Conservation Issues: California Chaparral

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What Is Chaparral?

Chaparral is a diverse, sclerophyllous shrub-dominated plant community shaped by a Mediterranean-type climate (hot, dry summers and mild, wet winters), a complex mixture of relatively young soils (Specht and Moll, 1983), and large, infrequent, high-intensity fires (30–150 year fire return interval) (Keeley and Zedler, 2009; Keeley et al., 2004; Lombardo et al., 2009). Large expanses of dense chaparral vegetation cover coastal mesas, canyons, foothills, and mountain slopes throughout the California Floristic Province (Figure 1), southward into Baja California, and extending north into the Rogue River Valley of southwest Oregon. Disjunct patches of chaparral can also be found in central and southeastern Arizona and northern Mexico (Keeley, 2000).

Along with the four other Mediterranean-type climate regions of the world with similar shrubland vegetation (Central Chile, Mediterranean Basin, South Africa, and southwestern Australia) (Table 1), California has been designated a biodiversity hot spot (Myers et al., 2000). Twenty-five designated locations in all, these hot spots have exceptional concentrations of endemic species that are undergoing exceptional loss of habitat (Myers et al., 2000; Rundel, 2004). Although covering only 2.5% of the world's surface, Mediterranean-type climate regions contain 16% of the world's plant species (Rundel and Pompelli, 2002).

California Chaparral Biodiversity

California is renowned for its biodiversity (Stebbins and Major, 1965). Species richness in the region on a per-area basis is about seven times higher than anywhere else in the continental United States (Keeley and Davis, 2007). A significant amount of this richness can be found in chaparral, the state's most extensive plant community (Figure 2).

Of the 4846 native vascular plant species found in the California, 24% (1177 spp.) occur in chaparral (Table 2) and 44% (516 spp.) of these are considered rare (Keeley, 2005). In areas where chaparral is especially common, high levels of biodiversity and endemism occur, as explained later in the text. For example, California's South Coast bioregion (from Ventura County to Baja California and inland to the western edge of the Mojave Desert) contains the largest number of plant and animal species classified as either endangered, threatened, or of special concern in the contiguous 48 states (CPIF, 2002). San Diego County, where chaparral covers nearly 35% of the land surface (Unitt, 2004), has been cited as having more vascular plant species than in any other county in the continental United States (2314 spp. including 570 nonnatives) (Rebman and Simpson, 2006).

When comparing plant communities, chaparral also leads in the total number of rare plant species, having 18% more than expected by the area it occupies. Lower coniferous forests are similar to chaparral in the number of observed versus expected rare species per area, but have 30% fewer rare species (359 spp.) (Keeley, 2005).

Chaparral Community Types

A key difference in diversity between Mediterranean-type climate ecosystems is related to differences in vegetation structure. California, Central Chilean, and Mediterranean Basin shrubland ecosystems generally develop closed-canopy shrublands and woodlands that shade out most understory species (Keeley et al., 2012b). Consequently, in a mature community, plant diversity tends to be rather low, composed mostly of shrubs, a few herbaceous vines, and, in the case of Chile, lianas (long-stemmed, woody
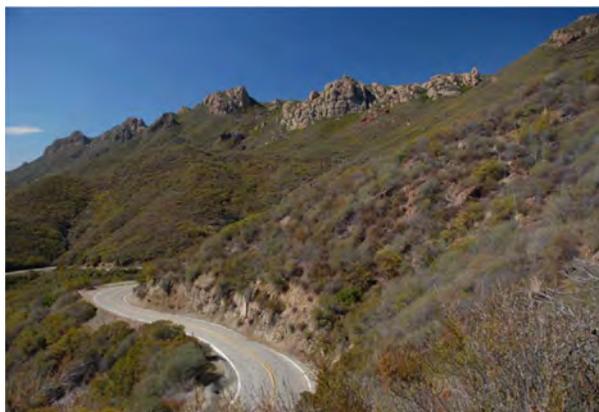
Figure 1   Mixed chaparral in the Santa Monica Mountains National Recreation Area, California.

Table 1   The five Mediterranean-type climate shrubland regions in the world

Location	Local name	Total vegetated area (km^2)[a]	Percent shrubland[a]	Native flora (% endemic)[b]	Number of threatened taxa[b]	Endemic fire followers	Soils
California	Chaparral	98,575	34	4300 (35)	718	Many	Young
Central Chile	Matorral	111,725	79	2400 (23)	700–2000 estimate[c]	None	Young
Mediterranean Basin	Maquis and garigue	1,286,950	45	25 000 (50)	4251	Many	Young
Southwestern Australia	Kwongan (heathlands) and mallee	430,875	63	8000 (75)	1451	Many	Old, nutrient-poor
Cape of South Africa	Fynbos and renosterveld	68,175	97	8550 (68)	1300	Many	Old, nutrient-poor

[a]Keeley et al. (2012a,b).
[b]Cowling et al. (1996).
[c]Royal Botanic Garden Edinburgh (2015).

vines). In the understory, there may be sparse populations of a few annual and herbaceous perennial species, but these populations fluctuate with annual precipitation. In contrast, shrub canopies are much more open and the diversity is higher in the two other Mediterranean-type climate shrublands, South African fynbos and southwestern Australian heathlands (Table 1).

Due to the closed-canopy structure of California chaparral, it can be easily viewed by the untrained observer as merely an amorphous green, dense carpet covering hundreds to tens of thousands of hectares. However, closer examination reveals significant biodiversity depending upon the spatial and temporal scales being considered. Since the species mix in chaparral can vary dramatically from one location to the next, there are a significant number of chaparral types that are distinctly different from one another.

