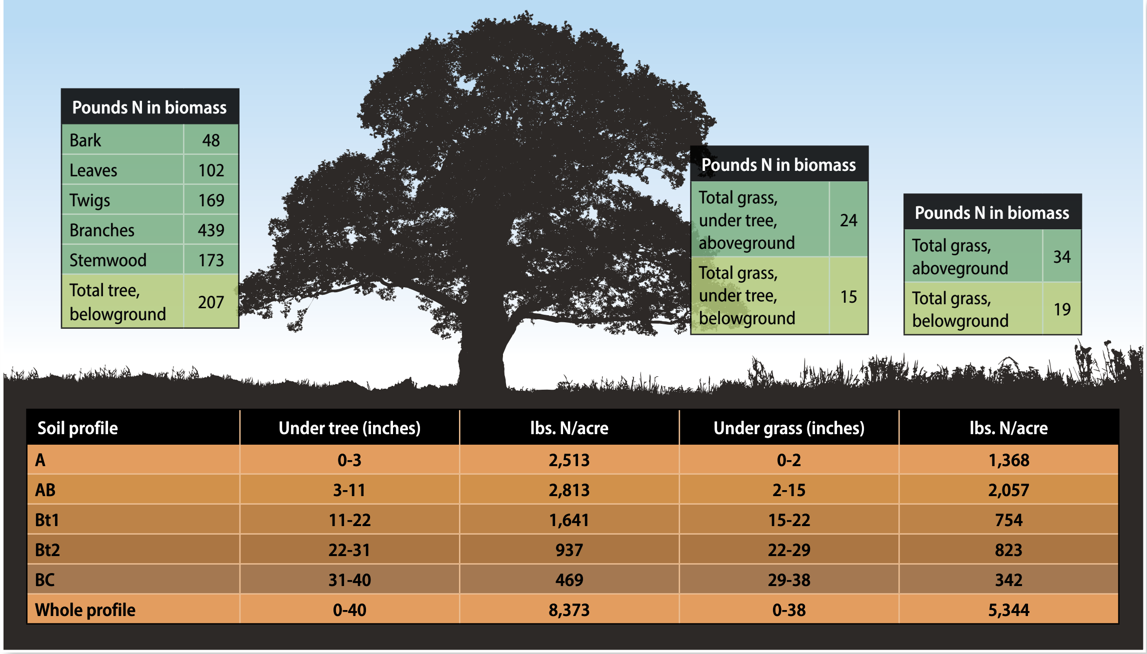
The oak woodlands occur in a ring around the Central Valley and along the coastal mountain

Figure 3. Oak woodlands are often a mosaic of oak, grass, and shrub patches.

ranges. The current oak woodlands have a composition of tree and shrub species similar to historic communities, but the understory is now dominated by introduced annual grasses and forbs. Native annual and perennial grasses and forbs are present in this annual-dominated understory, but many are remnants of their former composition. State and transition models for the oak woodlands are based on the fire cycle but may also include vegetation change mediated by disease and grazing (George et al. 1992; Eastburn et al. 2017).

Oak woodlands are a multilayered mosaic of tree, shrub, and grassland patches (fig. 3). In some locations these mosaics have been correlated with geological substrate (Cole 1980) and soil characteristics (Harrison et al. 1971). However, other researchers have found each of these vegetation types on most soil depths, slopes, aspects, and all geological substrates, suggesting that disturbance (fire) and biological factors (competition, grazing, and browsing) are important determinants of the patchy distribution of these vegetation types (Wells 1962; Callaway and Davis 1991). Given this mosaic of multilayered vegetation types, there is wide amplitude in expected species composition and amounts on the same soil series or association within an ecological site.

Oak trees are an important component of the ecosystem, serving a valuable role in retention of nutrients that, in turn, contribute to long-term ecosystem sustainability (fig. 4). Nutrient cycling studies have shown that oak trees create islands of enhanced fertility through organic matter incorporation and



Pounds N in biomass	
Bark	48
Leaves	102
Twigs	169
Branches	439
Stemwood	173
Total tree, belowground	207

Pounds N in biomass	
Total grass, under tree, aboveground	24
Total grass, under tree, belowground	15

Pounds N in biomass	
Total grass, aboveground	34
Total grass, belowground	19

Soil profile	Under tree (inches)	lbs. N/acre	Under grass (inches)	lbs. N/acre
A	0-3	2,513	0-2	1,368
AB	3-11	2,813	2-15	2,057
Bt1	11-22	1,641	15-22	754
Bt2	22-31	937	22-29	823
BC	31-40	469	29-38	342
Whole profile	0-40	8,373	0-38	5,344

Figure 4. Nitrogen cycling, with major pools of nitrogen (lb/ac), for an oak woodland–grassland ecosystem in the Schubert watershed at University of California Sierra Foothill Research and Extension Center, northeast of Marysville, CA. *Source:* O'Geen et al. 2010.

