MANZANITA

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Botanical Diversity of the California Floristic Province

by Dylan O. Burge, PhD

In the far western United States and northern Mexico, a unique combination of geology, geography, and climate has led to the development of a botanically hyper-diverse region—the California Floristic Province, frequently referred as the "CFP" (Figure 1). The CFP has a Mediterranean-type climate, with mild, wet winters and hot, dry summers. As in other regions of Mediterranean-type climate around the world—parts of South Africa's Cape, southwestern Australia, central Chile, and the Mediterranean basin itself—there is an abundance of unique species with specialized characteristics that are suited to the climate, including many beautiful bulbs, a host of diminutive annuals, a high diversity of conifers, legions of hard-leaved shrubs, and a bewildering array of succulents (Figure 2). Like other Mediterranean-type climate regions, the CFP is recognized by scientists as a biodiversity hotspot of global significance, with a flora that is distinctive from the rest of North America, and indeed from the rest of the world. The region is home to more than 5,000 species of plants, making it one of the most botanically diverse non-tropical regions in the world. To put this high concentration of diversity into perspective, consider that these 5,000 species account for more than one quarter of the species that are thought to live in the whole of the United States and Canada. What is more,

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Figure 1. A map of the California Floristic Province (colored portions). Colored regions inside the state of California are based on a classification of major ecological regions used in *The Jepson Manual*; please refer to "Patterns of Diversity within the CFP" for details on the reasons for recognizing these regions. From top to bottom, NW stands for the Northwestern Region, CaR refers to the Cascade Ranges Region, SN refers to the Sierra Nevada Region, GV refers to the Great Central Valley Region, CW refers to the Central Western Region, and SW refers to the Southwestern Region.

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An Alternative California Floristic Province

by Bart O'Brien

Floristic provinces, by definition, are geographic areas with fairly uniform floras. Such areas typically share additional defining characteristics such as climate type, latitude, and/or geology. For the California Floristic Province (CFP), nearly everyone agrees that the additional primary defining characteristic is its Mediterranean-type climate of hot dry summers and cool wet winters.

Globally, the concept of a Mediterranean-type climate defines the boundaries of all the other parts of the world with the above-mentioned attributes: the Cape Floristic Province in South Africa, the Southwest Australia Province in Australia, the Central Chile Province in Chile, and the Mediterranean Region (itself composed of several subsidiary floristic provinces).

For the CFP, it is comparably easy to differentiate the southern and far eastern boundaries as these are readily recognized deserts: the Great Basin, the Mojave Desert, and the Sonoran Desert. But the northern and nearer eastern boundaries of the CFP are not uniformly agreed upon. These areas are shown as "Vancouverian" on the map opposite and are dominated by redwood forests, mixed evergreen forests, mixed coniferous forests, and yellow pine forests. (Forests—defined here as tree-dominated ecosystems with a closed canopy—are relatively rare elements of the world's Mediterranean-climate areas). The first three forest types are found in northwestern California, while the yellow pine forests dominate the Sierra Nevada. Forests require more water to thrive than do the woodlands, shrublands, and grasslands that typify the vast majority of Mediterranean-type climate ecosystems, and California's forests are no exception to the rule. The Sierra Nevada gains large quantities of precipitation during the winter months but also receives summer rainfall from near ubiquitous afternoon thunderstorms. Northwestern California, particularly in coastal forests, receives tremendous amounts of summer precipitation from the nearly ever-present fog drip. The floral affinities of the dominant plants in these botanically rich areas are to the cooler, wetter, non-Mediterranean-climate to the north and not to the warmer, drier, Mediterranean-climate to the south. However, the Sierran flora and the Klamath-Siskiyou flora include many unusual endemic species and a number of disjunct genera and species that further complicate the matter of defining boundaries.

This map was created by staff at Rancho Santa Ana Botanic Garden in the mid-1990s though a reinterpretation of the Geographic Subdivisions of California map in the 1993 edition of *The Jepson Manual*.

Calycanthus is a good example of a disjunct genus: California spicebush (*C. occidentalis*) is found only in California; Carolina spicebush (*C. floridus*) is found on the east coast of the United States from Virginia south to the Florida panhandle and Louisiana. False bugbane (*Trautvetteria caroliniensis*) is an example of a disjunct species: It is found only in the Klamath-Siskiyou and Cascade regions of California, then to British Colum-

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Figure 2. Diversity of the California Floristic Province. From left to right, top to bottom: ground iris (*Iris macrosiphon*), buck brush *(Ceanothus cuneatus*), Veatch silktassel (*Garrya veatchii*), Baja liveforever (*Dudleya ingens*), Cleveland's bush monkeyflower (formerly *Mimulus clevelandii*, now *Diplacus clevelandii*), southern mountain misery (*Chamaebatia australis*), Fremont's death camas (*Toxicoscordion fremontii*), chalk dudleya (*Dudleya pulverulenta*), and Applegate's Indian paintbrush (*Castilleja applegatei*).

37 percent of the plants found in the CFP are *endemic* to that region—found there and nowhere else in the world. Thus, the CFP is both highly botanically diverse and strongly endemic (see Box 1, Diversity Versus Endemism), contributing a disproportionate amount to the floral distinctiveness of North America, and to the diversity of life on Earth.