V.L. Holland (1977) was the first to develop a thorough classification of California vegetation. Using a "top-down" approach, he divided the state into geographic regions and then considered ecological relationships. Holland and Keil (1989) expanded upon this, ultimately identifying 11 different chaparral community types. Six of these types are recognized by dominant species (chamisal or chamise, redshanks, manzanita, *Ceanothus*, scrub oak, and mixed), four geographically (maritime, channel island, montane, and semidesert) and one geologically (serpentine). Chamise (*Adenostoma fasciculatum*), redshanks (*Adenostoma sparsifolium*), and *Ceanothus* chaparral can form stands ≥ 1000 m^2, with the identifying species comprising nearly the entire canopy. Manzanita (*Arctostaphylos* spp.) and scrub oak (*Quercus* spp.) can also form nearly pure stands, but typically in smaller patches.

In an update to the California Natural Diversity Database, R.F. Holland (1986) examined the literature and divided the chaparral further by identifying 44 different chaparral community types. In keeping with V.L. Holland's original methodology, maritime chaparral was separated into northern, central, and southern forms. For example, southern maritime chaparral was differentiated from the other two by geology and locale: growing in "weathered sands within the coastal fog belt" and "restricted to Torrey Pines State Natural Reserve and a few scattered nearby localities." *Ceanothus* chaparral was subdivided into different types including buckbrush (*C. cuneatus*) and bigpod *Ceanothus* (*C. megacarpus*) chaparral.

Sawyer et al. (2008) diverged from Holland by attempting to identify plant "alliances," also known as vegetation groups, determined by the most common species present. Using this "bottom-up" approach, they identified over 70 different shrubland
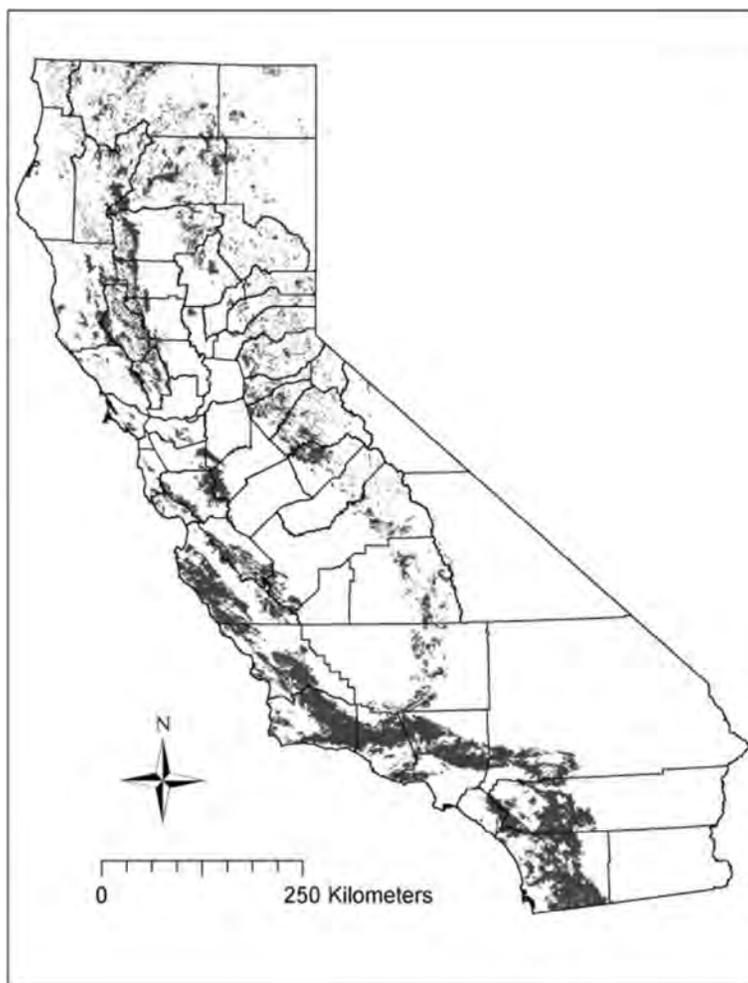
Figure 2   Primary distribution of chaparral in California. Map from Keeley, J. E. and Davis, F. W. (2007). Chaparral. In: Barbour, M. G., Keeler-Wolf, T. and Schoenherr, A. A. (eds.) *Terrestrial vegetation of California*. Berkeley, CA: University of California Press.

Table 2   Life-form for selected California native vascular plant species and those associated with the chaparral

Life-form	All native species	% All native species[a]	Chaparral species	% Chaparral species[a]	Chaparral-only species
Annual herb	1469	30	415	35	27
Perennial herb	2524	52	460	39	24
Shrub	599	12	228	19	54
Tree	84	2	22	2	2
Others	170	4	52	4	3
Total	4846	–	1177	–	110

[a]Rounded %. From Keeley and Davis (2007).

alliances that can be considered chaparral (those containing at least two common chaparral shrub taxa: *Adenostoma*, *Arctostaphylos*, *Ceanothus*, *Cercocarpus*, *Garrya*, or shrub forms of *Quercus*).

   This shrubland alliance classification scheme can be useful for land managers and conservation efforts because it allows for the identification of threatened plant communities. However, the lack of specific parameters in determining the existence of an alliance makes the scheme problematic when attempting to measure biodiversity or conducting ecological research because plant populations from one community usually blend into another. Consequently, it is difficult to determine when one alliance ends and another begins. The scheme can also ignore smaller species groupings. For example, the current classification includes distinct stands of cliff spurge (*Euphorbia misera*) that exist on Point Loma in San Diego County under the broader California sage scrub category.