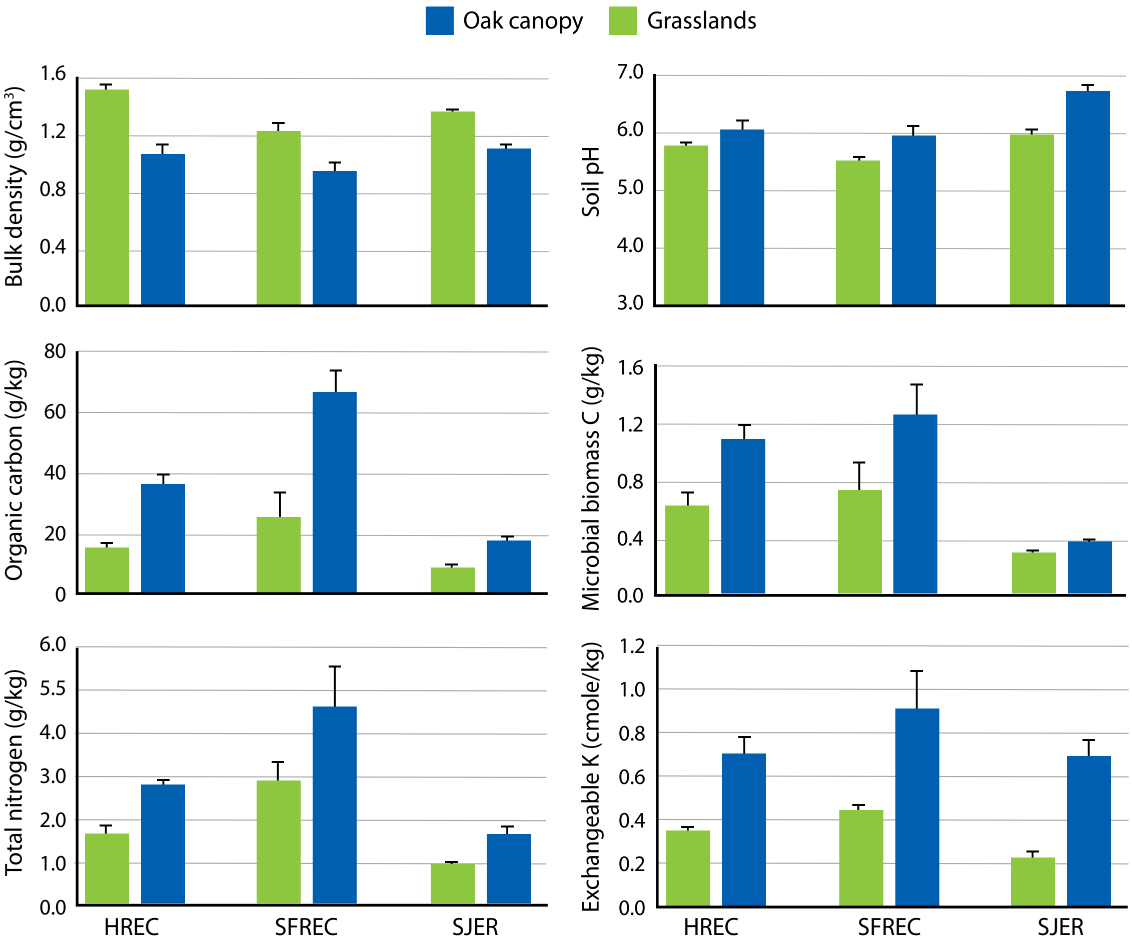


Figure 5. Selected soil quality and fertility parameters for the 0 to 5 centimeters surface soils beneath an oak canopy and adjacent grasslands for three oak woodland sites. *Source:* O'Geen et al. 2010.

nutrient cycling. Compared to adjacent grasslands, soils beneath the oak canopy have a lower bulk density, higher pH, and greater concentrations of organic carbon, nitrogen, and exchangeable potassium (fig. 5), especially in the upper soil horizons (Dahlgren et al. 1997). Removal of oak trees results in loss of soil fertility over a 10-to-20-year period (Kay 1987; Dahlgren et al. 1997).

Major Plants

While around 2,000 plant species exist in the oak woodlands, a few tree, shrub, and herbaceous species dominate the species composition. Blue oak, interior live oak *(Quercus wislizeni)*, and coast live oak *(Q. agrifolia)* are dominants in the oak woodlands (fig. 6). Coast live oak and blue oak are common dominant trees in the Coast Range. Other trees include toyon *(Heteromeles arbutifolia)*, madrone *(Arbutus*

Figure 6. Blue oak (A), interior live oak (B), and coast live oak (C) are dominant species in the oak woodlands.

menziesii), and coffeeberry *(Rhamnus californica)*. The shrub layer, if present, may include narrowleaf goldenbush *(Ericameria linearifolia)*, chamise *(Adenostema fasiculatum)*, black sage *(Salvia mellifera)*, and coast sagebrush *(Artemesia californica)*. In the Sierra Nevada foothills, dominant trees include blue oak, interior live oak, and foothill pine *(Pinus sabiniana)*. Black oak *(Q. kelloggii)* occurs at upper elevations in the transition to coniferous forest. Dominants in the shrub layer, when present, may include wedgeleaf ceanothus *(Ceanothus cuneatus)*, manzanita (*Arctostaphylos* spp.), and poison oak *(Toxicodendron diversilobum)*. At lower elevations and lower rainfall, the oak woodlands are often an oak savanna. With increasing elevation, rainfall, and slope, the interior live oak and shrub component increases.

The understory is dominated by annual grasses and forbs of European origin. Soft chess *(Bromus hordeaceus,* formerly *B. mollis)*, ripgut brome *(Bromus diandrus,* formerly *B. rigidus)*, and wild oats *(Avena fatua)* are the most prevalent grasses in the foothill oak woodlands, and filaree (*Erodium* spp.) is the most prevalent forb. Native perennial grasses such as purple needlegrass and blue wildrye *(Elymus glaucus)* may also be present. Patches on shallow soils are often dominated by filaree or other low-growing forbs. Deep soils with higher water-holding capacity are often dominated by wild oats and other tall annual grasses. Oak canopies influence species composition of the understory. Studies have shown that oak canopies favor wild oats, soft chess, and ripgut brome (Holland 1980; Ratliff et al. 1991).

Animals

Of the 632 terrestrial vertebrates (amphibians, reptiles, birds, and mammals) native to California, over 300 species use oak woodlands for food, cover, or reproduction, including at least 120 species of mammals, 147 species of birds, and approximately 60 species of amphibians and reptiles (Tietje et al. 2005). Many of these species are on state and federal threatened and endangered lists.

California quail *(Callipepla californicus)*, Beechey ground squirrels *(Spermophilus beecheyi)*, and Botta pocket gopher *(Thomomys bottae mewa)* are common in oak woodlands, as are Audubon cottontail *(Sylvilagus audubonii vallicola)* and deer (*Odocoileus* spp.). The rich rodent and lagomorph population is an important food source for common predators, including bobcat *(Lynx rufus californicus)*, coyote *(Canis latrans)*, and the Pacific rattlesnake *(Crotalus viridis oreganus)*. The value of this site for food or cover changes seasonally with the vegetation. In habitat planning, each plant community and each species' needs must be considered individually and collectively.

Chaparral

Historic Plant Communities

The distribution of chaparral, little changed since the start of the Holocene, is greatest in the Transverse and Peninsular ranges of central and southern California, but it is also important in the Sierra Nevada foothills and along the Coast Range. There is little evidence that chaparral is replaced by other vegetation types after a century without fire. Most changes result from changing dominance patterns within the shrub flora. Ceanothus, an obligate fire seeder, varies markedly in its longevity. Some species (e.g., *Ceanothus tomentosus)* appear to be relatively short-lived, on the order of 30 to 50 years, while others persist longer (e.g., *C. greggii*). Some obligate fire seeders such as manzanita (*Arctostaphylos* spp.) are much longer-lived and persist for a century or more (Keeley and Davis 2007).

