

FREMONTIA

JOURNAL OF THE CALIFORNIA NATIVE PLANT SOCIETY



LICHENS AND BRYOPHYTES
TEJON RANCH REVISITED
BIGCONE DOUGLAS-FIR
VEGETATION MAPPING AND RE-MAPPING

FREMONTIA

VOL. 45, NOS. 1&2, JUNE 2017

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California Native Plant Society

Michael Kauffmann, Editor
Beth Hansen-Winter, Designer

ISSN 0092-1793



CALIFORNIA NATIVE
PLANT SOCIETY

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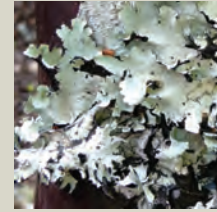
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Printed by Modern Litho: www.modernlitho.com

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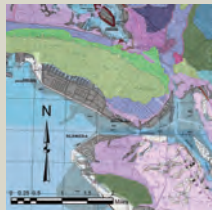
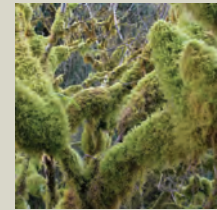


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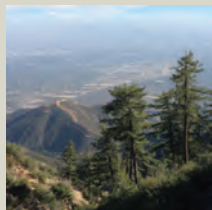
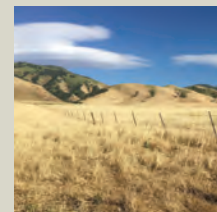


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On the cover: Lichens glow at sunrise, decorating the upper redwood (*Sequoia sempervirens*) canopy in Redwood National and State Parks. Photo by Marie Antoine.



The bright orange splash of lichen at the peak of this outcrop tells us something—there's nitrogen input at that spot. In this case, the source is birds perching and pooping on the rock's summit. Photographs by Shelly Benson unless otherwise noted.

SEEING LICHENS... AND WHAT THEY TELL US ABOUT OUR ENVIRONMENT

by Shelly Benson

Lichens are found all around us, growing in nearly every habitat and on any stable substrate. Yet, they are often overlooked because many people are unsure of what lichens are. I once heard someone speak on the topic of how words affect our ability to see. The speaker's point was that an object right under your nose could go unnoticed until you have a word for it. By naming

the object, a recognition link is made and one cannot help but see it in one's surroundings. As a lichenologist, my mission is to help people "see" lichens. When I lead nature walks, I explain the basics about lichens and point out examples of the different lichen growth forms: foliose, fruticose, and crustose. Almost immediately, people begin to observe lichens everywhere. They

can't believe that they had been walking blindly past this diverse group of organisms for so long. Seeing the amazing colors, shapes, and textures of lichen can give great enjoyment. But that's not all—lichens are widely used as indicators of air quality, climate, and old growth forests; once you learn to see lichens you can discover the stories that they tell about our environment.

WHAT IS A LICHEN?

It is a composite organism made up of fungus and a photosynthesizing partner (photo-partner). Last summer a team of lichenologists announced their discovery that many lichens contain two types of fungi (see NEWS FLASH). The photo-partner can be either a green alga or a cyanobacteria. In a few lichens, both types of photo-partners are present. This oddity is interesting because these lichens represent a symbiotic relationship between three kingdoms of life: fungi from Kingdom Fungi, green algae from Kingdom Protista, and cyanobacteria from Kingdom Eubacteria (formerly Kingdom Monera). Additionally, like many other organisms, lichens have numerous species of bacteria that live on and in them.

The lichen relationship is an example of a mutualistic symbiotic relationship—the partners benefit from living together. The fungal partners provide general protection for the photo-partner. This includes a structural ‘home’ within which the photo-partner lives. Chemical compounds found in fungal tissue are unpalatable or even toxic to some critters, thereby protecting the photo-partner from herbivory. Other chemical compounds in fungal tissue function as ultraviolet filters which protect the alga or cyanobacteria from the sun’s harmful rays. In return, the photo-partner feeds the fungi by producing sugars through photosynthesis. In addition to producing sugars, lichens that contain cyanobacteria (collectively called cyanolichens) also transform atmospheric nitrogen into a form that the fungi can use. Living together as a lichen, the partners are able to colonize a much wider range of habitats than if they were on their own.

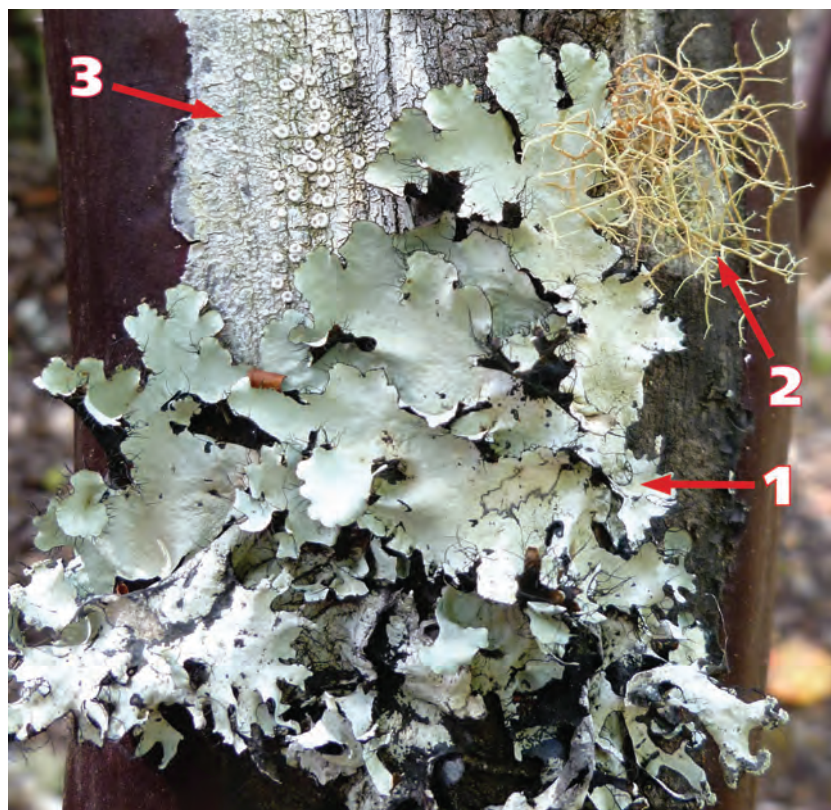
Lichens are valuable as biological indicators because they are responsive to environmental change. Lichens give the general impression of being tenacious little organisms based

NEWS FLASH: Two’s Company, Three’s a Lichen?

Recent scientific findings from Spribille *et al.* (2016) change our understanding of the lichen relationship. For over 140 years we thought that lichens were made of a fungus and an alga or cyanobacteria. Spribille’s team discovered that many lichen species contain two types of fungi. The first type (the one we already knew about) is typically in the group ascomycetes—the sac fungi. The previously unseen fungal partner is a newly discovered lineage of yeast in the group basidiomycetes—the club fungi, which include gilled mushrooms. These yeasts appear to be responsible for producing some of the unique chemical compounds found in the lichen’s fungal tissue. There is still much more to learn about these yeasts and their role in the lichen relationship.

on their ability to exist on bare rock in the baking desert or survive exposure to the extremes of outer space. However, they are actually quite sensitive to environmental conditions. Lichens are passive organisms and they have few mechanisms to mitigate changes in their surroundings.

Unlike plants, lichens have no barriers to protect themselves from extreme conditions. They have no waxy cuticle or stomata to prevent water from leaving or pollutants from entering the lichen. They don’t have roots either. There is no active uptake of water or nutrients in li-



Lichens can be categorized into three general growth forms, similar to how we group plants as herbs, shrubs, and trees. The lichen growth forms are: 1) foliose= leafy, with a distinct upper and lower surface; 2) fruticose= shrubby or hair-like; and 3) crustose= thin crust tightly attached to its substrate.



TOP: Cyanolichens, such as the lungwort lichens (*Lobaria* species), are sensitive to pollution and their presence in an ecosystem indicates clean air. • BOTTOM: Sunburst lichens, orange foliose lichens in the genera *Xanthoria* and *Xanthomendoza*, are broadly considered nitrogen-loving species.

chens. They are at the mercy of the atmosphere for providing moisture, along with dissolved nutrients, which are passively absorbed across the entire surface of the lichen body. The lichen has no way of discriminating between nutrients and pollutants. So, pollutants dissolved in rain water are also absorbed by the lichen.

Lichens are biologically active only when they are wet—that's when the photo-partner is photosynthesizing and making sugars, and the fungi are growing or making structural repairs. When the lichen dries out, it goes into a state of suspended animation and no metabolic activity occurs. In this dry state, lichens can withstand extreme conditions, giv-

ing the false impression that they are tough organisms.

The composite nature of lichens is a key factor in their sensitivity to environmental change. The symbiotic relationship between the fungi and photo-partner is relatively fragile. When the lichen is stressed—by pollution or climate extremes—the balance between the partners is upset. Usually, the stressor affects the physiology of the photo-partner, thus disrupting photosynthesis. The result is that the relationship falls apart and the lichen dies.

AIR QUALITY

Lichens were first used as indicators of air quality in the early 1800s when the onset of the Industrial Revolution brought a marked increase in coal burning. People across Europe documented the disappearance of lichens in urban areas as pollution levels rose. Lichens can be used to indicate a variety of different pollutants including semi-volatile organic compounds, radionuclides, metals, ozone, and fluorine, as well as nitrogen- and sulfur-containing compounds.