The remarkable diversity and endemism of the CFP have been noticed and studied since the time that the early California explorers—including the likes of David Douglas and Thomas Nuttall—returned to Europe and the eastern United States carrying specimens that boggled the minds of late nineteenth century botanical luminaries. Now, nearly two hundred years after the early explorers focused the lens of science on the botanical diversity of the CFP, new kinds of research are revealing how geology, geography, and climate conspired over millions of years to produce the unique environment of the CFP, and how the remarkable plants of the region migrated, diversified, and survived.

Forged in Fire and Ice: the Geoclimatic History of the CFP

Charles Darwin and Alfred Russell Wallace, fathers of the theory of evolution by natural selection, were both heavily influenced by the writings of Charles Lyell, a geologist whose book *Principles of Geology* was on the shelf of every Victorian naturalist worth his or her salt. Lyell's most important idea was that the earth must be extraordinarily ancient. Today, most people take it for granted that the earth is billions of years old, but this is a relatively recent idea, even among scientists. Armed with the dizzying thought that life on Earth might have evolutionary roots that go back hundreds of millions of years, Darwin and Wallace made the intellectual leap to infer that miniscule genetic changes might, over the course of millions of years, lead to major differences among organisms. This idea of deep evolutionary time is what allows modern scientists to understand the evolutionary roots of life on Earth. In addition, the concept of deep evolutionary time implies that life on Earth has experienced almost incomprehensible upheavals of climate and geology, albeit over long spans of time. These changes have determined, in large part, the course of evolution. Acting over millions of years, geology and climate (sometimes simply called geoclimate) have determined how plants evolve, migrate, and survive. Mountains rise and fall through time, creating new climates along their slopes; tectonic shifts alter the shape of the coastlines, which interact with powerful ocean currents to cause changes in land temperature. For the formation of the CFP, the most important geoclimatic events were the recent cooling and drying of the planet, the uplift of the rugged north-south trending mountain ranges that cut the CFP off from the rest of North America, and the development of cold-water upwelling along the coast of western North America.

Prior to the beginning of the Pliocene, a short geologic epoch that scientists define as

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bia, Montana, Wyoming, New Mexico, the eastern United States, and eastern Asia—an extremely unusual pattern of distribution.

All of this leads to three possible lines of thought:

1. A traditional view that the entire non-desert area from southwestern Oregon to northwestern Baja California is the CFP.
2. A competing view that highly forested areas with significantly greater amounts of precipitation should not be included in the CFP: this view would lead to a more cohesive flora.
3. A compromise view that the Sierran flora and the Klamath-Siskiyou flora have multiple affinities and are best considered as transition zones between the Vancouverian Floristic Province and the CFP.

When one studies the regional similarity matrices at the species level (Burge et al. 2016, 10), it is evident that the flora of the Great Central Valley (a region that includes both the Sacramento Valley and the San Joaquin Valley) is the least related to its immediately adjacent geographic subdivisions (TJM2, page 42). The relatedness values for the Great Central Valley (GV) range from a low of 26 percent for both Northwestern California (NW) and the Cascade Ranges (CaR), to a high of just 39 percent for the Central Western Region (CW). Many scientists classify and map most of the San Joaquin Valley as steppe or desert—and therefore NOT part of the CFP—due to its very low rainfall. Portions of the flora of the San Joaquin Valley share a significant number of plant taxa with the Mojave Desert.

As the vegetative cover of the state is further mapped and understood, and the patterns of plant species distribution become clearer, it is likely that a more detailed and correct map of the CFP will emerge. Even now, it is possible to map the extensive coast redwood forests of Santa Cruz and Monterey counties as Vancouverian. n

Reference

Burge, Dylan O., James H. Thorne, Susan P. Harrison, Bart C. O'Brien, Jon P. Rebman, James R. Shevock, Edward R. Alverson, Linda K. Hardison, José Delgadillo-Rodríguez, Steven A. Junak, Thomas A. Oberbauer, Hugo Riemann, Sula E. Vanderplank, and Teri Barry. 2016. "Plant Diversity and Endemism in the California Floristic Province." *Madroño* 63(2): 3-206.

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beginning about five million years ago (Figure 3), the earth was a much warmer, wetter place, with lush rainforests, tropical woodlands, and highly diverse temperate deciduous forests covering virtually all of western North America, with a flora reminiscent of what is found today in the eastern United States. At that time many cold-sensitive plants that are now found exclusively in the CFP, like redwood (*Sequoia sempervirens*), ironwood (*Lyonothamnus floribundus*), and California nutmeg (*Torreya californica*) extended over a vast swath of North America; close relatives of the redwood, for example, ranged over much of the northern hemisphere, including Europe and Asia.

By the beginning of the Pliocene the Sierra Nevada was very well developed and

Seep monkeyflower (*Mimulus guttatus*, recently re-classified as *Erythranthe guttata)*, a member of a plant genus that probably diversified rapidly beginning in the Pliocene. Red Hills, California.