Current Plant Communities

Chaparral is composed largely of evergreen, sclerophyllous shrub species that range from 3 to 13 feet in height (fig. 7). Other growth forms include soft-leaved subshrubs, perennial herbs, and geophytes (bulbs and corms). Annual herbs are less abundant in mature chaparral but can be present in abundance in early and late successional stands of chaparral (Keeley and Keeley 1984). Sparse stands of trees can occur within chaparral, typically within transition areas, with conifers at higher elevations and oaks at lower elevations (Hanes 1977; Keeley and Keeley 1984). Depending on the species composition and underlying topography and soil, the structure of chaparral can

Figure 7. Fire-adapted chaparral is composed largely of evergreen, sclerophyllous shrub species that range from 3 to 13 feet in height.

range from low, monotonous, smooth-textured vegetation to more heterogeneous stands approaching the vertical structure of woodlands (Keeley 2000).

From inland and high elevations to coastal locations, chaparral occurs in both large continuous stands or within a mosaic of vegetation types, including coastal sage scrub, annual grasslands, oak woodlands, conifer forests, and wetland habitats (Heady 1977; Hanes 1977; Callaway and Davis 1991). Chaparral near the coast tends to occur in disjunct patches occupying more mesic sites, whereas coastal sage scrub is distributed more extensively in drier habitats (Kirkpatrick and Hutchinson 1980; Malanson and O'Leary 1994). Mountain foothill and high-elevation stands of chaparral are larger and more continuous. Coastal sage scrub occurs in smaller patches generally restricted to steep and south-facing exposures (Keeley 2000; PSBS 1995). Oak woodlands often border chaparral in more mesic areas (e.g., adjacent to stream channels, ravines, north-facing slopes) that have developed deeper soils (Griffin 1977). Oak woodlands are thought to develop within late successional chaparral in areas with more developed soils (Cooper 1922; Wells 1962). The native grassland-chaparral interface is not well understood; however, research has shown cases of type conversion from chaparral to non-native annual grasslands with frequent fire or mechanical disturbance (Zedler et al. 1983).

The species composition of a particular chaparral stand is largely influenced by fire. Chaparral generally returns to prefire structure and composition within a normal fire regime (Keeley 1986); however, considerable research has documented various effects of fire regime on species mortality (Keeley 2000). Frequency of fire has been shown to affect chaparral species composition, where short fire intervals may eliminate obligate seeding species in favor of resprouters (Keeley 1986, 1992). Additional research has shown that fire temperature or intensity also has a strong influence on postfire species composition (Davis et al. 1989; Rice 1993; Tyler 1995). Stand age following fire is thought to influence the reproduction of species based on reproductive strategies. Research has shown that seedling recruitment is more common for resprouting species in old (> 56-year) stands of chaparral, whereas seedling recruitment for obligate seeding species is extremely uncommon (Keeley 1986, 1992). This research has led to the conclusion that short-interval fires may adversely affect the presence of obligate resprouting species in favor of obligate seeders.

Major Plants

The floristic composition of chaparral varies depending on biogeography, local habitat characteristics, and fire history. Of the many growth forms present in chaparral, woody evergreen perennials are the dominant plants and, as such, exert the most influence on the habitat. Chamise (fig. 8) is the most common

Figure 8. Chamise is the most common and widespread species within the chaparral vegetation type.

and widespread species within the chaparral vegetation type (Hanes 1971). This species occurs in most stands of chaparral and is the dominant plant in drier habitats (Keeley 2000). The ubiquity of this species is likely explained by its many adaptations to drought, fire, and disturbance (Hanes 1977). Other common shrubs include several species of manzanita and ceanothus, silk-tassel bush (*Garrya* spp.), oaks *(Quercus* spp.), redberry (*Rhamnus* spp.), sumac (*Rhus* spp.), laurel sumac *(Malosma laurina)*, mountain mahogany *(Cercocarpus betuloides)*, toyon *(Heteromeles arbutifolia)*, holly-leaf cherry *(Prunus ilicifolia)*, and mission manzanita *(Xylococcus bicolor)* (Holland 1986).

Soft-leaved subshrubs are less common in true chaparral than in coastal sage scrub but occur within canopy gaps of mature stands, and they may be more prevalent following fire (Holland 1986; Keeley and Keeley 1984; Sawyer and Keeler-Wolf 1995). Common species include California buckwheat *(Eriogonum fasciculatum)*, sages (*Salvia* spp.), California sagebrush *(Artemisia californica)*, and monkeyflower (*Mimulus* spp.). Suffrutescent and perennial herbaceous species commonly include deerweed *(Lotus scoparius)*, nightshade (*Solanum* spp.), Spanish bayonet *(Yucca whipplei)*, rock-rose *(Helianthemum scoparium)*, golden yarrow *(Eriophyllum confertiflorum)*, golden stars (*Bloomeria* spp.), Brodie (*Brodiaea* spp.), onion (*Allium* spp.), and bunch grasses (*Nassella* spp. and *Melica* spp.) (Holland 1986; Keeley and Keeley 1984; Sawyer and Keeler-Wolf 1995).

Animals

The abundance and diversity of wildlife in California's chaparral are not commonly recognized. The iconic, but now extinct, California grizzly bear *(Ursus arctos californicus)* and the majestic California condor *(Gymnogyps californianus)*, which nearly became extinct and remains endangered, are the chaparral's most famous animal residents. Chaparral habitat supports nearly 50 species of mammals, but none live exclusively in chaparral. Some are found primarily in mature chaparral and others in young chaparral and along ecotones between chaparral and other plant communities. Several prefer riparian areas in and near chaparral. Predators in California's chaparral include mountain lions *(Puma concolor)*, bobcats *(Lynx rufus)*, and coyotes *(Canis latrans)*. These predators prey on black tail deer *(Odocoileus hemionus columbianus)*, rabbits, and ground squirrels (Quinn 1990).