Lichens are being used to monitor nitrogen-based pollutants across the country as part of a US Forest Service program that tracks forest health (Jovan 2008). Two such pollutants are nitrogen oxide and ammonia, which result from fossil fuel combustion and agricultural activity. There is an increasing interest in using lichens to monitor nitrogen pollution because of the growing concern over the ecological effects of nitrogen deposition. These effects include the following: reduced drinking water quality, eutrophication of estuaries, nitrate-induced toxic effects on freshwater biota, changes in plant community composition, disruption in nutrient cycling, and increased emissions from soil of nitrogenous greenhouse gases (Fenn *et al.* 1998).

An easy, low-cost method for



Fog lichens (*Niebla homalea*) form small, shrubby tufts, typically on coastal rocks. Their shrubby growth form intercepts wind-blown fog, enabling these lichens to become hydrated and begin photosynthesizing without a rainfall event.

monitoring air quality is to assess lichen community composition (which species are present and their abundance). Some lichens are very sensitive to nitrogen and begin to die-off when nitrogen levels rise. Other lichens are nitrogen-loving and flourish in high nitrogen environments. As nitrogen deposition increases, there is a distinct shift in lichen community composition: nitrogen-sensitive species drop out of the picture and nitrogen-loving species move in. By monitoring the proportion of nitrogen-sensitive species to nitrogen-loving species in an area, we can estimate the amount of nitrogen deposition.

Lichen-based estimates for nitrogen deposition are backed by a quantitative benchmark. Research was done within California's major forest and shrub vegetation types to determine the threshold for nitrogen deposition, above which the lichen community begins to shift towards nitrogen-loving species. This benchmark is known as the critical load. The critical load ranged from

3-8 kg N ha⁻¹ yr⁻¹ for mixed conifer forests, chaparral, and oak woodlands (Fenn *et al.* 2010). Lichens are among the most sensitive organisms to nitrogen pollution, so keeping deposition amounts below the critical load is expected to protect all components of these ecosystems from adverse effects of nitrogen.

Nitrogen deposition can be measured using mechanical air quality sensors. However, the benefit of using biological indicators is that they tell you where pollutants are affecting the ecosystem—locations where the lichen community composition is changing. Additionally, lichen monitoring can be conducted throughout the landscape; whereas, mechanical sensors are restricted to areas with good access for installing and maintaining the equipment.

CLIMATE

Within the last two decades a growing body of literature shows that lichens are sensitive to climatic conditions and are good indicators

of our changing climate (Jovan 2008, Geiser and Neitlich 2007, Van Herk 2002). Lichens, like plants, respond predictably along climate gradients. They sort themselves into geographic zones that share similar temperature and moisture conditions.

Temperature is an important factor in explaining lichen distribution because it affects the rate of photosynthesis and basic metabolic processes. Going from the California coast to the inland mountains you cross several temperature zones, each characterized by a unique assemblage of lichens. The relatively moderate temperature at the coast supports a lichen community that is distinctly different from those found in warmer areas like the Central Valley or cooler areas like the Sierra Nevada Mountains.

As the climate warms, these temperature zones will change in size and location—so, too, will the distribution of lichen communities. Lichens restricted to cooler forests, currently found at mid to high elevations, will likely experience a



Methuselah's beard, *Usnea longissima*, indicator of old growth forest habitat. Photograph by Richard Droker.

shrinking range. Provided the species are not dispersal-limited, they are expected to move up in elevation or migrate northward in search of more suitable growing conditions.

Lichens are also closely tied to moisture regimes due to their passive method for obtaining water and nutrients. They only colonize habitats with atmospheric conditions that meet their hydration needs. The physiology of some species

requires frequent periods of wetting while others can stand regular and long episodes of dehydration. As climate change alters moisture

regimes, lichen physiology is directly affected and we expect to see corresponding shifts in the lichen community composition.

One particular group of lichens stands out as being intimately linked to coastal climate. The fog lichens, those in the genus *Niebla* (the genus name means fog in Spanish), are found only in maritime regions. Aside from one species that stretches up into Alaska, North America's fog lichens are



Green stubble lichen (*Calicium viride*), indicator of old growth forest habitat. Photograph by Eric Peterson.

concentrated along the California coast from Sonoma County south into Baja California. As the name indicates, these lichens are restricted to a narrow section of shoreline within the fog zone—an area that receives a significant amount of summer fog. During the summer when there is little to no rain, fog lichens depend on regular moisture input from fog.

The fate of fog lichens is uncertain in the face of climate change. California's climate models don't agree about predictions for coastal fog. If the frequency or duration of fog decreases, it will likely lead to a reduction of fog lichens.

OLD GROWTH FORESTS

Old growth forests and woodlands are increasingly rare. In order to preserve biological diversity, conservationists are interested in protecting as many remaining old growth stands as possible. To do that, they have developed a number of tools to rank stands in terms of importance. One tool uses lichens as indicators of stand age and continuity (Rose 1976). Mature forests develop an architecture not found in younger stands. Most importantly, they include a range of tree sizes and ages. This structure provides an array of unique microhabitats and microclimates that in turn support unique groups of lichens. The overall lichen diversity, in combination with the frequency of old growth associated species, is used to evaluate stand quality.

A group of very tiny lichens called pin lichens, those in the genus *Calicium*, are broadly known as old growth indicators (Selva 2003). Even lichenologists have a hard time seeing these lichens because you need to have your nose within two inches of them before you can see their characteristic 1-2 mm tall pin-like stalks. Pin lichens, also called stubble lichens, grow on bark or dead wood and a dense patch of the lichen can

give a twig the appearance of a five o'clock shadow. One species of pin lichen, *C. adpersum*, is listed as rare in California (CRPR 2B.2). While habitat specificity is what makes these lichens good indicators of old growth stands, it also means that their fate is inextricably linked to the survival of that habitat.

Another indicator of old growth forest is Methuselah's beard, *Usnea longissima*. This species is also rare in California (CRPR 4.2). In contrast to the tiny pin lichens, *U. longissima* is California's largest lichen. It hangs from old growth conifers and hardwoods with garland-like strands typically reaching more than a meter in length.

Opening your eyes to lichens can be personally fulfilling. Also, the stories the lichen community has to tell can inform environmental policy and ecosystem management. But the first step toward seeing and learning from lichens is to increase lichen awareness. The California Lichen Society's effort to designate lace lichen (*Ramalina menziesii*) as the California state lichen was a significant move in that direction. On January 1, 2016 California became the first state to list a lichen as a state symbol. With this important public acknowledgement of an often overlooked group of organisms comes a tremendous potential to reach California's school-age kids as they learn about the state's symbols. Lichens now have a place alongside the California poppy, redwood, and grizzly bear. Today, more people than ever are seeing lichens. Naturalists young and old, scientists, and policy makers are beginning to understand the important role lichens play in the environment.

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LICHEN CONSERVATION IS COMPLICATED

by Rikke Reese Næsborg

The conservation aim for rare, threatened, or endangered (hereafter, “rare”) organisms is to maintain populations, so that they are able to sustain themselves. This can be a difficult task even for well-known populations of large, showy-flowered vascular plants, but the task is far more daunting for inconspicuous, poorly understood taxa, such as lichens. Conservationists generally strive to include as many different organisms as possible when designating land for conservation. However, they face special challenges with lichens because they are composite organisms that often occupy different habitats than other rare taxa.

THREATS

Lichens in general are sensitive to changes in their environment. This sensitivity can be attributed to three properties of lichens. (1) They do not have roots to absorb water and



Peltigera gowardii grows entirely submerged in fresh water and is one of the few aquatic lichens. It is associated with cyanobacteria that give it a translucent, dark green or brownish color under water. *Peltigera gowardii* grows in pollution-free, cold-water mountain creeks with little or no sediment or disturbance. It is endemic to North America and threatened by hydrological changes, recreational activities, erosion, and logging (Poulsen and Carlberg 2007). Photograph by Rikke Reese Næsborg.

WHY CARE ABOUT LICHENS?

Lichens serve many functions in the ecosystem.

- Some lichens are considered pioneer species capable of colonizing and breaking down bare rock. Lichens trap dust and silt as they grow, and when they die organic material is added to the minerals of the rock (Brodo *et al.* 2001). These processes nucleate soil formation that fosters growth of other organisms such as vascular plants.
- Lichens contribute nutrients to the ecosystem by adding organic material to the soil when they decompose. Those with a cyanobacterial partner can bind nitrogen from the air, so they are important components of the nitrogen cycle. As much as 50% of the total nitrogen input in some old-growth forests has been attributed to lichens (Brodo *et al.* 2001).
- Lichens serve as a food source for a wide variety of animals, including muskoxen, deer, voles, flying squirrels, slugs, and mites. Up to 90% of a reindeer's winter diet may consist of lichens (Brodo *et al.* 2001), and many birds use lichens as a nesting material. Invertebrates such as water bears live in the intricate microtopography of lichens.
- Many lichens contain unique chemical compounds that serve functions such as reflecting excess sunlight, aiding in gas exchange, or deterring herbivory. Some of these chemical compounds even have properties that benefit humans, such as antibacterial, antibiotic, cytotoxic, antiviral, and antitumor functions. Some lichen compounds are promising novel sources of natural non-genotoxic anticancer drugs (Molnár and Farkas 2010).

nutrients from their substrates, nor do they have a waxy cuticle to control hydration. Instead, lichens passively absorb water and nutrients from their environment, which consequently also leads to absorption of atmospheric pollutants that happen to land on their surfaces (McCune and Geiser 2009). (2) Each lichen is a composite organism, consisting one or more fungi (Spribille *et al.* 2016) in a symbiotic relationship with green algae and/or cyanobacteria. The lichen symbiosis is delicate and therefore vulnerable to dissociation. Changes in environmental conditions, especially increased pollution, can alter the symbiotic balance between the fungi and the algae/cyanobacteria, resulting in a breakdown of the relationship (McCune and Geiser 2009). (Read more about air pollution and lichens in the article “Seeing Lichens” in this issue). (3) Many lichens are slow to colonize new habitats due to long generation times and limited dispersal distances, rendering them sensitive to landscape-level disturbances (Silleet *et al.* 2000).