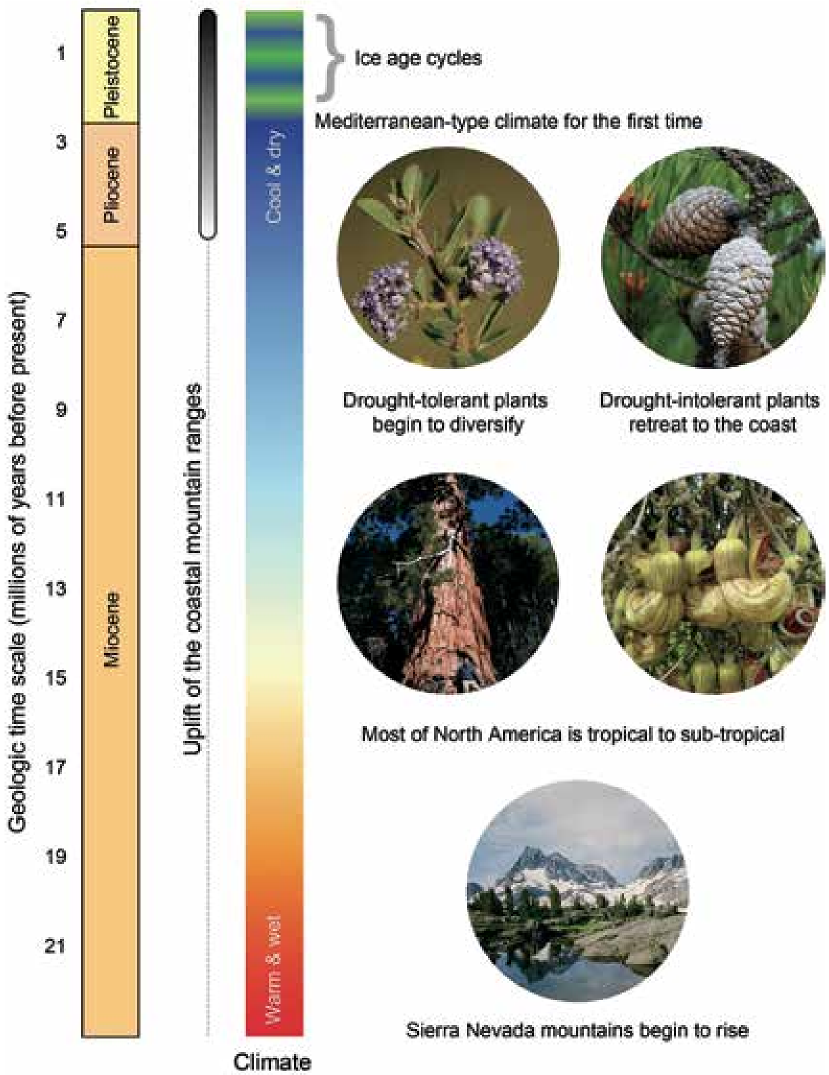

Figure 3. (Right) A timeline for development of the CFP. Images are, from top to bottom, left to right: buck brush (*Ceanothus cuneatus*), Monterey pine (Pinus radiata), giant sequoia (*Sequoiadendron giganteum*), California pipevine (*Aristolochia californica*), and a scene from the Banner Peak area, Ansel Adams Wilderness, California.

presented a formidable mountain rampart similar to what we see today, except that at the beginning of the Pliocene its rivers would have drained directly into the Pacific Ocean, as the mountains of the Coast Ranges had not yet begun to rise. During the late Pliocene and into the next geologic era, the Pleistocene (beginning about two and a half million years ago; Figure 3), the earth cooled and dried. As the climate changed, tropical forests contracted southward and deserts expanded dramatically. Overall, cold-sensitive plants began to disappear, the survivors becoming restricted to small areas of suitable climate. Despite the loss of many species, the cool and dry conditions drove diversification of some plant groups. Many herb lineages were spurred into evolutionary innovation, spawning new drought-adapted species. Well-known examples of CFP-associated groups that probably began to diversify in this way during the Pliocene include the monkeyflowers (*Mimulus*; recently split into two separate genera, *Diplacus* and *Erythranthe*), beardtongues (*Penstemon,* Figure 4), and *Ceanothus*.

While the Pliocene pulse of evolutionary innovation was in full swing, a major geological event was taking place. This was the formation of the westernmost chain of mountains in western North America, the Coast, Transverse, and Peninsular Ranges, all of which formed in roughly the past three million years (Figure 5). Uplift of these ranges created the Central Valley of California, and added to the geoclimatic complexity of the region, creating unique coastal environments entirely walled off from the extremes of heat and cold found in the interior. Uplift of these ranges, and continued erosion of the early Sierra Nevada, exposed a fantastic diversity of rocks, including serpentinite, that weathered to form chemically unusual soils. This archipelago of soil islands spurred further adaptation and the formation (speciation) of new soil-specialized plants.