Although many bird species travel over and through the chaparral, only a few reside year-round. Common birds in chaparral ecosystems include the wrentit *(Chamaea fasciata)*, western scrub jay *(Aphelocoma californica)*, California towhee *(Melozone crissalis)*, spotted towhee (*Pipilo maculatus)*, and California thrasher *(Toxostoma redivivum)*. Birds especially common in chaparral for several years after a fire include Costa's hummingbird *(Calypte costae)*, sage sparrow *(Artemisiospiza belli)*, Rufous-crowned sparrow *(Aimophila ruficeps)*, lazuli bunting *(Passerina amoena)*, Lawrence's goldfinch *(Carduelis lawrencei)*, and black-chinned sparrow *(Spizella atrogularis)* (Quinn 1990).

Postfire succession of birds (Alten 1981; Wirtz 1979), reptiles (Simovich 1979), mammals (Quinn 1990; Wirtz 1977), and insects (Force 1982) has been studied. In general, wildlife habitat may be optimized by maintaining chaparral in many age classes, by restricting the size of burned or treated areas, by protecting trees, and by enhancing water sources (Quinn 1990).

Coastal Scrub

Southern coastal scrub is distributed along the southern and central coast to the south San Francisco Bay Area (Rundel 2007). It extends south into Baja California. The community is sometimes called soft chaparral due to the predominance of soft, drought-deciduous leaves in contrast to the hard, waxy-cuticled leaves on sclerophyllous plants of California's chaparral communities. The northern coastal scrub is distributed along the coast from Santa Barbara County to the Oregon border (Ford and Hayes 2007).

Southern coastal scrub on some sites is replaced by chaparral types (Mooney 1977; Gray 1983), but the usual trend of vegetation change in undisturbed stands is toward shrubs of various ages and size classes. Southern coastal scrub is fire adapted, and most species sprout readily from crowns after burning. The coyote bush *(Baccharis pilularis)* stands in northern coastal scrub have been considered a seral stage in the progression from grassland to woodland or forest (Ford and Hayes 2007).

The extent of southern coastal scrub has been drastically reduced and fragmented by agricultural conversion, urbanization, grazing, altered fire intervals, and air pollution (Taylor 2005). While most of the native shrubs remain part of the composition, native annual and perennial grasses and forbs, historically present, have been displaced by the invasion of alien annual grasses and forbs.

Major Plants

Dominant plants of the northern coastal scrub include coyote bush *(Baccharis pilularis)*, yerba santa *(Eriodictyon californicum)*, coast silk-tassel *(Garrya elliptica)*, salal *(Gaultheria shallon)*, and yellow bush lupine *(Lupinus arboreus)*. Herbaceous species include western blue-eyed grass *(Sisyrinchium bellum)*, Douglas iris *(Iris douglasiana)*, and several native grasses.

Typical species in the southern coastal scrub include California sagebrush, black sage *(Salvia mellifera)*, white sage *(Salvia apiana)*, California buckwheat *(Eriogonum fasciculatum)*, coast brittle-bush *(Encelia californica)*, and golden yarrow *(Eriophyllum confertifolium)*. Larger shrubs include toyon *(Heteromeles arbutifolia)* and lemonade berry *(Rhus integrifolia)*. Several native and introduced grasses and forbs are part of this community, and cacti and succulents may occur in some locations.

Animals

The coastal sage scrub community hosts a great diversity of organisms. Of the many animals that live in the coastal sage scrub, 120 are considered rare, threatened, or endangered. Of these, the blue-gray gnatcatcher *(Polioptila caerulea)* and Stephen's kangaroo rat *(Dipodomys stephensi)* are on the federal list of endangered species. Protection of this unique habitat is critical to the survival of a diversity of animals, including nearly 150 different species of birds and more than 150 different butterfly species (CDFG 2011)

VEGETATION DYNAMICS AND DISTURBANCE

Introduction

The woody and herbaceous plant communities of the annual rangelands are adapted to fire and drought, and fire is a major driver of vegetation change. Beginning with European colonization of California, the invasion of non-native annual grasses and forbs has had a strong influence on grassland and understory dynamics as well as on woody plant regeneration. Cultivation, grazing, and drought facilitated the invasion of non-native plants. More recently, nutrient enrichment resulting from air pollution has influenced herbaceous species composition. Climate change holds the prospect of more change as the amount and timing of rainfall are forecasted to change over the coming decades. Conversion of woodlands to grasslands has resulted in permanent, often irreversible changes to woody plant communities. Grazing and browsing have short- and long-term effects on herbaceous and woody plant communities.

Fire

Fire strongly influences the structure of annual rangeland plant communities. Lightning-caused fires, while infrequent, have surely influenced the structure of these communities. Native Americans used fire as a management tool to enhance habitat and to manage food and fiber plants. While fire is a natural part of annual rangeland ecosystems, fire frequency has changed from frequent burning by Native Americans and early ranchers to infrequent burning today. McClaren (1986) and McClaren and Bartolome (1989) estimated oak woodland fire return intervals of about 25 years prior to European settlement. After settlement, the return interval was around 7 years due to burning by settlers. In the 1940s, Sampson (1940) estimated that oak woodland burning by ranchers resulted in return intervals of 8 to 15 years. While prescribed burning continues today, urbanization and air quality concerns have reduced the use of fire as a management tool. Today, fire frequency is more likely to be 25 to 50 years or longer. Prescribed burning and mechanical and chemical brush control have been used to remove the shrub and tree layers but have been used infrequently since the beginning of the twenty-first century (Murphy and Crampton 1964; Murphy and Berry 1973).

Historic fire regimes for chaparral are not well documented, but it appears that the fire return interval was in the range of 50 to 150 years (Conard and Weise 1998). However, the fire interval has changed due to anthropogenic ignitions and fire suppression, and it may be closer to every 50 to 70 years. Minnich (1989) estimated a 70-year fire return interval for chaparral sites in San Diego County, but fire interval varies spatially. The fire return interval for coastal shrublands tends to be longer than for inland regions (Keeley and Fotheringham 2000). An increasing interval between fires increases the risk of catastrophic fire with far-reaching ecological and economic impacts (Allen-Diaz et al. 2007).

Figure 9. Chamise resprouts from the base of the shrub following fire.