HOW DO CALIFORNIA LICHENS OFFICIALLY ATTAIN “RARITY” STATUS?

California Native Plant Society (CNPS) partners with the California Lichen Society (CALS) to promote conservation of rare, threatened, and endangered lichens. Information about rare lichens is collected by CALS Conservation Committee, submitted to the California Natural Diversity Database, and subsequently included in CNPS’s Inventory of Rare and Endangered Plants. Each lichen taxon proposed as a Lichen of Conservation Concern undergoes a rigorous sponsorship process by CALS to understand taxonomy, biogeography, and threats before status is recommended. The sponsorship includes a 90-day technical review, followed by publication of a comprehensive status review for comments by both experts and amateurs. Because lichen biogeography is poorly understood, a one-year waiting period is required before final decisions about ranking and listing are made (Sims *et al.* 2014).

As of March 2017, the following 13 lichens were registered in the CNPS inventory: *Calicium adpersum*, *Cladonia firma*, *Graphis saxorum*, *Hypogymnia schizidiata*, *Mobergia calculiformis*, *Peltigera gowardii*, *Ramalina thrausta*, *Solorina spongiosa*, *Sulcaria isidiifera*, *Sulcaria spiralis*, *Texosporium sancti-jacobi*, *Thamnolia vermicularis*, and *Usnea longissima*.

Because of these properties, lichen-rich habitats worldwide are negatively affected or destroyed by

anthropogenic influences, such as habitat degradation or loss, habitat fragmentation (Bergamini *et al.*, 2005), climate change (Ellis *et al.*, 2007), and air pollution (Jovan 2008). Of these, habitat loss, especially of virgin forest (Wolseley 1995), is probably the most devastating threat to lichens because local populations are removed. Since most forests reach economic maturity long before they reach ecological maturity, naturally heterogeneous forests in many parts of the world are converted to monospecific, even-aged stands with short rotation periods to maximize economic profits (Thor 1999). The effect on both species richness and community composition of lichens is dramatic and devastating. Lichen floras of natural forests are unique; similar communities are not found in secondary or fragmented forests (Bergamini *et al.*, 2005). These unique lichen communities not only depend on the habitat and moisture regimes found in virgin forests, but



Hypogymnia schizidiata was described as a new species in 2002, and it is considered rare throughout its limited range. Like other tube lichens, it has hollow branches, but the surface of these branches characteristically disintegrates into flakes, giving it a “schizidiate” appearance. The species grows on bark and exposed wood of both conifers and hardwoods in woodlands, forests, and chaparral (McCune 2006). Until recently, the known global distribution was limited to four islands: Cedros and Guadalupe Islands in Mexico, and Santa Cruz and Santa Rosa Islands in California. In 2015 it was discovered on the San Francisco Peninsula. Destruction of habitat by fire may be the greatest threat in California. Photograph by Rikke Reese Næsborg.

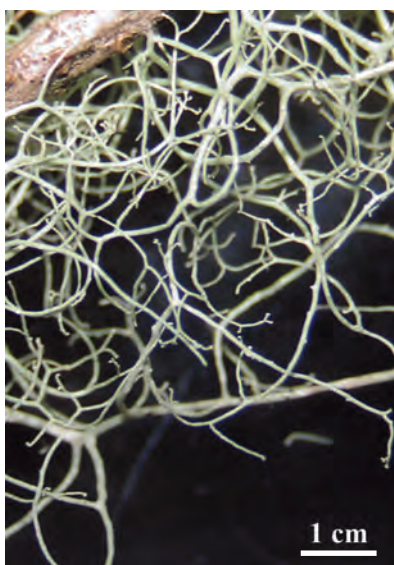
they also rely on long-term ecological continuity for dispersal and establishment.

Structural changes in the agricultural landscape and urbanization also pose serious threats to lichens. Large-scale modern agricultural practices eliminate minor and marginal habitats such as remnant trees, stone walls, alleys, and old barns that serve as refugia for lichens in a changing environment (Thor 1999). Furthermore, nitrogen compounds generated by agricultural activities and by combustion of fossil fuels are known to have harmful effects on lichens (McCune and Geiser 2009).

SPECIFIC PROBLEMS WITH CONSERVATION OF LICHENS

Since each lichen is a composite organism, lichen conservation must deal with at least two very different species. Even though the fungus is typically the object for conservation efforts (Scheidegger and Goward 2002), the delicate nature of the symbiosis creates challenges unique to lichens. Developing conservation strategies for lichens is additionally complicated by the fact that the distributions and ecologies remain unknown for most lichen taxa. Moreover, many lichens, particularly inconspicuous crustose species, await scientific description or have yet to be discovered altogether. This is probably especially true for rare taxa.

While it is possible to cultivate and breed many other species in captivity (e.g., Hanson and Nelson 2015), the delicate symbiosis of lichens is poorly understood and notoriously difficult to duplicate in captivity (Honegger 1996) which prohibits our ability to artificially augment lichen populations. Transplantation of symbiotic propagules and lichen fragments can be successful for some species (Schei-



Ramalina thrausta resembles a tiny, pendent shrub with filamentous branches that are curled over at the tips. These curly tips have earned it the poetic common name “angel’s hair.” The species is mainly found on dead twigs of both conifers and hardwoods in moist, cool forests of the boreal zone, and it is considered uncommon throughout its global range. It is mainly threatened by air pollution and timber harvest (Carlberg 2006). Photograph by Tom Carlberg.

degger *et al.* 1995; Sillett *et al.* 2000), but this conservation approach will be inherently more challenging for sexually reproducing lichens because their reproductive units (spores) contain only the ascomycete fungus, and also for crustose species because of their small sizes. Conservation must instead be based on strategies that protect suitable habitats for the long-term, but the lack of knowledge about lichen ecology means these decisions often rely on guesswork. Management decisions are further complicated by the fact that many lichens have specific habitat requirements that are not shared by other organisms in the same community, so special lichen-specific management considerations may be needed. As a result, lichen preferences are often not taken into account when planning reserves, and an overall ecosystem approach of conservation often fails to successfully protect these incon-

spicuous organisms (Scheidegger and Werth 2009).

Compared to more well-known organisms such as vascular plants, mammals, or birds, a large proportion of lichen taxa have cosmopolitan distributions. Most of these widespread lichens are unevenly distributed throughout their range, but they frequently receive low conservation priority even in parts of the world where they are truly rare. Genetic research into a given species may reveal that there are actually two or more geographically distinct taxa, such that lack of protection could reduce or even extirpate genetic diversity (Scheidegger and Goward 2002). Some lichens are rare throughout their widespread range. For example, species of *Lobaria*, *Sticta*, *Nephroma*, *Pannaria*, and *Calicium* are associated with boreal and temperate forests that are open and ancient. Previously, these forests were kept open by populations of large, grazing herbivores, but a combination of declining or disappearing large grazers as well as logging of ancient forests has rendered these habitats increasingly scarce. In many areas, the above mentioned lichens are now restricted to manmade parks, wood pastures, and hunting reserves that have remained unchanged for many years (Wolseley 1995). Some lichen genera are narrow endemics, and there are also many local, endemic species within widespread genera. Endemic species may either represent emergence of “new” taxa via speciation or reflect relict survivors after extensive range reduction (Galloway 1997). Regardless of origin, rare endemics are often considered high conservation priorities—that is, if we know enough about their distributions and ecologies to offer effective protection measures.

CONSERVATION STRATEGIES

In order to maintain viable population sizes over time it is vital that

current large populations of rare lichen species receive strict protection. Such large populations serve as propagule sources for expanding the ranges and therefore enhancing the long-term survivability of rare species. Of course, the success of these conservation efforts is only possible if adjacent or nearby future habitats for range expansion are appropriately managed, such that suitable habitats (e.g., old trees for epiphytes or open soil patches for soil-dwelling species) will continue to be available for colonization within the landscape (Scheidegger and Werth 2009). Often, it is necessary to considerably reduce or altogether halt harvest of forest resources since many lichens are extremely sensitive to environmental changes (Jovan 2008).

A successful conservation strategy typically combines habitat protection with efforts to maintain or improve the size, distribution, and genetic structure of lichen populations. This does not necessarily mean that habitats, forest stands, or even entire landscapes must be completely off limits, as long as the lichen populations can retain viable effective population sizes and populations in different areas are able to interbreed to maintain genetic diversity (Scheidegger and Werth 2009). Large populations with high genetic variability are expected to have a higher probability of survival as well as a higher evolutionary potential to cope with future environmental changes.