   A geographically/ecologically based classification scheme like Holland (1977) provides a better tool for research because the units are functional ecological communities rather than a cluster of a few defining species (Zedler, 1997). For example,

Vasey et al. (2014) investigated the possible influence of fog on the compositional diversity of central maritime chaparral. They found a distinct shift from *Arctostaphylos*-dominated chaparral in coastal sites to *Adenostoma*-dominated chaparral in the interior. They also found significant endemism on the coast within *Arctostaphylos* and *Ceanothus*, thus displaying greater change in chaparral diversity across the broad landscape (gamma diversity) than chaparral in the interior. Such findings could stimulate comparative research of other maritime chaparral types (see later text). This finding also identifies a potential threat from climate change. Coastal *Arctostaphylos* and *Ceanothus* communities will likely come under threat if fog decreases.

Measuring Chaparral Biodiversity

There is no single measure of biodiversity for any community type, let alone chaparral. It can be based on landscape or biome diversity or evolutionary relationships such as species diversity or other measures that reflect genetic diversity. It can also focus on ecosystem processes and diversity and be based on characteristics such as the variety of responses to fire like resprouting, reseeding, or colonizing from outside the burned habitat. The most commonly used metric for measuring diversity is species diversity.

Species diversity is of interest at different spatial scales. For example, *point diversity* measures how many species are within a single square meter of soil surface. More commonly, *alpha diversity* (α) measures the diversity of larger areas, such as 1000 m^2 within a single community (Table 3). When one is interested in how species change across the broader landscape within the same community type (eg, chaparral), *gamma diversity* (γ) is being expressed. Alternatively, *beta diversity* (β) is generated by the juxtaposition of different plant communities within a certain area (eg, chamise chaparral, oak woodland, and conifer forest). These types of diversity measures are illustrated in Figure 3.

Historically, ecologists developed a number of species diversity indexes (e.g., the Shannon–Wiener, Simpson, Sørensen, and Whittaker indexes) that include patterns of abundance of individual species.

Figure 3   Different measures of diversity. *Alpha diversity* (α) is the expression of diversity within a single community over a large area as in this patch of chamise chaparral. *Gamma diversity* (γ) is a measure of how species change across the broader landscape within the same community (e.g., chaparral). *Beta diversity* (β) is generated by the juxtaposition of different plant communities on the landscape (e.g., chamise chaparral, oak woodland, and conifer forest).

Table 3   Species diversity in various Mediterranean-type climate regions

Community	Diversity	
	Species/1 m^2	*Species/1000 m^2*
Coastal chaparral (2nd year)	7.1 (0.5)	46.5 (2.1)
Interior chaparral (2nd year)	12.2 (0.9)	53.0 (2.8)
Arizona chaparral (spring and fall 1st year)	25.2 (2.0)	107.3 (9.3)
South African fynbos	15.2 (1.1)	63.8 (4.0)
West Australian heathland	13.6 (2.9)	65.0 (–)
Western Mediterranean maquis	8.9 (3.3)	35.6 (8.3)
Eastern Mediterranean maquis (open-canopy)	27.8 (2.1)	105.2 (10.3)

Number of species per unit area. Standard error in parentheses.
Modified from Keeley, J. E., Fotheringham, C. J. and Rundel, P. W. (2012). Post-fire regeneration of chaparral under mediterranean and non-mediterranean climates. *Madroño* **59**, 109–127; Keeley, J. E., Bond, W. J., Bradstock, R. A., Pausas, J. G. and Rundel, P. W. (2012). *Fire in mediterranean ecosystems: ecology, evolution and management*, 528 p. Cambridge: Cambridge University Press.

These can be useful as a means of illustrating different community structures such as comparing California interior chaparral and southwestern Australian heathland. Although these two communities have roughly similar species diversity at the different scales, chaparral is structured very differently from heathland (Keeley et al., 2012b). Cover in chaparral is predominantly from a few dominant shrubs and the vast majority of associated species are subordinate, comprising relatively little cover. In contrast, the heathland has many species that generally share the space equally in the community.

In an interesting study of shrublands in the Santa Ynez Mountains of the central coast of California, it was found that shrub species diversity generally increased at higher elevations, on steep slopes with significant topographic variability, in rocky conditions, and where potential soil moisture and total canopy were low (Moody and Meentemeyer, 2001).

Diversity Within Individual Plant Taxa

Arctostaphylos, one of the chaparral iconic shrub genera, provides an example of the community's notable gamma diversity.

With its characteristic thin, red bark and urn-shaped flowers, the genus *Arctostaphylos* is remarkably adaptable. It is a major component of the montane chaparral community, growing in granitic soils above 1400 m with an average annual rainfall over 90 cm, as well as in sandy soils found in the southern maritime chaparral of Del Mar, California, with an average annual rainfall of 33 cm (Halsey, 2005). The threatened endemic Ione manzanita (*A. myrtifolia*) is mostly restricted to a narrow corridor in Amador County, California, where it grows in acidic soils with high aluminum content.

Within a 35 km diameter circle, centered near San Luis Obispo on California's central coast, one can find seven localized endemic species of manzanita (*A. obispoensis*, *A. pilosula*, *A. luciana*, *A. rudis*, *A. pechoensis*, *A. osoensis*, and *A. morroensis*). Similar to Ione manzanita, these seven species are confined to edaphic "islands," outcroppings of particular soil types (serpentine, Monterey shale, granitic, and Pleistocene sands) where chaparral is typically found among a landscape of forest, coastal scrub, and grassland. These islands may have served as genetic reservoirs for the genus, with different species migrating onto and off the soils during the numerous Ice Ages (Kauffmann et al., 2015).