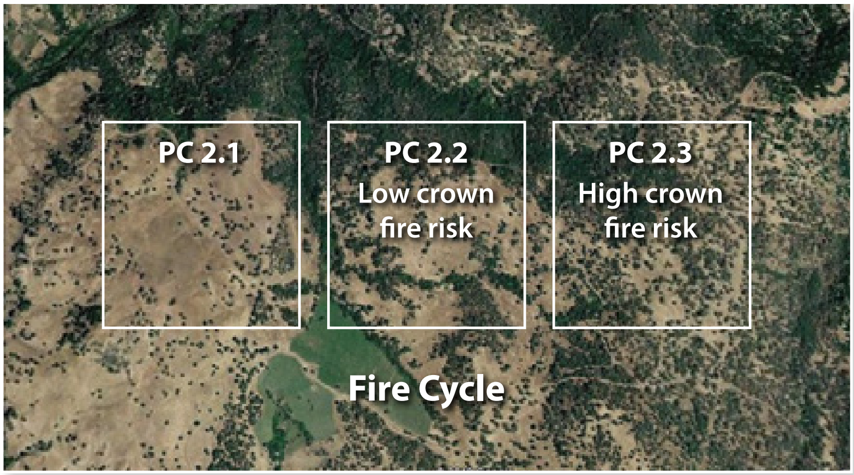


Figure 10. Three vegetation states representing early, middle, and late in the fire cycle are visible in this aerial photograph of a foothill oak woodland. The early state (PC2.1, 0% to 20% canopy cover) is a savanna state with little or no shrub layer immediately following fire. The middle state (PC2.2, 20% to 60% canopy cover) shows an increase in the shrub layer but low risk of crown fire, and the late state (PC2.3, 60% to 100% canopy cover) represents a shrub layer that has grown into contact with the tree layer, increasing crown fire risk. Frequent fire tends to result in oak woodland vegetation states dominated by an oak–annual grass community. Protection from fire and grazing results in a gradual increase in shrubs, contributing to increased fuel loads and increased risk of crown fires.

Most woody plants in the annual rangelands are either adapted to occasional fire or are able to persist in fire-prone ecological regimes. Some resprout following fire from belowground burls (fig. 9); some produce large amounts of dormant seed that persist for long periods of time and are stimulated to germinate by heat or chemical processes initiated by fire; and some woody plants exhibit both adaptations (Keely 1977). Live oak and chamise resprout following fire, while shrubs such as ceanothus are stimulated to germinate by fire. Blue oak tends to be a weak resprouter, which contributes to poor regeneration.

Following fire, oak woodlands often have a savanna structure until shrubs and small trees begin to fill the space between the existing trees. Competition between the species that germinate or resprout following fire or other disturbances, mediated by weather and soil moisture conditions, greatly influences the vegetation states present in oak woodlands. Tree, shrub, and grass patches are all possible vegetation states on some soils, geological substrates, and aspects (see fig. 3). Shallow soils, coarse and rocky soils, and southern aspects sometimes limit vegetation to shrub-dominated states. Frequent fire tends to result in vegetation states dominated by an oak–annual grass community (fig. 10). Protection from fire and grazing results in a gradual increase in shrubs, contributing to increased fuel loads. As the shrub canopy reaches into the tree canopy, the potential for crown fires increases (George et al. 1992). Protection from browsing reduces hedging, allowing the oak canopy to reach the ground layer and increasing the chances for ground fires to become crown fires. Crown fires can top-kill oak trees. While interior live oak *(Q. wislizeni)* will resprout vigorously, blue oak may not resprout vigorously in some locations. Grazing and browsing may slow the recovery of woody plants following fire (Johnson and Fitzhugh 1990). Vegetation dynamics for many oak woodland sites have been compiled in state and transition models and published by USDA NRCS in ecological site descriptions on the USDA Natural Resources Conservation Service website, https://www.nrcs.usda.gov/wps/portal/nrcs/main/national/technical/ecoscience/desc/.

Chaparral undergoes a rapid succession from largely herbaceous flora immediately after fire to relatively dense woody vegetation in a short time period, with minimal loss of species (Hanes 1971; Zedler and Zammit 1989). Immediately after a disturbance, usually fire, the grasses and forbs initially dominate. Within 2 to 5 years, the seedlings of chaparral plants and the shrubs resprouting from their crown or germinating in response to fire become dominant. Their more aggressive root systems exploit deeper water reserves, and they will eventually shade out the forbs and grasses and replace them. By the fifth year, shrubs are tall enough to shade out the shorter herbs and approach a climax community.

Early research suggested that without fire chaparral would develop into oak woodlands or grasslands (Sampson 1944; Wells 1962). Chaparral succession to oak woodlands may occur in mesic situations adjacent to current stands of oak woodlands (Callaway and D'Antonio 1991), but often examples are found of chaparral stands greater than 100 years old showing little evidence of further succession (Zedler 1981; Keeley 1992). This research has shown that in addition to remaining stable and reproductively viable following long periods without fire, some chaparral species (most resprouting species) sexually reproduce largely within older stands (Zedler 1981; Keeley 1992). Additional research has shown that high-frequency burning of chaparral in the presence of non-native grasses can cause type conversion from shrublands to non-native grasslands (Wells 1962; Zedler et al. 1983; Keeley 1990). So, while chaparral appears to be fire adapted, it can remain healthy for long periods without fire, and too-frequent fire may cause conversion to grassland.

Large areas of southern California coastal scrub and chaparral are being altered by the invasion of non-native grasses. Most coastal scrub and chaparral species are adapted to intense but infrequent fire. Under these conditions, there is an ephemeral postfire community consisting of annual and perennial herbaceous species that dominate for only 1 to 3 years before the shrub canopy closes. With an increase in fire frequency, recruitment of fire-adapted native woody species may be hindered, slowing the formation of a closed woody canopy. Under these conditions, non-native grasses and other herbaceous species persist longer after fire, and grasses may dominate patches in mature coastal sage scrub and chaparral communities. However, the exact role of non-native grasses during recovery of these plant communities from fire remains unclear (Pec and Carlton 2014). Deposition of oxidized nitrogen associated with urban pollution sources appears to strengthen the competitive ability of non-native grasses. Therefore, the relationship between invasive grasses, fire, and loss of coastal scrub appears to be exacerbated by nitrogen deposition, which increases exotic grass biomass more rapidly than native plants (Weiss 1999; Allen et al. 2005; Fenn et al. 2010; and Kimball et al. 2014).

Volatilization of nitrogen, and to a lesser degree potassium, are important fire-associated nutrient losses. Some nitrogen is recovered or replaced by nitrogen-fixing legumes such as lupine (*Lupinus* spp.) and deerweed (*Lotus* spp.), as well as nonleguminous plants such as California lilac (*Ceanothus* spp.). The interrelationships among soil microorganisms, heating rates associated with wildfires or prescribed burns, soil moisture at the time of a fire, and various nitrogen-fixing plant species have been studied, but much remains to be learned about the dynamics of nutrients in chaparral systems. Soil erosion following fire results in large losses of all nutrients (Conrad et al. 1986).