Despite the reality that lichen conservation is faced with many challenges such as limited knowledge about ecology and distribution as well as habitat loss and fragmentation, progress is being made here in California (see sidebar on page 9). On January 1, 2016 California was the first of the United States to designate a state lichen (lace lichen, *Ramalina menziesii*) to promote awareness about lichens.

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Bryophytes in all their glory, growing in the North Coast redwood forest. All photos by Marie Antoine.

A BIT ABOUT BRYOPHYTES

by Marie Antoine

Although there is much overlap in the ecology of lichens and bryophytes, they are fundamentally different groups of organisms. A lichen is a symbiotic system where a fungus farms a population of green algal and/or cyanobacterial cells. In other words, lichens represent a highly successful fungal nutritional mode. Bryophytes, on the other hand, are plants.

The word “bryophyte” translates to “moss plant.” Mosses are indeed bryophytes, but liverworts and hornworts are also bryophytes. Technically speaking, bryophytes are an informal group composed of three separate phyla: Bryophyta (mosses), Marchantiophyta (liverworts), and Anthocerotophyta (hornworts). These are ancient land plant lineages, and their divergence from tracheophytes (lignified vascular plants) occurred

relatively soon after plants colonized land. For the past 400 million years or so, bryophytes have been adapting and evolving to exploit a broad range of habitats where they can avoid competition with tracheophytes.

While mosses, liverworts, and hornworts are only distantly related to each other, there are certain features that unite them. Bryophytes are often referred to as “non-vascular plants” because they lack ligni-

fied vascular tissue. Lignins impart structural support and rigidity in the conducting tissue of tracheophytes, which include all other land plants except bryophytes. The lack of lignin means bryophytes can only be relatively small plants. Bryophytes anchor to their substrates with hair-like rhizoids, instead of roots. All bryophytes lack seeds; they reproduce sexually via spores and asexually via fragmentation or production of tiny clonal propagules called gemmae. Furthermore, all bryophytes require liquid water for fertilization because of their swimming sperm.

Seeds and sperm may be familiar concepts, but several of the other features uniting bryophytes involve less intuitive aspects of their life cycle. All land plants have the same fundamental life cycle of alternating heteromorphic multicellular generations: the haploid generation (with one set of chromosomes) is the gametophyte that makes gametes (eggs or sperm) and the diploid generation (with two sets of chromosomes) is the sporophyte that makes spores. Bryophytes have a dominant gametophyte, and their sporophytes are short-lived, unbranched, and nutritionally dependent on the gametophyte. This situation is reversed in tracheophytes, where the sporophyte is dominant, relatively long-lived, and branched, while gametophytes are variously reduced and retained on the sporophyte. In other words, the green fuzzy moss is a gametophyte, but the green leafy tree is a sporophyte.

HOW CAN YOU TELL VARIOUS BRYOPHYTES APART?

The first thing to do is determine whether the gametophyte is leafy or thalloid. If the plant is leafy, you will be able to see tiny leaves attached to tiny stems. On the other hand, a thallus is a plant body that is

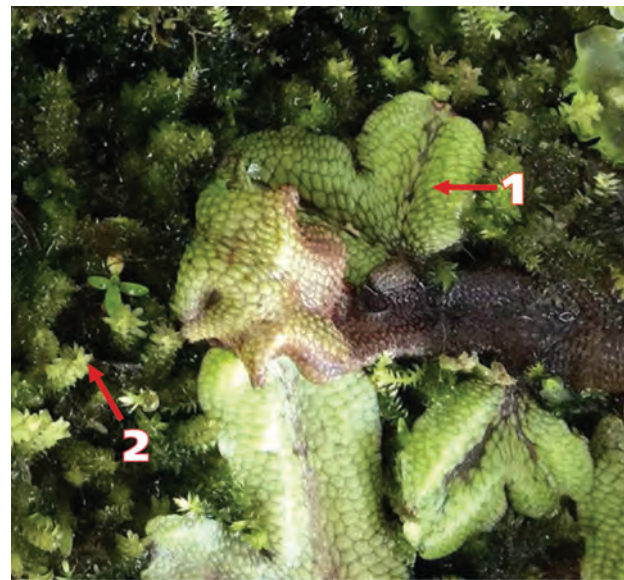
not differentiated into leaves and stems. Thalli may be strap-shaped or form a rosette. If the plant is reproductive, the appearance of the sporophyte is also diagnostic.

Mosses are the most familiar group of bryophytes, and with over 13,000 species they are also the most diverse. All mosses have leafy gametophytes and their leaves are spirally arranged upon the stem.

Many mosses have a flattened, feather-like appearance, but examination with a hand lens will show the leaves are indeed spirally arranged. The moss sporophyte consists of a small brownish spore capsule attached to the parent gametophyte via an unbranched stem. The sporophyte stem is wiry and durable, and it often persists after the spore capsule has shed its spores or been picked off by some hungry animal. The spore capsule itself has a neat little lid that pops off when the spores are mature. In most mosses, the mouth of the spore capsule is lined with tiny intricate teeth that flex with changes in humidity and thereby promote spore dispersal.

Liverworts are the second most diverse group of bryophytes with approximately 5,200 species. Most liverworts are leafy and could be mistaken for mosses upon first impression. However, close examination of a leafy liverwort will reveal that, unlike mosses with their spirally arranged leaves, liverwort leaves are arranged in two or three distinct rows. There are two lateral rows of leaves, and most leafy liverworts also have a third row of leaves on the ventral surface (not surprisingly, these are called underleaves).

Although more than 85% of all liverworts are leafy, the thalloid liverworts are probably more familiar to most people because of their prevalence as greenhouse or nursery weeds. Thalloid liverworts may be either complex or simple. Complex thalloid liverworts are many cell layers thick, which allows for tissue differentiation and turret-like



TOP: *Kindbergia* showing "feather moss" morphology. • BOTTOM: Thalloid (1) vs. leafy (2) bryophytes.

dorsal air pores. In contrast to complex thalloid liverworts, simple thalloid liverworts are only a few cell layers thick and their fragile translucent bodies do not have differentiated tissues or dorsal air pores.

Whether belonging to a leafy or a thalloid liverwort, the liverwort sporophyte is uniformly ephemeral. A fragile, transparent stem expands via turgor pressure to elevate the shiny blackish spore capsule, and the whole structure collapses after the spores are released. If you have access to a compound microscope, squash-mount a liverwort spore cap-



Polytrichum moss with mature sporophytes

sule and check out the beautiful helical structures that are mixed in with the spores. These little spring-like structures, called elaters, enhance spore dispersal and are unique to liverworts.

Hornworts are the third and least common group of bryophytes. They are arguably a relictual group, with fewer than 200 species worldwide. All hornworts have a thalloid gametophyte, and the thallus is usually a distinctive bluish-green color because of symbiotic cyanobacteria that live inside and provide a nitrogen source to the hornwort. The “horn” part of the plant is the sporophyte, which is essentially just an elongating spore capsule. Hornworts have a number of characteristics that make them unlike any other land plants. For example, each cell has only one large chloroplast, whereas all other land plants have multiple chloroplasts per cell.

WHAT ARE BRYOPHYTES NOT?

First of all, bryophytes are not parasites, although you will often find bryophytes growing upon other plants. This habit is called epi-

phytism, where epiphyte means “on the surface of a plant.” Many lichens are epiphytic as well. Both bryophytes and lichens lack roots. This means they cannot tap into their host’s sugar and water supply like parasitic mistletoes do. Epiphytic bryophytes and lichens use their rhizoids to cling to the outer surface of their host tracheophyte

and they do not penetrate their host’s bark or leaf cuticle. These epiphytes simply use their hosts as substrate. Growing upon the bark, wood, or leaves of tracheophytes is an excellent strategy for reaching moisture, nutrients, and sunlight without having to compete directly with tracheophytes for these resources.

If epiphytic bryophytes and lichens do not harm their substrates, then why do we see more epiphytes on dead or dying branches?

Again, we must return to the issue of competition. As a tree or branch dies, it loses its leaves. With fewer tracheophyte leaves, there is more light available for the epiphytes. More light means more epiphyte growth, and voilà, the dead branch or tree appears unusually cloaked in epiphytes. Epiphyte growth may be also be enhanced by minerals leaching out of dying foliage and twigs, but the epiphytes themselves are not responsible for the tracheophyte’s decline.

Here is another myth to dispel: bryophytes are not

primitive precursors to tracheophytes. You will often see this claim even in textbooks and scientific papers, and this erroneous thinking likely arises from the chauvinistic belief that “bigger is better.” Bryophytes represent a fundamentally different strategy in land plant evolution. Bryophytes and tracheophytes diverged shortly after plants first colonized land, and from the beginning bryophytes pursued a disparate strategy from tracheophytes. The bryophyte strategy involved elaboration of the gametophyte, and the tracheophyte strategy involved elaboration of the sporophyte. It is interesting to consider the ultimate role of the sporophyte (spore dispersal) vs. the role of the gametophyte (successful fertilization) and the characters that would be advantageous in each case. What makes sense for a large plant does not make sense for a small plant, and there are some fascinating morphological, anatomical, and physiological processes underlying bryophyte success. The numbers speak to the success of the bryophyte strategy: in terms of diversity, they are second only to the flowering plants. Their small size, intricacy of form, and unique physiology make bryophytes per-

Thalloid liverworts *Conocephalum* (complex) and *Pellia* (simple).



fectly suited to inhabit niches that are unavailable to tracheophytes.