The ability of the genus to adapt to hostile environmental conditions can also be seen in its drought-resistant leaves, its symbiotic relationship with mycorrhizal fungi that facilitate the absorption of nitrogen and phosphorus from nutrient-poor soils (Read, 1983), and its dependence on chemicals produced by fire for successful seed germination (Keeley, 1987). *Arctostaphylos* adaptive radiation has led it to become the most species-rich shrub genus in California.

A high level of diversity applies to another common chaparral shrub genus as well, *Ceanothus*. Within a distance of 100–300 km, depending on the steepness of the local terrain, one can discover an estimated local turnover rate of 50% in *Ceanothus* species (Cody, 1986). This is especially true along the central coast where the influences of a steep climate gradient and geographic variation shape central maritime chaparral (Vasey and Parker, 2014; Vasey et al., 2014) (**Figure** 4). The nonresprouting, shallow-rooted species (∼80% of *Ceanothus* spp. California) are renowned for their ability to survive severe water stress. Ironically, they are also more susceptible to mortality during extreme drought because of their shallow root formation (Pratt et al., 2008).

Faunal Diversity

California is ranked first in the United States in mammal diversity, fourth in bird diversity, and fifth in reptile diversity. California is also one of the five top-ranking states for the number of animal species at risk (Stein, 2002). Many of these species can be found in the chaparral.

Although most bird species are not restricted to one plant community, the California thrasher (*Toxostoma redivivum*) and the wrentit (*Chamaea fasciata*) are exceptions. Both are nearly exclusive to chaparral. The thrasher's narrow distribution inspired Grinnell (1917) to coin the now famous term ecological "niche." Referring to the chaparral, he wrote,

> These various circumstances, which emphasize dependence upon cover, and adaption in physical structure and temperament thereto, go to demonstrate the nature of the ultimate associational niche occupied by the California Thrasher.

Erickson (1938) did an extensive study of the wrentit and found that individuals generally restrict movement to a territory of 0.8 ha or less. Noell (1969), one of Erickson's students, conducted research on the thrasher and found that although its territory size appeared to be substantially larger than that of the wrentit's, it remains a chaparral-centric species as Grinnell described.

The endangered California gnatcatcher (*Polioptila californica*) is a key indicator species within the coastal California sage scrub community, a closely related native shrubland to chaparral. In contrast to woody chaparral, this community is characterized by generally brittle subshrubs such as California buckwheat (*Eriogonum fasciculatum*), California sagebrush (*Artemisia californica*), and various aromatic sages (*Salvia* spp.).

Twenty-five percent of all butterfly species north of Mexico inhabit southern California, with 154 permanent residents and 14 migrants (Ballmer, 1995). San Diego County alone is home to over 600 native bee species, half of which are found in shrubland plant communities. This is more than any other comparable region in the United States (K.-L. J. Hung, unpublished data). Fourteen species of walking-stick insects (*Timema* spp.) have evolved multiple variations of cryptic coloration in relation to their host plants,
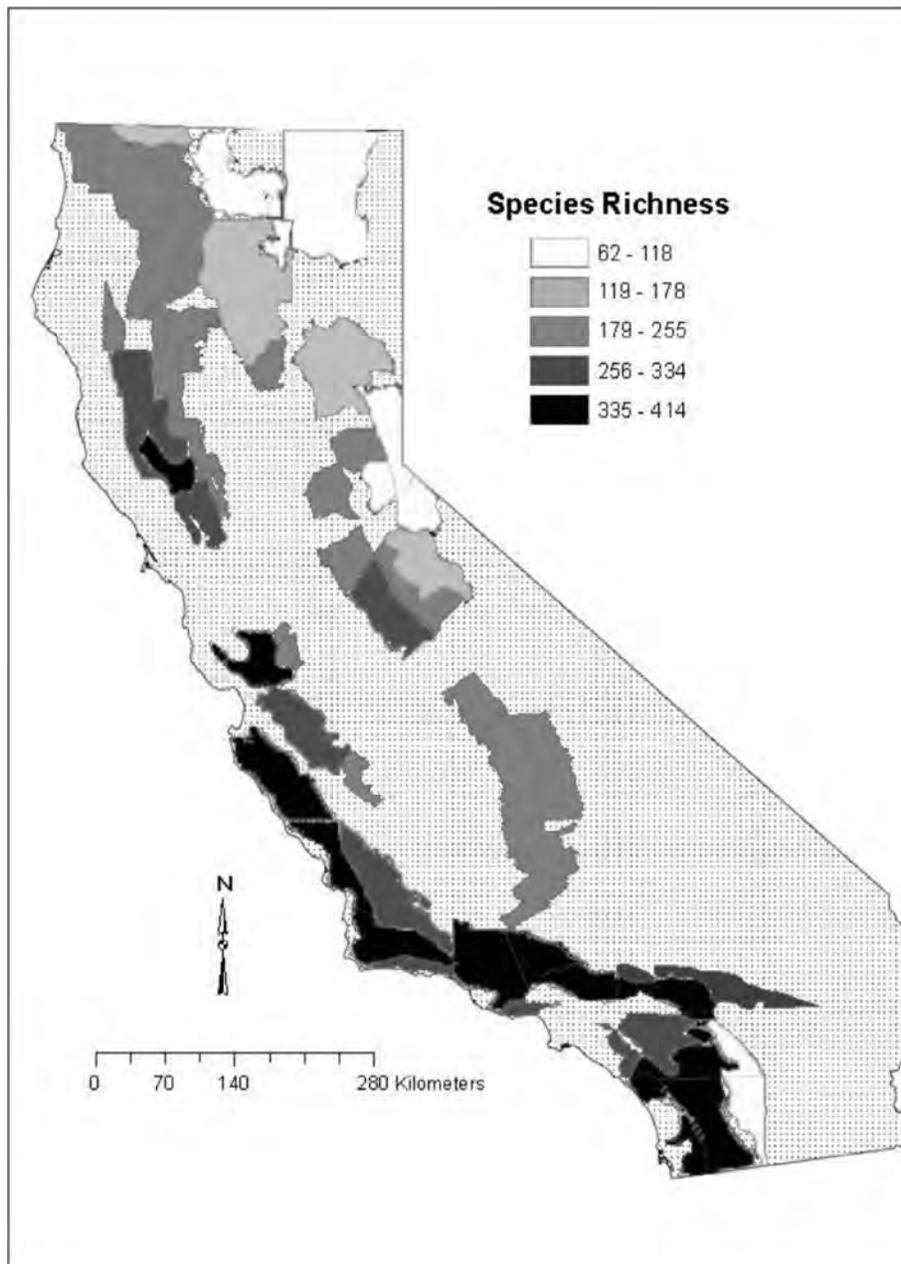
Figure 4   Observed pattern of chaparral plant species richness in 74 subregions containing 90% of the total chaparral area in California. Lighter areas represent the most richness. Data from Keeley and Davis (2007).