North America's climate became even colder and drier during the height of the Pleistocene, when the earth entered its most recent series of glacial cycles, during which cold, wet periods of glacier advance alternated with warm, dry periods of glacier retreat, each period lasting thousands of years. During this time the very stable climate adjacent to the Pacific Ocean along the west coast of North America turned into a crucial refuge for species that soon disappeared over most of North America. Many of these species are now found only in the coastal CFP, where they persist under comparatively mild climatic conditions. Iconic examples of these types of plants include Monterey pine (*Pinus radiata*, Figure 6), ironwood (*Lyonothamnus floribundus*), and redwood (*Sequoia sempervirens*). Such plants are often referred to as paleoendemics because they are endemic to the CFP but probably did not originate here; rather, they belong to seemingly ancient evolutionary lineages, many of them with a fossil record extending back millions of years.

Box 1 Diversity Versus Endemism

In the 21st century, the scientific study of the diversity of life on Earth has become a discipline unto itself, with all the terms, definitions, and semantic ins and outs that come with scientific discourse. When scientists talk about biodiversity in a particular geographic region (for example, the CFP), they make a key distinction between the concept of diversity, the total number of species that are present in a region, and endemism, the proportion of those species that are found only there. This is an important topic because one of the fundamental observations of biodiversity science is that diversity is highly heterogeneously distributed on the globe. For example, most of the planet's plant and animal species are found only in the tropics—the tropical regions contain both high diversity and high endemism. And within the tropics there are hotspots, places where unusually high concentrations of diversity and endemism occur; examples include the island of Madagascar, where 80 percent of all species are endemic, and the Hawaiian Islands, where about 90% of the native plants and land animals are endemic. This is an important idea because it means that conservation efforts worldwide must be designed to account for heterogeneity. For example, it has been estimated that more than 50 percent of the world's plant and animal species are restricted to just 1 percent of the planet's surface (including water and land). This means, theoretically at least, that humans could totally protect half of life on Earth by setting aside just 1 percent of the planet for biodiversity. Sadly, this is an almost impossible scenario, because these regions of biodiversity are, like the CFP, split across different countries with different methods of protection, making it difficult to plan for conservation. However, scientists have found that by focusing on understanding patterns of biodiversity, regardless of international boundaries, they can improve understanding of how biodiversity develops and how best to maintain it.

Figure 4. The beardtongues (genus *Penstemon*), a plant genus that probably diversified rapidly beginning in the Pliocene. Left: showy penstemon (*Penstemon spectabilis*), Sierra Juarez, Baja California, Mexico; right: Cedros Island penstemon (*Penstemon cedrosensis*).

Figure 5. Trinity Mountains, part of the North Coast Range. Mount Eddy area, California. Foxtail pines (*Pinus balfouriana*) in the foreground.

Figure 6. Monterey pine (*Pinus radiata*), a coastal, heat-intolerant paleoendemic of the CFP. Isla Cedros, Baja California, Mexico.

It was during the Pleistocene that the CFP began to develop a Mediterranean-type climate. Other arid regions existed then, for example the vast deserts, but the climate that developed in the CFP was totally unique in the history of North America: a combination of hot, dry summers and mild, wet winters. It is difficult to piece together exactly what events of the Pleistocene finally tipped the geoclimatic scale in favor of a Mediterranean-type climate in western North America, but fossil pollen data suggest that ocean currents played a crucial role. Beginning in the Pleistocene, the Pacific Ocean off the coast of western North America became dominated by the California Current, which flows from north to south and delivers cool water from the vicinity of Alaska and Siberia, like a gigantic oceanic conveyor belt. This water absorbs heat from the land in the summer, though the effect of this absorption lessens as distance from the coast increases.

The cooling effect of the California Current is augmented by the prevailing north-westerly winds along the coast of western North America, which cause upwelling of cold, nutrient-rich water along the coast. Because of the properties of the Coriolis effect (the tendency of air and water to rotate around the earth at different speeds depending on latitude), surface water is deflected west, at a right angle to the direction of the wind, and is replaced by cooler, nutrient-rich water from deep in the ocean. Upwelling cools coastal waters and generates fog: when upwelling cold water comes into contact with ocean air laden with moisture from the Pacific, the water condenses into fog. Not only do these fog belts result in cool, forgiving conditions during the hottest part of the summer, creating ideal habitat for plants like fog-harvesting redwood (*Sequoia sempervirens*), they also prevent summer storms—moisture condensed to form fog never has a chance to reach land and power thunderstorms. Because other storms are deflected during the summer by a seasonal northward shift of the polar jet stream, the net effect is an absence of rainfall in the CFP from late spring to early fall, a time when most of North America experiences rainfall.

Though the ocean has always exerted considerable influence over the climate of the CFP, most of the region does not enjoy the direct cooling effects of fog and cool sea air. Long, scorching summers are the norm in most of the interior CFP. However, it is not the same kind of heat that other parts of the continent experience during the summer. What makes a Mediterranean-type climate unique is that the hottest part of the year occurs at the same time as the driest part of the year (hence the well-known phrase, “it’s a dry heat”). In virtually every other terrestrial environment, even parts of the Arctic, the warmest part of the year is also the wettest, but in a Mediterranean-type climate the time of year when plants need the most water—when temperatures are high and evaporation happens fast—is also the time when water is in shortest supply. As a consequence, most plants do not thrive in Mediterranean-type climates. With this factor in mind, it is easy to understand why many of the most successful groups of plants in the CFP are almost unknown outside this region.