WHERE DO BRYOPHYTES LIVE?

The short answer is: almost everywhere where they can avoid competition with tracheophytes. This competition may be either direct (imagine a moss trying to compete for space with a redwood tree) or indirect (imagine a deciduous tree dropping a thick layer of leaves and smothering a thalloid liverwort). The same concept applies to lichens, and this is one of the reasons why you will often find bryophytes and lichens growing together. Generally, bryophytes and lichens have the advantage on any substrate where tracheophytes are disadvantaged. This includes hard impermeable substrates with poor water retention, such as rock, bark, and tracheophyte leaf cuticles. Tracheophytes cannot usually exploit these substrates because they need to sink their roots into a dependable water supply. Here is where we encounter one of the profound physiological differences between bryophytes and tracheophytes.

Most tracheophytes and other liv-

ing organisms (including us) have a water physiology called homeohydry, where cellular water content must remain within certain boundaries or else the organism will die. Bryophytes have a type of water physiology called poikilohydry. This word means “varied water.” When water is available, bryophytes are physiologically active. When water ceases to be available, they undergo an orderly shutdown of cellular processes and remain dormant until water returns. Lichens are also poikilohydric. The advantage of poikilohydry is that bryophytes and lichens are liberated from reliance on soil water, so they can grow on surfaces like rock and bark. The disadvantage is that these organisms will be dormant whenever ambient water is unavailable. It is important to point out that poikilohydry and desiccation tolerance are not synonymous. All bryophytes and lichens are poikilohydric, but degree of desiccation tolerance ranges widely among species from different habitats. A bryophyte or lichen growing on a desert rock can tolerate more extreme drying-wetting cycles than can a related species growing on a log in a humid forest.

While many bryophytes and li-

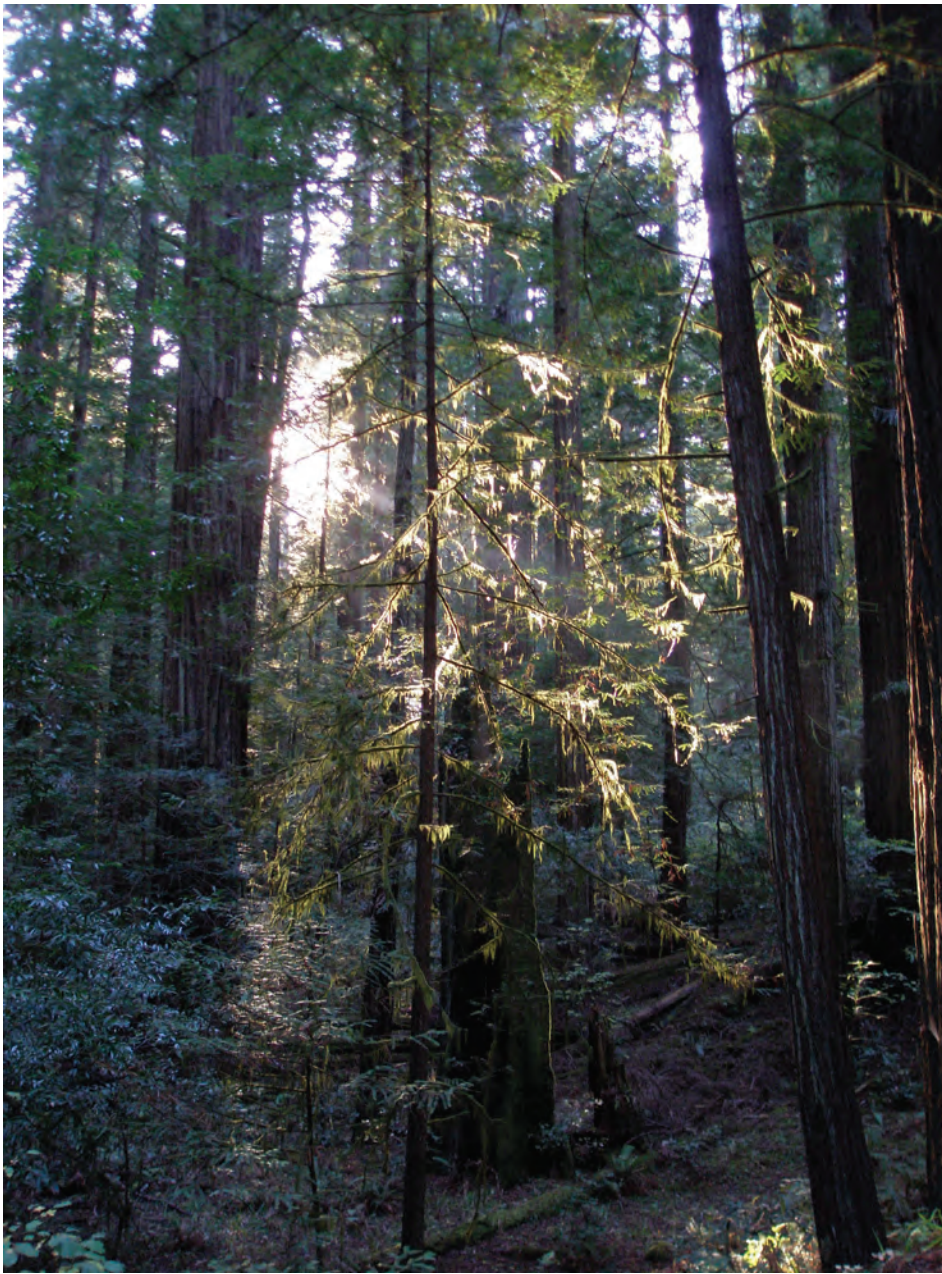


Leafy liverworts *Porella* and *Frullania* on alder trunk.

chens thrive on hard surfaces, there are certain conditions that promote bryophyte dominance on softer substrates. The combination of deep shade and high humidity is one such

BELOW LEFT: Leafy liverwort *Scaparia* (fertile, with flimsy sporophytes in variable stages of development) growing amidst a collection of mosses. • BELOW RIGHT: Hornworts with their “horn-like” sporophytes.





Isoetecium (the icicle moss) growing on dead lower branches.

condition where bryophytes can colonize soil. Most bryophytes are considered “shade plants” in that they can achieve positive carbon balance at very low light levels. Another bryophyte-favorable substrate is provided by soft, wet, decaying wood on the forest floor. With adequate light tracheophytes will colonize this habitat, as in the “nurse log” phenomenon where young trees establish on fallen logs. In the deep shade, however, bryophytes

reign supreme. You will find relatively few lichens in these dark, wet niches. Prolonged hydration and low light levels can be a dangerous combination for lichens. Most lichens need regular cycles of wetting and drying to maintain the balance of the symbiosis, lest the fungus respire the system to death. Many bryophytes, on the other hand, will thrive under conditions of near-constant hydration.

Waterlogged soils can be prime

bryophyte habitat. These soils often lack sufficient oxygen to support the roots of tracheophytes. Bryophytes, on the other hand, can simply absorb oxygen across their entire surface area from the air or water around them. One moss genus, *Sphagnum*, is considered an ecosystem engineer because of its ability to hold water and create conditions that exclude most other plants. This fascinating moss has unique anatomy and physiology that creates and perpetuates the vast northern peatlands (which is a topic deserving of its own article).

WHY SHOULD WE CARE ABOUT BRYOPHYTES?

Aside from their aesthetic charm, bryophytes have inherent value as contributors to biodiversity. They also play fundamentally important ecological roles, such as hydrological buffering and nutrient cycling. Imagine rain falling through the crown of a tree that is cloaked in mosses and leafy liverworts. The bryophytes absorb water and slowly re-

lease it, like so many green sponges, thereby buffering the canopy habitat, which is otherwise quite desiccating. This, in turn, provides viable habitat for other organisms. Every bryophyte colony is like a miniature forest with niche diversity and food webs of its own. Tiny animals are given shelter and protection from predators within the matrix of the bryophyte forest. Larger animals, particularly birds, use bryophytes as nesting material. Moss spore cap-

sules are nutritious snacks for insects, birds, and small mammals.

HOW ARE BRYOPHYTES FARING IN THE ANTHROPOCENE?

A major threat to bryophyte (and lichen) abundance and diversity is habitat destruction, whether through clear-cut logging, urban development, or collection for the horticultural industry. Another important vulnerability is air pollution. Recall the poikilohydric nature of bryophytes and lichens. All water and nutritional needs must be met through direct deposition from the atmosphere. While this is a handy strategy for making a living literally out of thin air, it also means bryophytes and lichens are unable to exclude harmful components in their environment. Lichens are classic indicators of air pollution, as certain species will disappear from polluted areas and be replaced by pollution-tolerant species. This is also true for bryophytes. You might recall the recent news from Portland, Oregon where street tree mosses revealed a previously unknown air pollution problem (i.e., heavy metal deposition). Climate change is another likely threat to bryophytes, although it remains to be seen how that will unfold.

WHERE MIGHT ONE LOOK FOR BRYOPHYTES?