primarily *Ceanothus* and *Adenostoma*. Studies suggest that the speciation of the genus is driven by diversifying selection for crypsis, adaptations that allow a species to avoid detection (Crespi and Sandoval, 2000).

Chaparral mammal diversity has been reduced significantly due to human population pressures, most notably causing the extinction of the California grizzly bear (*Ursus arctos californicus*). The last grizzly in southern California was shot near the southeastern corner of Orange County in Trabuco Canyon in the Santa Ana Mountains in January 1908. The final recorded grizzly bear sighting in the state occurred in 1924 around the vicinity of Sequoia National Park (Storer and Tevis, 1955). The loss of the grizzly has likely had cascading effects on the chaparral ecosystem. Beyond possibly predating on mesopredators and herbivores, grizzlies were known to establish tunnels throughout dense chaparral stands that facilitated easier movement across the landscape. These tunnels could have been used by other species as well.

Prior to the grizzly's extinction, four genera of large herbivores, many smaller herbivores, and numerous carnivores, including the large short-faced bear (*Arctodus simus*), dire wolf (*Canis dirus*), and saber-toothed cat (*Smilodon fatalis*), became extinct in California near the end of the Pleistocene between 11 200 and 10 800 BP (Owen-Smith, 1987; Stock, 1930). Many of these large herbivores may have been keystone chaparral species, having a disproportionately large impact on ecosystem function.

Owen-Smith (1989) suggested these Pleistocene mammals maintained widespread landscape diversity through disturbances and the modification of nutrient cycling. With the extinction of these large herbivores, the habitats they may have maintained disappeared along with the species that depended on them. The loss of megaherbivores would have likely allowed for the expansion of shrublands and woodlands because of their hypothesized physical disruption of such plant communities.

Pinter et al. (2011) reviewed vegetation and fire shifts in the Americas following the Last Glacial Maximum at the end of the Pleistocene. While the authors acknowledged that climate change exerted significant controls on the latest Pleistocene paleo-environments, they emphasized that climate was not necessarily the only control. Specifically, they noted that the extinction of megaherbivores, the concomitant increase in vegetation biomass, a sharp increase in burning and fire intensity, and the resulting changes in vegetation and vegetation structure across North and South America were synchronous with the abrupt arrival of humans to the Americas between 15 000 and 13 000 BP after crossing the Bering Sea land bridge from Asia. Data across the Americas support the hypothesis that humans played a crucial role in these transformative events as they progressively migrated over the landscape. For example, the faunal extinctions, vegetation changes, and increased burning first appeared in Alaska and then later in more distant regions. Spikes in charcoal at Pacific coastal sites in South America between 13 500 and 11 500 BP coincide with paleobotanical shifts toward shade-intolerant vegetation.

Megaherbivores in the Caribbean region lasted longer than mainland counterparts by 8000 years until humans arrived.

It is likely that continued burning by Native Americans caused the reduction of native shrubland habitat in California near areas of occupation, especially along the central coast (Keeley, 2002). Cooper (1922) provided interesting evidence that "dense chaparral once covered extensive areas which are now grassland or under cultivation." It is likely that many of the nonnative grasslands seen today were once shrublands.

Influence of Geology

California's unique biological diversity has also been shaped by its physical geography, one of the most geologically complex in the Western Hemisphere (P. Abbott, personal communication, 3 November 2001). Due to the conjunction and movement of three tectonic plates, floating upon the Earth's surface like frosting, California is an accumulation of leftovers: seafloor sediments, fragments of foreign terrain, and chunks of recycled crust jumbled together like slabs of lithified lasagna.