Although the tandem action of heat and drought are a crucial aspect of how Mediterranean-type climates affect plant life, winter conditions are also notable. The winters in a Mediterranean-type climate are mild, with moderate rainfall and relatively little frost or snow except in the mountains. This means that frost-tender plants are able to survive. Thus, the CFP provides a refuge for plant lineages that tolerate hot summers but would not be able to survive in regions with very cold winters. In addition to the coastal paleoendemics listed above, many iconic CFP endemics fit this bill, for example, tree-anemone (*Carpenteria californica*), spicebush (*Calycanthus occidentalis;* Figure 7), and California pipevine (*Aristolochia californica*).

It is comparatively easy to see how climatic conditions of today probably affect the extent of different kinds of vegetation. Indeed, this is how the CFP was first characterized. It is much more difficult to look backward in time and infer how the extent of the CFP may have changed over the last several million years. Scientists believe that this climatic region shrank dramatically during the cooler, wetter periods of Pleistocene and expanded again when warmer, drier conditions prevailed. However, some pockets of Mediterranean-type climate probably existed continuously in western North America over the last three million years, allowing for the evolutionary origin and persistence of plant lineages that were adapted specifically to this unusual climate.

Evolution and Ecology in the CFP

For many decades, the high rate of endemism in the CFP has been attributed to the large number of habitat types in the region, which includes microclimates arrayed over rugged, complex terrain as well as the chemically unusual soil islands mentioned above. It was thought that these new, special habitats led to the origin of new taxa that were specifically adapted to unique soils, climates, or both. In the past, these taxa were often called neoendemics, since they seemed to have sprung into existence quite recently, at least compared to the so-called paleoendemics, many of which had fossil records going back millions of years. A lot of the best examples of neoendemic lineages in the CFP are soil specialists. For example, more than 10 percent of CFP-endemic species are serpentine endemics, and many of these most likely became new species as they adapted to serpentine. Another large group of neoendemics is found along the coast of the CFP, where the fog belt supports species with incredibly small geographic distributions, for example many species of *Ceanothus*, manzanitas (genus *Arctostaphylos*), and liveforevers (genus *Dudleya*; Figure 8). Although it is generally true that many of these narrowly distributed species are "young" in

Figure 7. Spicebush (*Calycanthus occidentalis*), an inland, heat-tolerant paleoendemic of the CFP. Butte Creek Canyon, near Chico, California.

Figure 8. Britton's liveforever (*Dudleya brittonii*), a fog-belt-specialized neoendemic of the CFP, with honey bee (*Apis mellifera*). North of Ensenada, Baja California, Mexico.

an evolutionary sense, the real explanation for their existence in the CFP may be something much simpler than the recent availability of new kinds of habitats.

One of the most important recent ideas about the CFP has to do with extinction, or more precisely, lack of extinction. The idea comes from research done by scientists at U.C. Santa Cruz and U.C. Davis, and suggests that high endemism in the CFP is due to a lower rate of extinction in the region, not because more species form there. This was long thought to be the case for paleoendemic lineages like the giant sequoia (*Sequoiadendron giganteum*), which apparently survive in the CFP because it is the only place where they were not killed off by cycles of climate change. However, we now know that this is probably true for neoendemics as well. Like the giant sequoia, these younger species may be "new relicts" which have persisted in the CFP due to its generally stable climate and the availability of rugged terrain, where plants can move up and down in elevation, or shift from a more southern to a more northern-facing aspect, to find optimal climates and avoid extinction during times of climate change.

The idea that extinction rates may be lower in the CFP for all plant lineages also has implications for management of the CFP under human-caused climate change. While the changes in climate induced by humans are happening many times faster than any past changes, the CFP should still provide a buffer in the same way it did in the past. This crucial idea incorporates a concept called **climate change velocity**, the speed at which a certain climate moves across the landscape. The more elevation diversity there is in an area, for example, the slower the velocity of climate change, since the types of climates that exist now at a given level will simply move upward a small distance along the topographic gradient. In this example, plants may be able to easily keep up with climate change by dispersing a short distance to a higher elevation. But in a very flat area—for example, the Central Valley of California—climate change velocity is expected to be high, and plants will have to disperse very long distances very quickly to keep up with climates that are suitable for them. Thus, in the Central Valley, more species are likely to be lost to extinction, and change in vegetation will happen very fast.

Overall, the breadth of recent and ongoing research on the ecology and evolution of the CFP is simply too extensive to cover in a single article. With the advent of new and powerful tools like digital floras (for example the Jepson eFlora, the online version of *The Jepson Manual*), faster DNA sequencing, and remote sensing (satellites, environmental sensor networks), many new insights are emerging. It is likely that scientists will learn more about a variety of subjects that in the past were difficult or impossible to study. For example, scientists will be able to learn more about the abundance of cryptic species that can only be identified using DNA sequencing, the effect of drought on CFP plants, and the influence of symbiosis (the interaction of plants with bacteria, fungi, and animals) on diversity and endemism. Overall, it is clear that the early twenty-first century is an exciting time to be a scientist—or a plant enthusiast—in the California Floristic Province.