No doubt after reading this *Fremontia* issue you will be out and about looking for lichens. As you examine epiphytic lichens growing on shrubs and trees, pay attention to the mosses and leafy liverworts that will likely be growing intermixed. As you examine rock-dwelling lichens, look in cracks and fissures for moss colonies. Venture into the shady nooks and crannies of your local forests and find luscious mosses carpeting the forest floor. Use a

headlamp and a hand lens to explore the intricate colonies of leafy liverworts on old wet redwood logs. Stroll (oh-so-carefully) along a stream bank and admire the thalloid liverworts growing on silty mineral

soil. Finally, search for hornworts on clay cutbanks or old gravel roadbeds. The more you look for these enchanting little plants, the more you will find the “green blur” coming into delightful and unexpected focus.

FURTHER READING ON GENERAL BRYOLOGY

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TOP: *Sphagnum*, the ecosystem engineer. • BOTTOM: Hummingbird nest with woven moss.

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A field biologist samples a stand of tufted poppy (*Eschscholzia caespitosa*) in the Inner Coast Ranges of Napa County with a backdrop of repeating floristic patterns (labeled and delineated). These patterns are guided by effects of soil, exposure, climate and fire. Repeat mapping takes advantage of definitions derived from vegetation sampling to accurately depict changes over time.

TIMES THEY ARE A CHANGING: VEGETATION MAPPING AND RE-MAPPING EFFORTS ACROSS CALIFORNIA

by Todd Keeler-Wolf, Rachelle Boul, Jennife Buck-Diaz, and John Menke

A vegetation map is a graphic representation of the patterns of vegetation such as woodlands, chaparral, and grassland arrayed across a landscape. Though vegetation maps have been produced for over 100 years, those created today far surpass a simple two-dimensional map. Geographic Information System (GIS) technology enables maps to represent a variety of “attributes” in addition to vegetation type. At the click

of a mouse, you can display not only the floristic variety of a given area’s vegetation, but also its structural attributes (such as height of the living vegetation), and even habitat quality for specific animals and plants. For example, a GIS map of Sonoma County vegetation highlights the tallest forests of large-diameter coast redwoods which can host nest sites for the endangered marbled murrelet, and can also differentiate largely non-native annual

grasslands from highly diverse patches of native wildflowers containing rare endemic plants. This information helps people explore and explain a wide variety of biological information for a mapped area. It is no wonder that today’s vegetation maps have become an indispensable tool for conservation planning and natural resource assessment.

The process of repeat vegetation mapping synthesizes and summa-

rizes changes for all vegetation covered by the map. This confers a unique status to vegetation mapping as the single best “landscape-level monitoring” tool amongst the arsenal of biological monitoring methods. For proper use, however, repeat mapping must be carefully done with appropriately set limitations. This article explores the value of repeat mapping through numerous examples across California, while highlighting the careful steps that must be taken to guarantee the highest comparison value.

INTERPRETING VEGETATION INFORMATION FROM THE PAST

The first vegetation map across California was spearheaded by A.E. Wieslander for the US Forest Service in the 1930s. Its quantitative nature and broad geographic scope, covering >40% of the state, has made it an important resource to revisit (Kelly and Allen-Diaz 2005, Thorne *et al.* 2008, etc.). However, there are problems using these beautifully produced maps as a basis of comparison to current vegetation conditions. They were made at a time when geodetic surveying (measurement of the earth) was less accurate and vegetation classification rules were less rigorous. There were no aerial photographs for reference, and they were hand-drawn from promi-

nent viewpoints such as hills and ridges by field mappers. This technique introduces a number of problems for accurate depiction of land-cover patterns. By necessity, the maps were drawn at a broad scale (less detail) to encompass the inherent uncertainties and to enable this huge effort to be completed over a manageable time frame (Figure 1).

Researchers interested in making detailed comparisons between the Wieslander map and current conditions must first generalize newer maps to compare “apples-to-apples.” Some results have been relatively inconclusive, however, analysis of the extensive field data collected to support these maps suggest broad landscape level changes at the tree line in both lower and upper elevations in the mountains of California, helping to confirm evidence of climate change patterns (Thorne *et al.* 2008, Wright *et al.* 2016).

Vegetation conditions prior to recorded history have also been considered, perhaps the most famous of these was produced by Kuchler (1977) for California as a “potential vegetation” map. This map synthesized scientific information on the status and distribution of plants before European history in the state, presumably when natural processes were running their course without the “control of man.” Though useful for conceptualizing past conditions, these maps are open to interpretation depending upon assump-

tions of historic controls on the extent and distribution of vegetation. For example, a 2010 map in the vicinity of the City of Oakland depicts how vegetation might have appeared 300 years ago prior to its first sighting by European explorers. This view is based on the landscape-level influence of Native American land management practices, which was not well understood when Kuchler developed his maps (Figure 2).

ORANGE COUNTY (20-YEAR INTERVAL)

In more recent efforts, the California Native Plant Society compared a 2012 vegetation map within Orange County (AIS 2015a) to an existing map produced in 1992 (Jones and Stokes 1993) to interpret differences between the maps and to guide future change analyses. Natural lands within Orange County include habitats such as open grasslands, coastal sage scrub, chaparral, and coast live oak woodlands. The vegetation in this region has undergone fragmentation due to urban expansion as well as multiple, widespread fires causing change and succession.

The Fire and Resource Assessment Program (FRAP 2014) publishes a statewide geodatabase of fire perimeters that includes wildfire history, prescribed burns, and other fuel modification projects. This resource allows users to understand

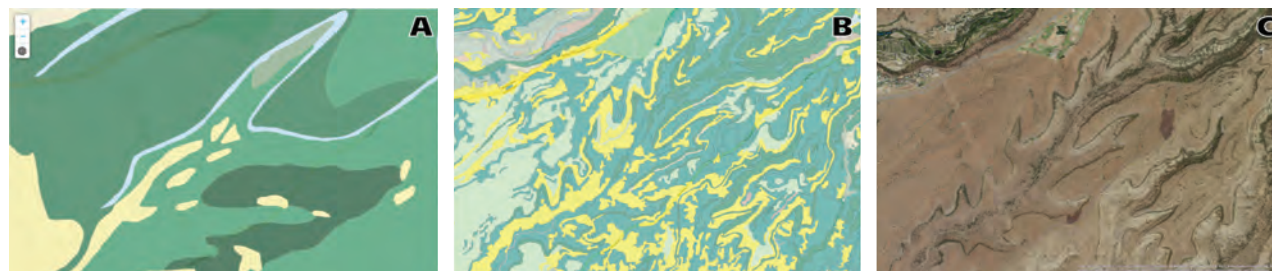
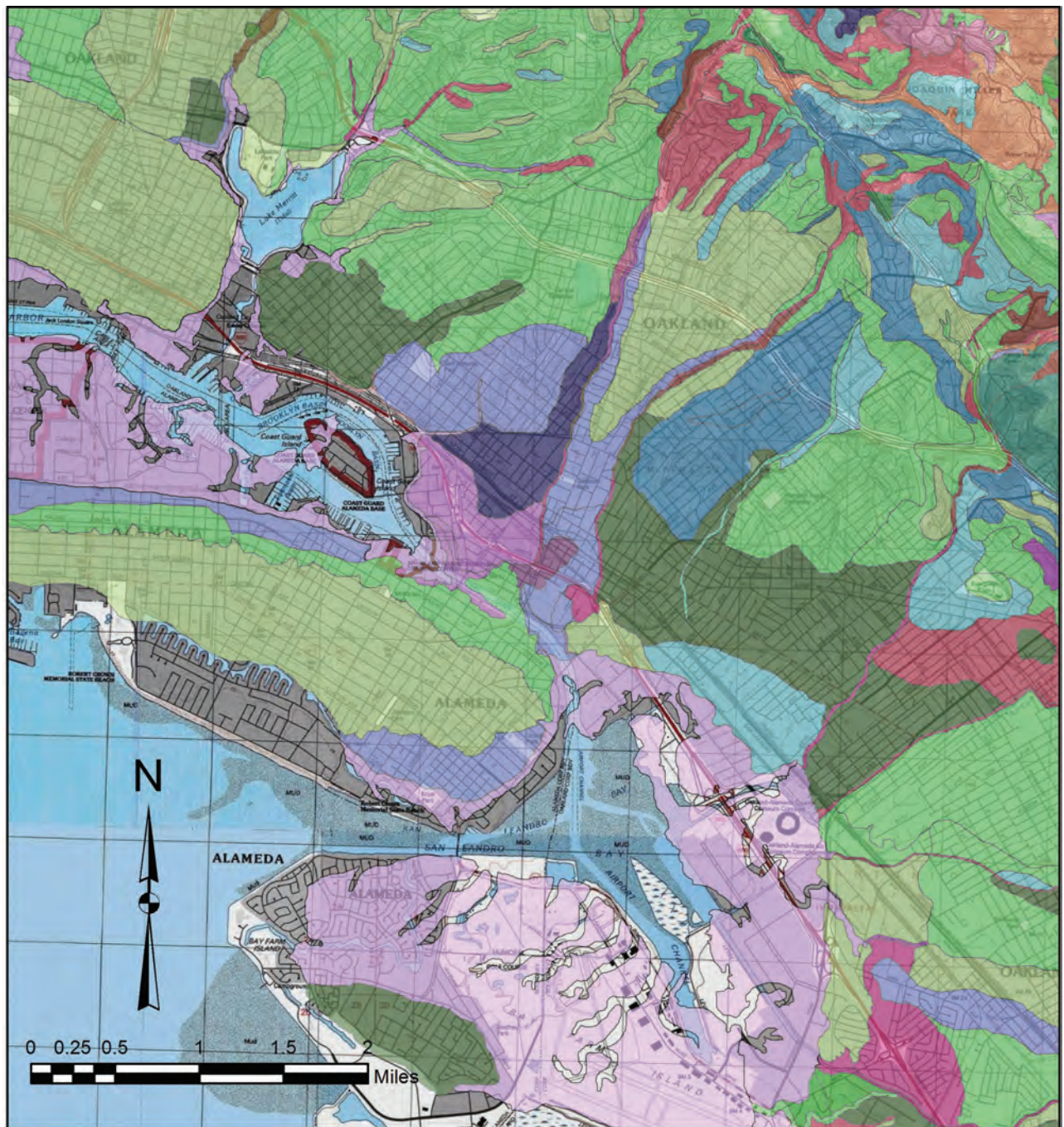


FIGURE 1. A comparison of Wieslander Vegetation Type Map (VTM) (A), 2010 northern Sierra Nevada foothill vegetation map (B), and recent color aerial imagery for the same area between Chico and Paradise in the northern foothills, depicted at 1:18,000 (C). the more accurate and detailed 2010 map is a result of quantitative vegetation classification and detailed aerial photography as a basis for the mapping, neither of which were available for the VTM mapping 75 years ago.