All this geologic pushing and shoving has created some remarkable landform variations. Mount Whitney and Death Valley, the highest and lowest spots in the lower 48 states, respectively, are within 129 km of each other. The movement has also created a complex mixture of young, nutrient-poor soil types where chaparral can be found, including those made from dense shale, sandstone outcrops, volcanic soils, iron-rich red gabbro, and serpentine. Outcrops of serpentine, a greenish, ultramafic (high in magnesium and iron) metamorphic rock that originates from heavy, accreted oceanic mantle, support hundreds of endemic species and subspecies representing a significant contribution to California's rich flora. It has been estimated that about 13% of the plant species endemic to the state are serpentine endemics (Safford et al., 2005). Considering that serpentine is relatively uncommon (it represents about 1.5% of the state's underlayment and is mostly restricted to the northern part of the state), it has an outsized influence on biodiversity.

Interestingly, California's active geology may have also been influential in creating the region's anthropological jigsaw prior to European contact. In addition to increasing the potential for allopatric speciation among plant and animal species, the enormous number of topographically distinct provinces helped to separate prehistoric human populations. Combined with the region's ecological diversity, this likely contributed to producing a remarkable amount of linguistic diversity in Native California cultures (Codding and Jones, 2013).

Influence of Climate

Climate change is a crucial driver of evolution. During the early Pleistocene when California's Mediterranean-type climate was being firmly established (Axelrod, 1981), combined with glacial/interglacial shifts, new selection pressures facilitated the rapid speciation of many chaparral plant taxa such as *Ceanothus* and *Arctostaphylos* (Raven and Axelrod, 1978; Stebbins, 1976). As recently as 15 000 years ago, chaparral covered the Vizcaino Desert in Baja California, about 300 km farther south than it does today (Rhode, 2002). Such changing climate patterns have also been responsible for interesting disjunctions in the distribution of some taxa. For example, populations of madrone (*Arbutus menziesii*) in southern California may be relics of a wider distribution, left behind in refugia as the species began to disappear in surrounding areas as the climate dried. Madrone remains a common species farther north. The nonresprouting, obligate seeding population of *Ceanothus tomentosus* in southern California presents an intriguing evolutionary puzzle as there is a second population in the central Sierra Nevada that resprouts (Schwilk and Ackerly, 2005). Since resprouting is considered the ancestral condition, the southern population may have lost this ability in response to the rapidly changing climate and the concomitant increase in fire due to the seasonality created by California's Mediterranean-type climate.

The lack of summer rain creates 6–7 months of drought, which usually begins in May and lasts through October. This has required plants to start their growing season in the winter when water is available and fostered a wide array of drought adaptations. These adaptations include summer deciduousness, the resistance to cavitation in the xylem (breaking of the water column by air) in taxa such as *Ceanothus*, and thick, evaporation-resistant leaves. Schimper (1903) was the first to describe these "sclerophyllous" leaves:

> *The mild temperature districts with winter-rain and prolonged summer-drought are the home of evergreen xerophilous woody plants*, which, owing to the stiffness of their thick, leathery leaves, may be termed *sclerophyllous* woody plants.

Seasonal drought has also increased the influence of slope aspect, the direction in which a mountain or hillside faces, creating diverse habitats within relatively small distances. Because of decreased solar radiation and thus reduced rates of evaporation, north-facing slopes are generally dominated by dense, more mesic vegetation communities with broad-leaved, obligate resprouting species such as toyon (*Heteromeles arbutifolia*), lemonade berry (*Rhus integrifolia*), and oaks (*Quercus* spp.). On sun-drenched south-facing slopes, less dense, xeric communities exist that are frequently composed of obligate seeding *Ceanothus* (*Ceanothus* spp.), chamise (*Adenostoma fasciculatum*), and California sage scrub taxa such as *Salvia* and *Eriogonum*.

Particularly instructive is the comparison of diversity patterns between California chaparral with its characteristic Mediterranean-type climate of a single rainy season and southeast Arizona with a bimodal rainfall pattern (Keeley et al., 2012a). Although the dominant shrub species are similar between these two regions, the postfire floras exhibit major differences. Arizona chaparral has both a spring growing season and a fall growing season, resulting in two very different postfire floras. These two floras are distinct in that the spring flora matches many of the same species found in California chaparral, whereas many of the fall floras have tropical affinities. Because of the two different floras, the total diversity of chaparral in Arizona is substantially higher than in California chaparral (Table 3). Other dissimilarities include the prominence of perennial grasses in Arizona, which is promoted by summer rains. This life form is largely nonexistent in California postfire chaparral because spring annuals are far better at persisting in landscapes dominated by a long summer drought. Some perennial grasses in California are tolerant of the long summer drought, such as *Stipa pulchra*, but they generally occur on clay soils rather than the rockier soils common to chaparral environments.

Influence of Fire

California chaparral has been shaped by a natural fire regime characterized by large, high-intensity crown fires with a fire-return interval, depending on the location, of 30–150 or more years (Keeley and Fotheringham, 2001; Keeley et al., 2005b; Lombardo et al., 2009; Safford and Van de Water, 2014).

In response to the natural fire regime, there is a rich diversity of long-lived dormant seeds, bulbs, and corms that are triggered by fire cues to germinate and resprout. As a consequence, chaparral exhibits dramatic increases in diversity after fire, represented primarily by annuals that comprise about a third of the chaparral flora, but postfire, they comprise about 50% (Figure 5).

Such plant diversity is typically highest in the first couple of years after a fire and much of this diversity is due to pyroendemics, species that are primarily concentrated immediately postfire. Several species typically have smoke-dependent germination and are extremely rare or uncommon except after fire (eg, *Emmenanthe penduliflora*, *Phacelia brachyloba*, and *Ehrendorferia chrysantha*). The seeds of *Arctostaphylos* species are also stimulated to germinate by chemicals found in smoke and charred wood. In contrast, *Ceanothus* species require a heat cue that modifies the seed coat to allow water to reach the embryo (Keeley, 1987).