Successional changes to southern coastal scrub following fire are complex and may vary with geographic region as well as fire interval, intensity, and seasonality. Some shrub species are strong resprouters that regrow and flower during the first growing season following a fire, while other species are weak- or non-sprouters that are more dependent on germination and seedling establishment, and they recover more slowly. In the northern coastal scrub, dominated by coyote bush, long intervals between fire and removal of livestock grazing facilitate succession to a shrub-dominated community (McBride and Heady 1968; Russell and McBride 2002). Livestock grazing and frequent fire can maintain a grassland. Without fire and grazing, northern coastal scrub expands into unmanaged fragments of land resulting from agricultural, urban, and industrial conversion.

In the annual grassland and woody understory, fire reduces thatch buildup and grass dominance, resulting in a shift in species composition toward forb dominance. When fire occurs, its effect is short-lived. The first growing season after a fire, forage production is commonly reduced by about 25 to 50 percent, partly because species composition typically is dominated by filaree and other forbs (Hervey 1949; Stromberg and Kephart 1996). The grass component is usually recovering by the second growing season following a fire, and by the third year species composition and productivity are back to prefire levels.

Invasion

The annual grasslands and the understories of annual rangeland woody plant communities are commonly dominated by annual grasses and forbs that invaded during the European colonization of California. While yearly and within-year variation in productivity and species composition are heavily influenced by prevailing weather, long-term change in annual grassland and oak woodland and shrub understory productivity, species composition, and ecosystem processes has been influenced by continuing waves of invasion (DiTomaso et al. 2007). Structural changes in invaded plant communities typically cause changes in canopy structure and reduced richness and diversity of native species.

In the annual grasslands, invasive plants have altered ecosystem structure and function, including hydrologic, fire, and nutrient cycles. Replacement of deep-rooted native perennial grasses by annual grasses and forbs that are largely rooted in the top 12 inches of the soil has changed patterns of soil moisture depletion, leaving a soil moisture niche for invading summer annuals such as yellow starthistle (Holmes and Rice 1996; Dyer and Rice 1997; Gerlach 2004). The use of deeper soil moisture by yellow starthistle may mimic the use of deeper soil associated with former native plants. Additionally, the loss of deep-rooted perennials has reduced the transfer of nutrients stored below 12 inches to the surface soil.

Non-native grasses and forbs, being prolific seed producers, have displaced most of the native perennial seed bank, resulting in extremely high seedling densities following fall germination. This is followed by high rates of self-thinning and turnover, potentially resulting in a large flux of nitrogen as these seedlings decompose (Eviner and Firestone 2007). This may contribute to high nitrogen cycling rates in exotic annual grasslands.

Alien annual grasses have been shown to reduce oak seedling growth and survivability by limiting soil moisture. Non-native grasses and forbs compete with seedlings of woody plants by depleting soil moisture at more rapid rates than perennials, especially in early spring when acorns are germinating and sending down their roots. Rapid soil moisture depletion rates in annual-dominated understories are devastating to oak seedlings, compared with more gradual depletion rates of perennial-dominated understories (McCreary 2001).

Grazing

Grazing animals consume forage, redistribute nutrients, and compact soil. However, the influence of these processes on vegetation change is not well documented (Jackson and Bartolome 2007) and is strongly affected by prevailing weather. Within the strong constraints exerted by prevailing weather, grazing can influence short- and long-term vegetation change. Grazing managers can manage these effects by controlling the season, intensity, frequency, duration, and distribution of grazing. The eighth publication in this series, “Grazing Management,” reviews the influence of these principles of grazing and their short-term effect on the annual grasslands and oak woodland understory. Grazing effects on the annual grassland or herbaceous understory, where most plants are annual and short-lived, tend to be short-term; however, grazing effects on longer-lived woody species tend to be longer-term.

Grazing effects on the herbaceous component of annual rangelands tend to reduce grass dominance and thatch buildup, which reduces light availability to the forb component of the composition. This same effect occurs with the removal of litter or residual dry matter by mowing. However, prevailing weather strongly influences production and species composition that results from manipulation of the grazing process (George et al. 2001).

Grass dominance and thatch buildup that results from removal of grazing can have devastating effects on forbs, some of which are critical habitat for insects or other animals. Weiss (1999) found that dwarf plantain *(Plantago erecta)*, a forb that is critical habitat for the bay checkerspot butterfly *(Euphydryas editha bayensis)*, is suppressed by competition from invasive grasses. Removal of grazing from this habitat can be devastating to the checkerspot caterpillars.

Strategically applied livestock grazing has the potential to engineer vegetation structures that meet the habitat needs of endangered animal species such as the San Joaquin kit fox *(Vulpes macrotis)* and the tiger salamander *(Ambystoma californiense)*. For example, the San Joaquin kit fox prefers a relatively open habitat and often disappears from ungrazed habitats. Barry et al. (2011) have reviewed grazing impacts and strategies that can be used to manipulate habitat for several animal species in California's annual rangelands.

Trampling, especially during the wet season, may result in soil compaction, but the effects are not uniform. Studies at the San Joaquin Experimental Range in Madera County have shown that compaction increases with moderate or heavy grazing, when compared with no grazing (Tate et al. 2004). Other researchers have also found increased soil bulk density in grazed compared with ungrazed pastures (Liacos 1962; Ratliff and Westfall 1971; Assaeed 1982). When grazing is removed, bulk density may decrease over a period of several years (Tate et al. 2004).

While grazing effects on the nutrient dynamics of annual rangelands have not been observed, it is generally accepted that grazing animals accelerate nutrient cycling by bypassing the decomposition pathway. However, nutrient redistribution is not uniform because livestock distribution is not uniform. Tate et al. (2000, 2003) found that livestock deposit excreta in patches reflecting their preferential use of a pasture landscape.

Grazing has positive and negative effects on oak woodland ecosystem sustainability. Positive grazing effects include reduced moisture competition between oaks and herbaceous understory, reduced habitat for rodents that consume oak seedlings and acorns, and elimination of ladder fuels that increase the risk of crown fire. Negative effects of grazing include increased soil compaction due to grazing during the wet season, consumption of acorns and oak seedlings, and reduced soil organic matter (McCreary 2001; Allen-Diaz et al. 2007).