SOURCE: Wieslander, A.E. 1935. A vegetation type map of California. *Madroño*. 3:140–144; Menke, J., *et al.* 2011. Northern Sierra Nevada Foothills Vegetation Project: Vegetation Mapping Report; Google, DigitalGlobe, 2016.



Potential Vegetation Alliances of the Oakland Area, Alameda Co. Caca. 1700 AD.

World Terrain Base		
Oakland_preHistoricVeg_working		
<all other values>		
VegName		
Adenostoma fasciculatum Alliance	Holodiscus discolor Alliance	Salix lasiolepis Alliance
Alnus rhombifolia Alliance	Juncus balticus - Juncus mexicanus Alliance	Sarcocornia pacifica Salt Marsh Alliance
Arctostaphylos (tomentosa, crustacea) Alliance	Leymus triticoides Alliance	Schoenoplectus acutus/californicus Alliance
Artemisia californica pure and mixed Alliance	Lupinus arboreus Alliance	Schoenoplectus acutus/californicus Alliance
Baccharis pilularis Alliance	Pinus attenuata Alliance	Sequoia sempervirens Alliance
Ceanothus oliganthus Alliance	Platanus racemosa Alliance	Shell Mound/Village Site
Corylus cornuta Alliance	Populus fremontii Alliance	Spartina foliosa Tidal Grassland Alliance
Danthonia californica Coastal Prairie Alliance	Quercus agrifolia /Quercus agrifolia /Grass-Herb Association	Tidal Mudflats, and Sandflats
Eschscholzia californica Alliance	Quercus agrifolia - Arbutus menziesii Association	Typha latifolia/angustifolia Alliance
	Quercus agrifolia - Chaparral Association	Umbellularia californica Alliance
	Quercus kelloggii Alliance	Upland Elymus glaucus Grassland Alliance
	Quercus lobata Alliance	Upland Nassella Grasslands & Forblands
	Red Osier Dogwood (Cornus stolonifera) Alliance	Zostera pacifica Eelgrass Beds
	Salix laevigata Alliance	

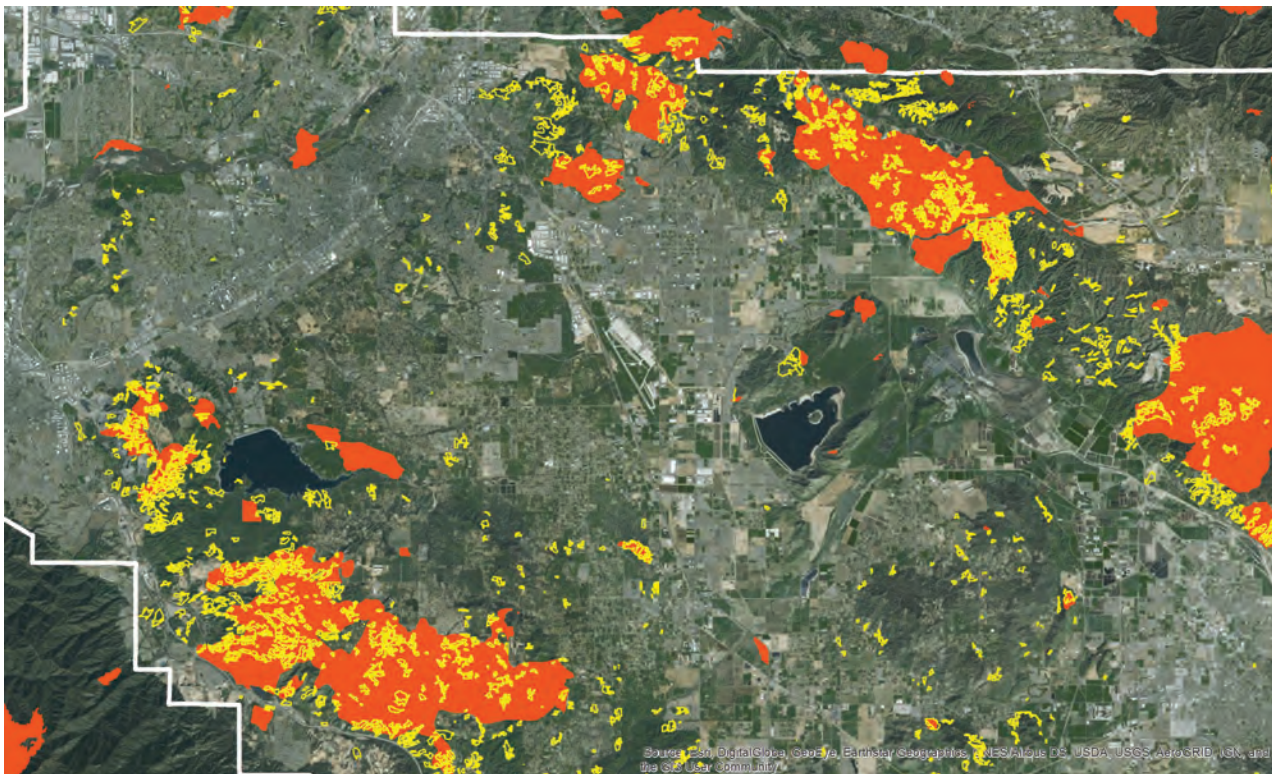


FIGURE 3. The western Riverside remap highlights significant change from coastal scrub dominated in 2001 to annual grasses in 2012 (this change is shown in yellow) in 2012 and the positional relationship to fire (shown in red) which occurred across an 11-year time span.

SOURCE: Aerial Information Systems, Inc. 2015b. Western Riverside County vegetation mapping update. Final vegetation mapping report. Prepared for the Western Riverside County Regional Conservation Authority. Redlands, CA.

and interpret landscape-scale vegetation change correlated with fire across California. Variation in the frequency, intensity, and scale of fire significantly alters the patterns of plant community regeneration. One important, rare vegetation type in this region are stands of Tecate cypress (*Hesperocyparis forbesii* Alliance), which grow along dry, exposed hillsides and ridgetops, stream banks, and arroyos. This species has a California Rare Plant Rank of 1B.1 and is threatened by trends of short fire return intervals, which destroy young trees before they are able to

reproduce and/or build up adequate seed reserves. In 2006, a large fire swept over the northern-most population of Tecate cypress, damaging the majority of the mature individuals. The 2012 map delineates only 38 acres of Tecate cypress compared to 196 acres delineated in 1992 (<20% of the 1992 extent). Much of the area previously mapped as Tecate cypress is now dominated by various shrub species. However, significant regeneration of the cypress has been observed, and this regeneration is documented in the 2012 map within the conifer density attribute

(currently at low levels 2-10%), regardless of the overall vegetation type. Supplementary attributes for each polygon allow users to identify and quantify more than just the existing vegetation type.

Mapping efforts represent single snapshots in time with unique interpretations of the distribution of vegetation in the region and allow users to better understand and interpret vegetation patterns across the region. However, differences between maps are not always straightforward. Careful map interpretation is needed to differentiate actual changes in vegetation composition from differences in classification, map scale, and resolution of delineation.

WESTERN RIVERSIDE COUNTY (11-YEAR INTERVAL)

Riverside County has faced challenges similar to Orange County in-

FACING PAGE: FIGURE 2. A hypothetical map of vegetation in the area now occupied by the city of Oakland immediately prior to the European discovery of the San Francisco Bay circa 1700. This map was created by studying remaining natural vegetation in the area and reviewing historic images and documents from the 1700s through early 1900s. A USGS topographic map backdrop shows the current arrangement of streets and landmarks. Changes have occurred in large areas of salt marsh (*Sarcocornia pacifica*, shown as lavender, lower left), now built-up as bay-fill and including the Oakland Coliseum complex, native grasslands and herblands occupied much of the city core, while redwood (*Sequoia sempervirens*) stands in the hills (orange color at upper right) still occupy roughly the same locations and area as they did 300 years ago.

SOURCE: Keeler-Wolf, T. 2010. unpublished map created for Oakland Museum of California.