As the chaparral shrub canopy returns 10–15 years postfire, these ephemeral species are present only as dormant seed banks in the soil and plant diversity is reduced. This is in contrast to the South African fynbos or southwestern Australian heathlands where postfire herbaceous perennials may persist indefinitely due to the more open-canopy nature of these shrublands.

Interestingly, the postfire bloom of geophytes from bulbs and corms appears to be stimulated not directly by fire, but by the additional sunlight that makes contact with the leaves once the chaparral canopy is removed by the flames (Tyler and Borchert, 2003).

It was once hypothesized that seeds of pyroendemics and common chaparral shrub species were prevented from germinating by allelopathic chemicals in the soil and that fire was needed to denature these chemicals and allow germination to proceed (Muller et al., 1968). However, this hypothesis has been rejected because it has been found that these seeds are innately dormant and that the suspected allelopathic chemicals actually increase postfire (Christensen and Muller, 1975; Halsey, 2004; Keeley, 1987).

As long as fire arrives above the lower limit of the natural fire-return interval of 30–40 years, the postfire chaparral ecosystem is extraordinarily resilient and vibrant. However, given increases in fire frequency due to human-caused ignitions, this resiliency can be interrupted. When keystone, nonresprouting (obligate seeding) shrubs, like most *Ceanothus* species, suffer closely spaced fires, their populations are often decimated and effect a type conversion to a less diverse, resprouting-dominated chaparral (Zedler et al., 1983). Such stands become more open and are often invaded by nonnative herbaceous weed species. Fire-return intervals fewer than 6 years have been shown to be highly detrimental to the persistence of nonresprouting chaparral species (Jacobsen and Davis, 2004). Multiple fires within a 6-year interval also reduce resprouting species, further opening the chaparral environment (Haidinger and Keeley, 1993).

The type conversion process and the concomitant loss of biodiversity usually begin with the elimination of obligate seeding shrubs leading to a combination of resprouting shrubs and native sage scrub species or resprouters and alien grasses. The process can ultimately lead to the complete replacement of native chaparral with nonnative grassland (Halsey and Syphard, 2015).

Faunal response to fire has not been adequately investigated in comparison to that of plants (van Mantgen et al. 2015). However, in an interesting study examining the response of birds to fire in San Diego County, it was found that a number of species colonized burned areas and then decreased as the vegetation returned over a 4-year period. These included the lazuli bunting
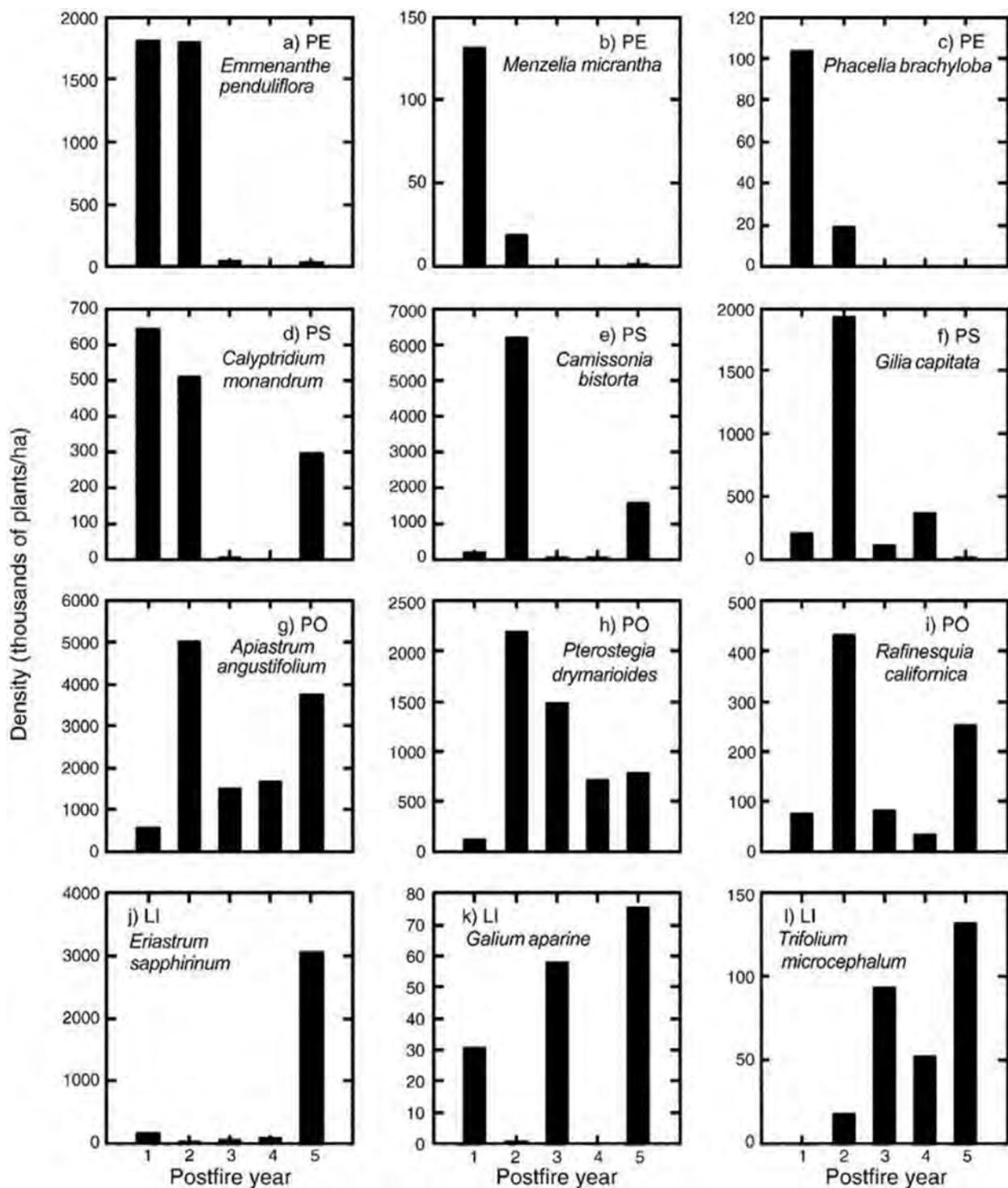
Figure 5   Changes in postfire flora. Postfire changes in the abundance of pyroendemics (a–c), fire specialists that persist during early succession (d–f), opportunistic species that expand after fire and then persist in gaps as determined by annual precipitation patterns (g–i), and species that increase later in succession (j–l). Reproduced from Keeley, J. E., Fotheringham, C. J. and Baer-Keeley, M. (2006). Demographic patterns of post-fire regeneration in mediterranean-climate shrublands of California. *Ecological Monographs* **76**, 235–255.