Burrowing animals, including ground squirrels *(Spermophilus beecheyi)*, gophers *(Thomomys bottae)*, and voles *(Microtus californicus)*, can have a dramatic effect on annual rangeland productivity and species composition. Ground squirrels and gophers disturb huge amounts of soil throughout most of the annual rangelands. Disturbed mounds are excellent microsites for germination and establishment of annual seedlings (Stromberg and Griffin 1996; Dyer and Rice 1997). Seed predation may also be an important effect of annual rangeland rodent populations. Voles and house mice *(Mus musculus)* have been shown to decrease wild oat numbers compared with foxtail barley and ripgut brome (Borchert and Jain 1978).

Pathogens

Disease may have a role in vegetation change. Barley yellow dwarf virus, transmitted by aphids, infects many introduced and native grasses in the annual grasslands and oak woodland understories, and it reduces survivorship and seed yield in some species (Malmstrom et al. 2005). Crown rust has been found to reduce biomass and reproduction in wild oats (Carsten et al. 2001). Sudden oak death is a fairly new disease affecting oaks in California and Oregon. It is caused by *Phytophthora ramorum*, which is a newly described pathogen. Plant species that are not killed by this disease act as a reservoir for the pathogen (Lee et al. 2011).

Climate Change

Because scientists are uncertain whether climate change will result in warmer, cooler, wetter, or drier conditions, the effect of climate change on individual plant performance and the structure of plant communities is uncertain. Warmer, wetter weather and elevated atmospheric carbon dioxide may increase productivity and result in changes in species composition. These changes may also cause some plant communities to increase in size and extent and others to decrease. Observed and predicted rise in carbon dioxide may facilitate invasions by non-native plants. Future species composition and structure of annual rangeland communities will be determined by a suite of global changes, potentially resulting in new dominant species and new community structures (Dukes and Shaw 2007; Shaw et al. 2011).

Because the effects of climate change cannot be determined by experimentation alone, scientists use global models to predict future precipitation and temperature patterns. Climate studies indicate that, on average, California ecosystems will experience warmer, wetter winters and slightly warmer summers, but there is no evidence that the seasonal Mediterranean climate will change. The winters will remain wet and cool and the summers dry and hot. However, the spatial and temporal distribution of winter precipitation, the frequency of extreme events, and the length of the growing season may change. These changes in temperature and precipitation will result in changes in ecosystem structure, function, and services (Dukes and Shaw 2007).

While the full extent of climate change impacts on rangeland forage production and species composition in California's annual rangelands is not extensively studied, one study forecasts changes in precipitation patterns on California rangeland production. It concluded that areas of the state suitable for cattle grazing would shift, as some areas become wetter and others become drier, depending on the climate model. Statewide, they predicted range forage production would decline between 14 and 58 percent (Shaw et al. 2011). Climate model projections suggest that forage production in Bay Area rangelands may be enhanced by future conditions in most years, but altered precipitation patterns could mean delayed germination, resulting in shorter growing seasons and longer periods of inadequate forage quality (Chaplin-Kramer and George 2013).

Scientists predict that if climate change results in warmer temperatures, lower humidity, higher winds, and drier fuels, fire ignition rates and spread will increase. Torn et al. (1998) forecasted that climate change will result in increased number of fires that escape containment in regions with large amounts of grass or brush fuels.

The distribution of vegetation may change in response to global climate change. Because some of California's oaks are constrained by climatic factors, some scientists have hypothesized that their range may be reduced and their location may shift to the north (Kueppers et al. 2005). Scientists studying life history strategies in California's Mediterranean shrublands hypothesize that climate change trends toward warmer winter temperatures will favor facultative sprouters, and increasing rainfall will favor nonsprouters and obligate resprouters, while reduced precipitation will favor facultative sprouters. Increasing fire probability will favor facultative species, while decreasing fire probability will favor obligate resprouting species. Because future climatic and fire regimes may favor one life history strategy over another, the distribution of shrub species and communities may change (Ramirez et al. 2012).

ECOSYSTEM SERVICES

Ecosystem services are the benefits humanity obtains from the environment, and they are generally categorized into four service types: provisioning, regulating, habitat, and cultural

Table 2. A selection of ecosystem services–related studies conducted in the annual grasslands and oak woodlands of California

Ecosystem services category	Services from oak woodlands–annual grasslands
Provisioning services	livestock production
	forage production
	water supply
	timber/fuel wood production
	genetic resources
Regulating services	climate regulation
	water and nutrient cycling
	moderation of extreme events
	pest control
	pollination
	resistance to weed invasion
Habitat services	plant diversity
	wildlife diversity
	migratory corridors
Cultural services	aesthetic
	recreation/tourism

Source: Adapted from categorization of ecosystem services in MEA 2005 and TEEB 2010.

(TEEB 2010; MEA 2005). California's annual grasslands and oak woodlands provide multiple benefits to society, including forage and livestock production, wildlife habitat, recreation, carbon sequestration, and drinking water supply (table 2). Management and conservation of rangelands is critical in maintaining ecosystem function and capacity to support goods and services over time. Services can be provided locally by an ecosystem, but the benefits to human well-being can also accrue across multiple scales (de Groot et al. 2010). For example, agricultural production can provide food at the local and global levels; managed watersheds and open space provide water and nutrient cycling and community value at the regional level; and conservation practices can provide carbon sequestration and climate-regulating functions at the global level.

Across California's annual grasslands and oak woodlands, there has been a historical focus on agricultural production, with the goal of sustaining the state and national food supply. However, there is increasing societal demand for provisioning agricultural goods (e.g., livestock and forage production) and additional services (e.g., abundant and high-quality water, wildlife habitat) through the management and conservation of these lands (Briske 2011). Balancing trade-offs between agricultural production and the maintenance of ecosystem services will be a key challenge. Here, we highlight an example of a framework for understanding multiple ecosystem service provisioning across a managed oak woodland–annual grassland system.