Patterns of Diversity within the CFP

Because it cuts across so many political boundaries, the CFP has never been the subject of a major flora treatment. As a result, our understanding of the CFP is broken along political lines. Botanists from Oregon know about diversity in the Oregon part

Box 2 The Problem of Circumscription

Plant taxonomists tend not to agree with each other. This fact is obvious from the extensive changes to the names of many plant groups between various editions of major floras, including *The Jepson Manual.* To be fair, many of these changes are due to individual taxonomists disagreeing with themselves and changing their minds about the plants they study, but a great majority of plant name changes are due to synthesis of new knowledge, for example, new specimens brought to light by exploration or by new genetic research. One of the major reasons why the name used for a particular plant might change over time (the plant itself does not change, of course, other than in an evolutionary sense) is due to a change in circumscription, the group of individual plants and populations that are considered to belong to a particular taxon (usually a species, subspecies, or variety). Most of taxonomy is based on what is called a typological species concept, which means that taxonomists create (the technical term is describe) a species by naming an individual physical herbarium specimen that they think represents the new species. Then the taxonomist lists other specimens (each one representing a different population) that they think belong to the same species. Later on, another taxonomist could revisit the same species and decide that a *different* set of populations should belong to this species. This is a change in circumscription. The key reason why it is difficult to conduct research on floras that span political borders is that, in some cases, scientists on each side of the border use different names for the same plant because they accept different circumscriptions of that taxon. This problem is most vexing near political borders, for example, where the Southwestern California Region and northern Baja California, Mexico are separated by an international border (Figure 1). It is crucial to note that multiple circumscriptions can be equally valid—there is no single objective way to select one over the other. Usually a decision is made based on the knowledge of the scientists and the information available to them, leading to changes in circumscription over time as new scientists take on particular groups of plants and develop their expertise.

of the CFP, Baja California botanists have a very good idea of the diversity in their region, and the same goes for California and Nevada. Each of these regions is the subject of major flora studies. At first blush, it would seem to be an easy undertaking to simply integrate botanical understanding across the various political factions of the CFP, but this is, sadly, not the case. These different groups of botanists often do not agree with each other (see Box 2, *The Problem of Circumscription*). For example, they may rely on different classifications, use different names for the same species, or break a species into different numbers of subspecies. An illustration of this type of problem can be seen in monkeyflowers (genus *Mimulus*). Recent research on monkeyflowers has resulted in a sort of tectonic taxonomic rift, with most botanists around the world agreeing to split the genus into two: the bulk of the species are now in the genus *Erythranthe*, and the remainder placed in the genus *Diplacus* (although, as of the printing of the second edition of *The Jepson Manual* in 2012, the name *Mimulus* is still used). Overall, the problem of producing a list of CFP plants is a bigger issue than it might at first appear. However, the problem was at least partially solved with the publication this year of the first list of plants found in the CFP.

Peter Raven and Daniel Axelrod were the first botanists to consider diversity and endemsim in the CFP, a task which they undertook in a landmark 1978 paper. Their work threw a spotlight on the strong diversity and endemism of the CFP, independent of any political units, and also brought forward many evolutionary concepts related to North American plant diversity, for example the idea of neoendemism versus paleoendemism, which was suggested by the fossil record. On the other hand, Raven and Axelrod did not publish an actual list of plants for the CFP, which limited the ability of future scientists to update their findings. That was the project that the author of this article took on, an effort of four years that required the knowledge of more than 12 geographic experts. The updated analysis of this list of CFP native and endemic plants revealed several striking patterns that were not well understood before. The most important of these is the remarkably strong floristic cohesiveness of the CFP, which transcends inconvenient political boundaries; a staggering 46 percent of CFP native plants extend out of the California part of the CFP into the Oregon, Nevada, and Baja California parts of the CFP. The connection is most evident in the north and south of the CFP; the Northwestern Region of California (Figure 1) shares 56 percent of its flora with the Oregon part of the CFP, while the Southwestern Region shares 43 percent of its flora with the Baja California part of the CFP. These connections underline the importance of using biotic regions, rather than political units, to conduct research and plan for conservation. Indeed, many of the problems with plant taxonomy in the CFP stem from decisions that are made based on knowledge that is skewed toward a single political unit.

The new analysis also revealed smaller-scale patterns of diversity and endemism within the CFP. For CFP-endemic plants, the greatest concentrations of diversity were found in the Central Western and Southwestern Regions of California (Figure 9B),