(*Passerina amoena*), black-chinned sparrow (*Spizella atrogularis*), and Lawrence's goldfinch (*Carduelis lawrencei*) (L. Hargrove and P. Unitt, unpublished data).

In contrast, the populations of resident species that depend on the chaparral cover, such as the wrentit, Bewick's wren (*Thryomanes bewickii*), and California thrasher, were reduced dramatically postfire. Future research examining what happens to

fire survivors of these species would be interesting. Several individuals of these species were seen taking refuge from the flames in a small *Eucalyptus* tree at the edge of the 2003 Cedar Fire (Halsey, personal observation). Since these birds' territories were no longer viable and the unburned areas were likely already occupied, the ultimate fate of these individuals may have been starvation.

Impact of Climate Change

It is predicted, for both wet and dry modeled scenarios, that California may lose up to 50% of its native shrubland due to the impacts of climate change alone (Lenihan et al., 2006). This is based on the prediction that changes in temperature and precipitation will alter the structure, composition, and productivity of all plant communities in California and that wildfires will likely become more frequent (Lenihan et al., 2006). Increased fire activity has already been linked to higher spring and summer temperatures in mid-elevation, Western forests (Westerling et al., 2006). Greater fire frequency will in turn likely increase the potential for type conversion from shrubland.

Safford and Van de Water (2014) suggested chaparral-type conversion is currently spreading northward from the southern part of California to the northern Santa Lucia Range and will likely continue to expand with climate change and population growth.

It is population growth, however, that poses the most immediate threat to chaparral, despite the fact that climate change will have significant impacts on plant community distribution long term. Development, accelerated fire frequencies due to anthropogenic ignitions, and habitat sacrifice in the name of fuel treatments will likely continue to be the most important factors compromising California's native shrublands (Keeley, 2006; Keeley et al., 2005a; Syphard et al., 2007).

Fuel treatments are vegetation-thinning or clearance projects conducted by prescribed fire or mechanical means that are intended to change fire behavior to facilitate control. Defensible space around homes has been shown to be effective in reducing home loss during wildfires. However, vegetation treatments beyond 33 m around homes have proven to be of little value, compromise habitat unnecessarily, and can be counterproductive by encouraging the spread of flammable, invasive weeds (Syphard et al, 2014). Fuel breaks far from homes can be helpful in controlling chaparral wildfires under mild weather conditions, but nearly only if they are placed strategically and are able to be accessed during fire-suppression activities (Syphard et al., 2011). The challenge presented to firefighting agencies is that the most dangerous chaparral wildfires occur during hot, dry weather and strong winds. Under such conditions, fuel treatments are mostly ineffective (Keeley et al., 2004, 2009). As a consequence, it is important to conduct a thorough cost/benefit analysis in determining the appropriate placement of fuel treatments to prevent unnecessary resource costs and habitat loss.

Preserving Chaparral Biodiversity

The increasing threat to the chaparral biodiversity underscores the urgency for government agencies and the public alike to better understand and appreciate California's native shrubland plant community. Such awareness will hopefully encourage actions to protect the chaparral and the ecosystem services it provides such as watershed integrity, moderating the impact of urbanization on local climates, and outdoor recreation. These types of services are necessary to maintaining the health and well-being of surrounding human communities (Watson and Zakri, 2005). Awareness will also help the public develop a better appreciation for the intrinsic value of the community and the organisms that occupy it. Protecting the chaparral's remaining species *for their own sake* aligns with objectives of the international Convention on Biological Diversity agreed to by 198 countries including the United States (CBD, 1992).

Of utmost importance will be for land management agencies, county planning departments, and firefighting agencies to recognize that the present distribution of chaparral does not necessarily reflect its future. As climate change continues and the population increases, fire patterns will change and natural habitats that may be taken for granted today will be changed or eliminated tomorrow.

The chaparral, and the remarkable biodiversity it supports, contributes to making California one of the richest temperate regions on Earth. As a consequence, it is essential that both local and regional land management plans emphasize the preservation of chaparral, especially old-growth chaparral (over 75 years old), by protecting large, contiguous stands from fragmentation, development, unnecessary clearance operations, and increased fire frequencies.

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