Case Study

During the mid-twentieth century, approximately 1.9 million acres of oak woodlands were cleared to create productive, open grasslands (Biswell 1954; Murphy and Crampton 1964; Bolsinger 1988). The UC Sierra Foothill Research and Extension Center (SFREC)—located in the northern Sierra Nevada foothills in Yuba County, California—has been a natural laboratory for oak woodland research (McCreary 2010). At SFREC, woody species (predominantly *Q. douglasii*, *Q. wislizeni, Ceanothus* spp., and *Toxicodendron diversilobum*) were actively cleared during the 1960s for forage improvement objectives, and selective woody species removal continued throughout the 1970s and late 1980s. The resulting gradient of woody cover (i.e., cleared open grassland, thinned savanna, and unthinned woodland) has served as a model managed landscape to assess trade-offs and synergies between multiple ecosystem service–based goals across different management scenarios.

State and transition models have been proposed as a framework to explicitly assess trade-offs and win-wins for ecosystem management options (George 1992; Eastburn et al. 2017). Spider diagrams are one approach to simply illustrate relative quantities of goods and services associated with different ecosystem management options (e.g., alternative vegetation states in a state and transition model). Figure 11 demonstrates the trade-offs and win-wins in ecosystem response based on alternative vegetation states adapted from George et al. (1992) and Huntsinger and Bartolome

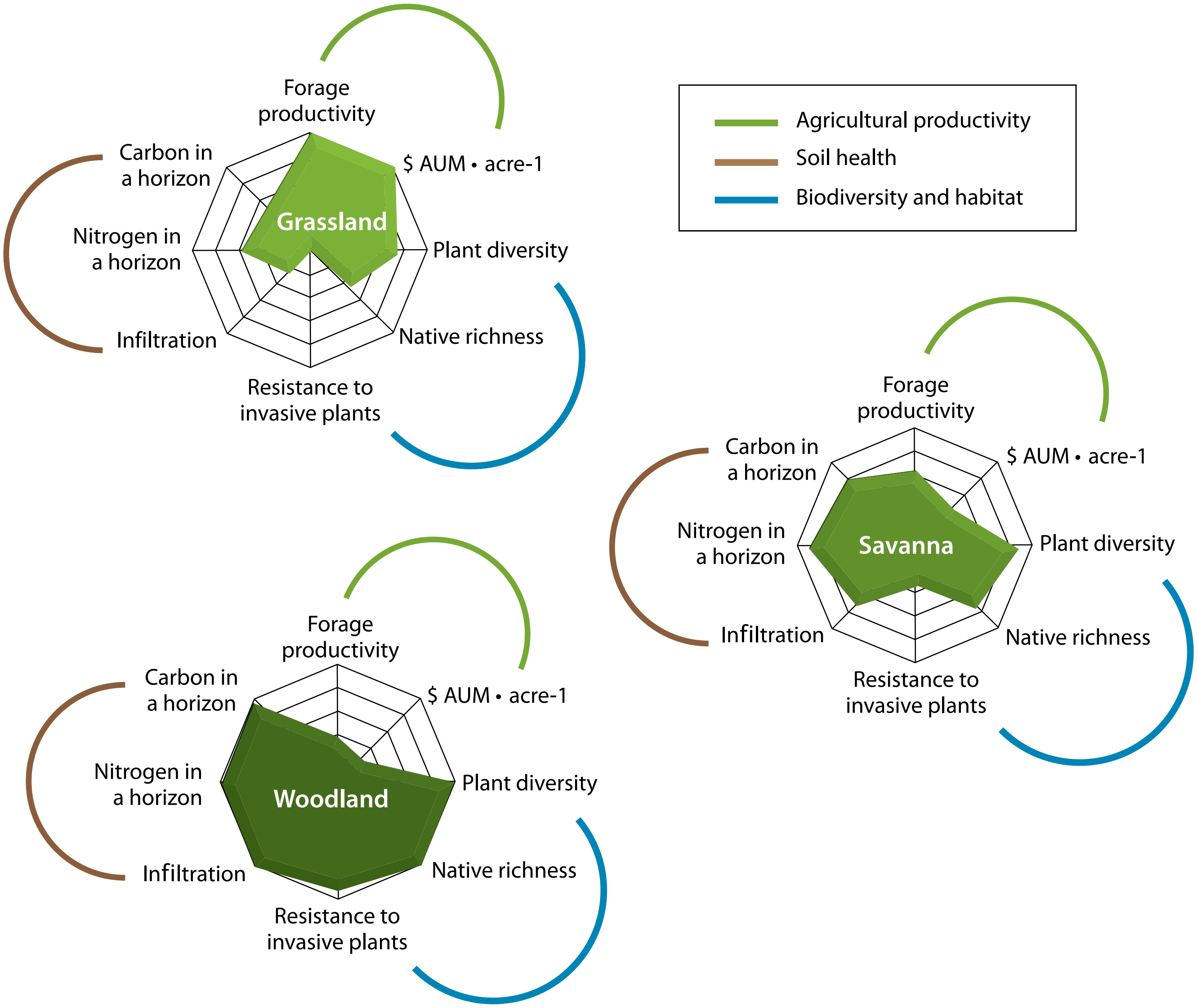


Figure 11. Spider diagrams illustrating the quantities of multiple goods and services under different ecosystem management options, resulting in alternative vegetation states: grassland (< 10% canopy cover), savanna (10–49% canopy cover), and oak woodland (> 50% canopy cover). Data on ecosystem service indicators were collected across 5,300 acres of managed oak woodland–annual grassland at the Sierra Foothill Research and Extension Center in Yuba County, California. *Source:* Adapted from Eastburn at al. 2017.

(1992) for the Sierra Nevada foothill gravelly-loam ecological site.

For each ecosystem service, the maximum distance from the center of the diagram represents the highest level of provisioning (i.e., relativized by maximum observed levels across all three states); therefore, the extent of area covered within each diagram allows for direct visual comparison of trade-offs and win-wins. For example, while the grassland state maximizes agricultural productivity, there are clear trade-offs for soil health, biodiversity, and habitat relative to the other management options. The savanna state highlights a local management opportunity to balance multiple ecosystem service goals.

At the landscape scale, maintaining a heterogeneous mosaic of vegetation patches optimizes the benefits of different ecosystem management options, including increased agricultural productivity, maintaining water and nutrient cycling capacity, protecting genetic resources, and enhancing the number of habitat types. Less apparent synergies exist that cannot be directly quantified; notably, conservation of oak woodland–annual grassland landscapes has been linked to socioeconomic sustainability (Huntsinger and Hopkinson 1996; Wetzel et al. 2012). Appropriate economic and social valuations for ecosystem services, taking into account trade-offs and synergies across space and time, remain an open question (de Groot et al. 2010; Villa et al. 2014).

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