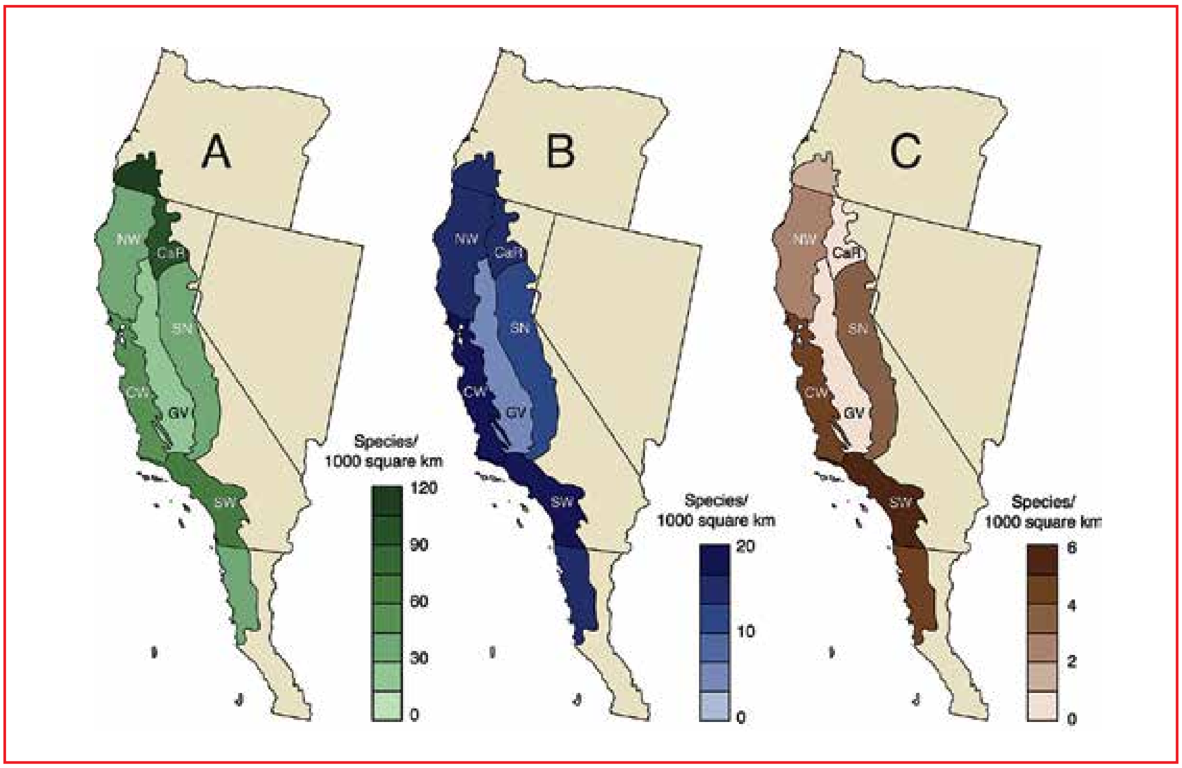

Figure 9. Diversity and endemism of the CFP subregions. Section "A" shows the number of native species per square kilometer; "B" shows the number of CFP-endemic species per square kilometer; "C" shows the number of subregional endemic species per square kilometer (for example, how many species are endemic to the Oregon portion of the CFP, per square kilometer of that region). Subregions inside California are based on a classification of major ecological regions used in *The Jepson Manual*; please refer to "Patterns of Diversity within the CFP" for details. From top to bottom, NW stands for the Northwestern Region, CaR refers to the Cascade Ranges Region, SN refers to the Sierra Nevada Region, GV refers to the Great Central Valley Region, CW refers to the Central Western Region, and SW refers to the Southwestern Region.

which together host more than 58 percent of CFP endemic species and are home to the largest number of CFP endemics per square kilometer. What may be of greater interest to rare plant enthusiasts, though, is the number of CFP-endemic species that are found only in single regions, species that are sometimes referred to as microendemics. The new analysis revealed that microendemics are also concentrated in the Central Western and Southwestern Regions of California, as well as in the nearby Baja California region of the CFP (Figure 9C); there are 177 species that are endemic to the Central Western Region of the CFP, 141 that are endemic to the Southwestern Region, and 136 that are endemic to the Baja California region. The Southwestern, Central Western, and Baja California portions of the CFP have long been considered centers of diversity within the CFP, so the new analysis quantifies this and draws attention to the fact that much of this justifiably celebrated endemic diversity is shared with Mexico.

Point Reyes ceanothus (*Ceanothus gloriosus* var. *gloriosus*), a fog-belt-specialized neoendemic of the CFP, with coyote brush (*Baccharis pilularis*) in the background. Point Reyes, California.

The Future of the CFP

Many prominent geologists are presently arguing for the recognition of a new geological era—the Anthropocene. This era would encompass just the past 66 years of the earth's history, a period during which the ecological processes of the biosphere have become dominated by humans. The activities of mankind have altered the chemistry of the atmosphere, increased the temperature of the planet more rapidly than ever before, and initiated the fastest mass extinction in the history of life on Earth. Fortunately, the CFP, which has long safe-guarded many plants from extinction, will probably continue to serve this function. However, the region is increasingly at risk from other impacts, such as urbanization, catastrophic fires, and non-native plants; the latter are becoming the dominant vegetation in much of the CFP. Nevertheless, the loss of plant species and habitats in the CFP is not inevitable and is reversible. The case has never been stronger for using cutting-edge research and smart conservation measures to preserve and recover habitats. A large part of this effort will be to continue the study of diversity and endemism patterns in the CFP, targeting places where new populations and species are most likely to be found. Overall, the more we know about patterns of diversity in the natural world, the better we will become at preserving biodiversity.

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Dylan Burge is broadly interested in the ecology and evolution of the CFP flora. His research is focused on Ceanothus *and the manzanitas (*Arctostaphylos*), particularly the role of climate and soil in the diversification of these genera. In his spare time, he enjoys photographing native plants and hiking in California's wild backcountry.*

Photos by the author.

The California Floristic Province. What Is It? *by Glenn Keator, PhD*

Deerbroom lotus (*Acmispon glaber*) in its summer condition without leaves

Goldfields (*Lasthenia californica*), a spring-flowering annual

The California Floristic Province (CFP) refers to a suite of plants adapted to a principally Mediterranean climate. The term is constantly used to define the majority of California's plant life. Technically, people use CFP to cover southwestern Oregon (Rogue River south) to northern Baja California, because of course political boundaries seldom correspond to floristic provinces. To understand the term better, we also need to talk about Mediterranean climates, found in only five regions of the world.

The main parameters of this unique climate are represented by the combination of wet, mild winters, the rain extending into spring, and long, (usually) hot, dry summers. While most other climates feature rain in summer and most other temperate climates have cold winters, the Mediterranean version is very different. If, then, you correlate the warmer, longer days of late spring and summer with the lack of precipitation, you see that our native plants—instead of growing during optimal conditions—have to adapt ways of growing earlier during shorter, cooler days, limiting or stopping growth entirely in late spring and summer.

There are many methods of dealing with this apparent conundrum:

Lose some or all leaves during summer, not winter. Examples: blue witch (*Solanum umbelliferum*) and deerbroom lotus (*Acmispon glaber*).

Die when conditions turn dry, just after producing seed (annuals). Examples: goldfields (*Lasthenia californica*) and California poppy (*Eschscholzia californica*).

Bury food and water underground in rhizomes, bulbs, corms, and tubers (geophytes) until favorable conditions return. Examples: white globe-tulip (*Calochortus albus*) and blue dicks brodiaea (*Dichelostemma capitatum*).

Die back to underground roots (summer-dormant perennials). Examples: blue-eyed grass (*Sisyrinchium bellum*) and checkerbloom (*Sidalcea malviflora*).

Store water in thickened stems and/or leaves (succulents). Examples: chalk dudleya (*Dudleya pulverulenta*) and Siskiyou lewisia (*Lewisia cotyledon*).

Consequently, you would expect plants of the CFP to belong to one of the categories above. The question is, do they?

The answer is far more complex than most people realize. First, plants of the coastal fog belt do not experience hot summers—think of redwood forests and coastal sand dunes. What's more, many of these habitats actually receive precipitation in the form of fog drip during the summer months. Do these plants fulfill our definition of Mediterranean-type vegetation? Of course not. Yet some of us simply call the coastal climate a modified Mediterranean climate and go along with categorizing this vegetation squarely in the CFP.

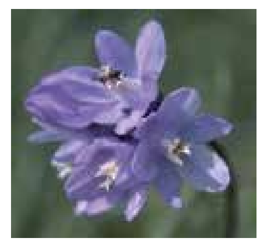
Second, plants of wetlands—swamps, bogs, marshes, permanent stream corridors, and more—have year-round water regardless of summer heat. These plants also do not qualify as typical of the CFP.

Third, plants of our higher mountains—the Klamaths all the way south to the highest mountains of the Peninsular Ranges in Southern California—have a very different climate: winter cold with a snow cover, snow melt and water availability in late spring and early summer, and dry conditions at summer's end and the start of fall. Such a climate is more typical of the inland regions of North America and is not a Mediterranean climate.

Finally, our deserts—areas with less than ten inches of annual precipitation—cover close to a third of the state, mostly in Southern California. Desert winters vary with altitude: High deserts are cold and snowy, low deserts are relatively winter-warm, but all deserts endure spotty water availability, except, of course, in desert riparian woodlands and oases. Desert plants show many of the adaptations mentioned above for Mediterranean plants but often have even more extreme expressions of these adaptations, including deeply probing roots found in several shrubs and small trees.

What does this do to our concept of the CFP? While deserts have never been included, the other regions mentioned are often lumped with the CFP, even though their climates and growing conditions differ sharply from those of the more typical habitats, such as chaparral, oak woodlands, grasslands, and coastal scrub. And, like most matters in the natural environment, there are intermediate conditions like, for example, the mixed-evergreen forests.

Chalk dudleya (*Dudleya pulverulenta*), a leaf succulent
Right: Blue dicks brodiaea (*Dichelostemma capitatum*), a geophyte



Another way of analyzing the CFP is to look at the major genera and their origins; most plants restricted to the CFP originated in warmer, drier climates, yet such water lovers as ashes, willows, cottonwoods, redwoods, and even many other conifers and shrubs have their roots in the more temperate regions of North America, including the Pacific Northwest. Are these plants truly representative of the CFP?

When all is said and done, it's obvious that there is no absolute line around the California Floristic Province—on the contrary, there is a great deal of interweaving and overlap with floras of other floristic provinces. n

Glenn Keator is chairman of the Friends *Advisory Council. He is a popular instructor of botany and field trip leader in the Bay Area, and he teaches the docent training course at the Regional Parks Botanic Garden. He is the author of a number of books on native plants.*

Photos by the author.

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