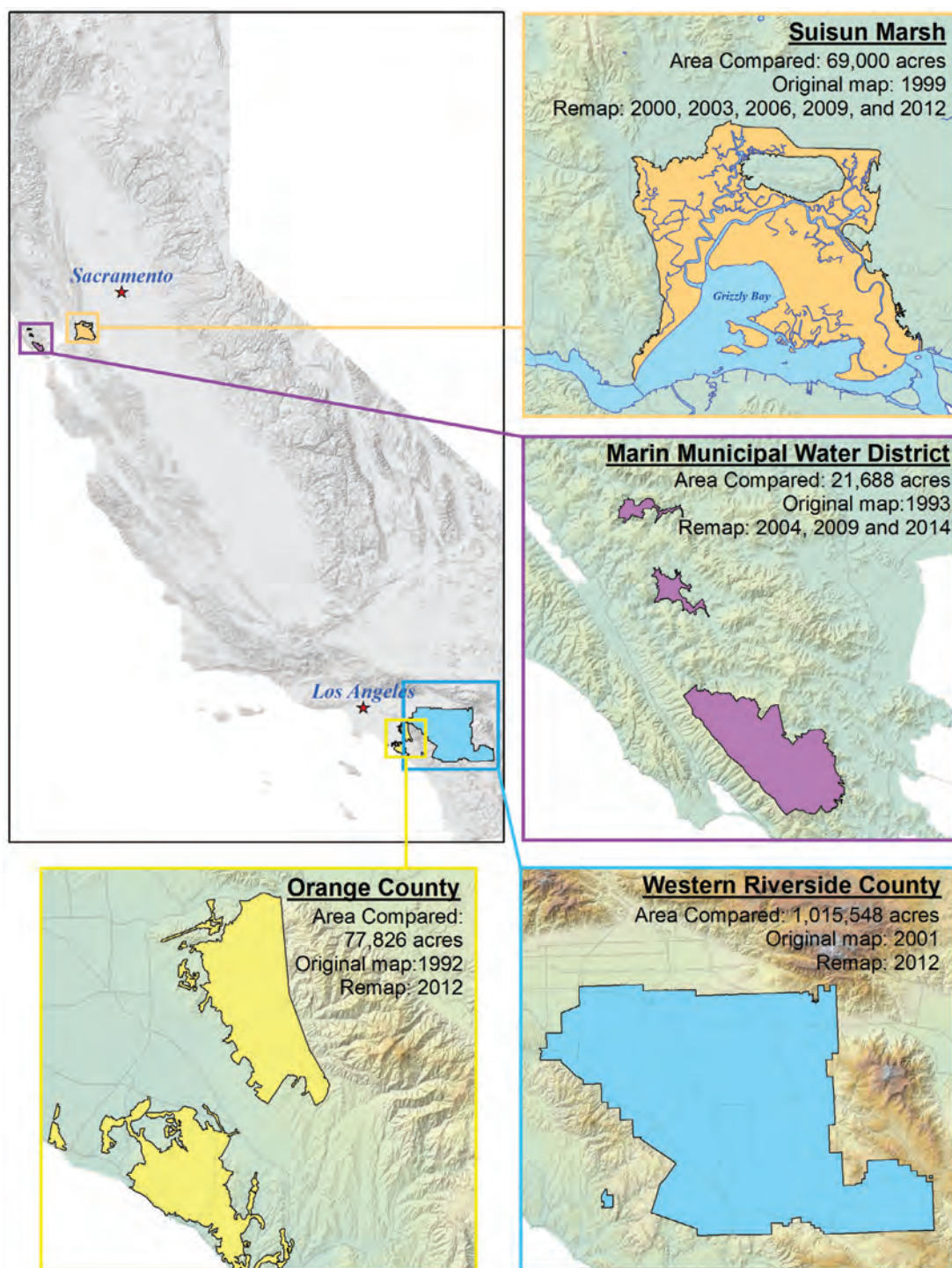


FIGURE 4. Select areas of California have been mapped and remapped at varying intervals to assess change over time.

Source: Boul, R. 2016.

cluding extensive wildfire and urban expansion. The area of focus for re-mapping included over one million acres of western Riverside County between the San Jacinto and Santa Ana Mountains (Figure 4).

This area supports coastal scrub, chaparral, grasslands, riparian corridors, and wetlands. Dynamics affecting vegetation change across the 11 year interval include fire across 119,000 acres, a significant decrease

category of the Coastal Sage Scrub Group which showed a loss of 13,795 acres.

Another illustration of change over time includes stands of chamise (*Adenostoma fasciculata* Alliance)

in average annual precipitation, increases in agricultural and human population, as well as substantial wetland and channel reconfiguration.

One advantage of this re-mapping effort was the use of the same mapping standards and floristic classification to ensure continuity between the two products (AIS 2005, AIS 2015b). This continuity allows a very accurate analysis of true vegetation change over time versus differences due to mapping technique. Change was detectable across both floristic and structural characteristics of vegetation and can be reported using various scales of classification, from the alliance level up to broader types such as those defined in a regional Multi Species Habitat Conservation Plan. For example, a loss of almost 5000 acres of Brittlebush scrub (*Encelia farinosa* Alliance) between 2001 and 2012 can also be aggregated within the more general cat-

that burned after the original 2001 vegetation map. While these stands may remain within the chamise Alliance, other attributes capture structural change in shrub cover, e.g. from 60% shrub cover to 10-25% shrub cover. Changes in shrub cover have direct impacts in relation to habitat preferences for various wildlife species. Other noted changes include post-fire increases in levels of non-native plant species, e.g. from category 0 (no exotics observed) to category 2 (high exotics). By implementing quantitative analyses for multiple aspects of vegetative change between the 2001 and 2012, informed management decisions can be made based on floristic characteristics as well as structural attributes and the overall quality of vegetation in the region.

MOUNT TAMALPAIS WATERSHED (4 MAPS / 5- TO 10-YEAR INTERVALS)

The Marin Municipal Water District developed and updated a Vegetation Mapping Plan in the Mount Tamalpais Watershed of southern Marin County, in part to address wildfire risk and the severity of Sudden Oak Death (SOD) caused by the plant pathogen *Phytophthora ramorum*. The original baseline vegetation map, created in 1993 by East-West Forestry Associates noted tanoak as the most abundant tree, two years prior to the arrival of SOD. In 2004, Aerial Information Systems Inc. (AIS) created a vegetation map using modern imagery and the MCV classification system through a process known as heads up digitizing. Their map was updated in the spring of 2009 and again in 2014, so that over a ten-year period, photo interpreters from AIS produced three vegetation maps that spatially rep-



FIGURE 5. Vigorous spread of common reed (*Phragmites australis*) from 1999 to 2015 in the Grizzly Island Wildlife Area complex, along the edge of Suisun Bay in Benicia, CA.

SOURCE: Vegetation Classification and Mapping Program (VegCAMP). In prep. 2015 vegetation map update for Suisun Marsh, Solano County, California. A report to the California Department of Water Resources. California Department of Fish and Wildlife, Sacramento, CA.

resent the response of vegetation to this devastating pathogen (AIS 2015c).

In 2004, AIS mapped nearly 19,000 acres of mixed hardwoods, redwood and Douglas-fir forests, serpentine and mixed chaparral, maritime coastal scrub and native grasslands within the Mount Tamalpais watershed. This important region is located in the middle of a diverse belt of mixed broadleaf and conifer forest, paralleling the San Andreas Fault between the Bolinas Ridge and Ross Valley. Vegetation was mapped in stands one acre or larger and assigned a vegetation type as well as attributes such as cover density of conifers and hardwoods as well as understory shrub cover where visible.

By measuring the cover of hardwood trees in each stand, photo interpreters evaluated how much of the existing trees (mainly tanoak or coast live oak) in the canopy died over time. Updates to the original 2004-baseline map highlighted additional SOD affected areas, quantified hardwood cover loss created from previous die-offs, and captured floristic change caused by the resultant hardwood death. The most recent effort, conducted in 2014, goes a step further by evaluating all polygons containing hardwoods (roughly 13,000 acres) and individually quantifying the total area of canopy openings created by SOD.

This effort revealed that the watershed has lost nearly all its existing stands of tanoak forest, in addition to suffering a serious decline in

coast live oak trees in the adjacent nearby grasslands. The final product depicts a total of over 2,500 acres of forest and woodlands that have been reclassified from vegetation containing pure and mixed tanoak to other vegetation types where tanoak is not a component of the canopy. The

final product incorporates the information gathered from each of the three mapping efforts over the 10-year period into one coherent geospatially referenced database, giving biologists and other users effective decision-making tools for the management of habitat loss and change, increased fire danger, and other hazards resulting from standing dead and downed trees.

SUISUN MARSH (7 MAPS / 3-YEAR INTERVALS)

The vegetation of Suisun Marsh is likely the most mapped vegetation in the entire state of California. The current methodology, adopted in 1999, utilizes the National Vegetation Classification (USNVC) which is now a state standard for vegetation mapping in California. The summer of 2015 marked the start of the 7th triennial vegetation survey of Suisun Marsh and was conducted by the Vegetation Classification and Mapping Program within the California Department of Fish and Wildlife.

Suisun Marsh is located in Solano County and is part of the San Francisco Bay/Sacramento-San Joaquin River Delta estuary ecosystem. It is one of the largest contiguous brackish marshes remaining in the United States, covering almost 70,000 acres of tidal and managed seasonal wetlands. The amount of information that can be gleaned from such a long, on-going, fine scale mapping project can make your head spin. Examples include: detecting and

monitoring changes in preferred habitat for the endangered Salt Marsh Harvest Mouse, tracking the spread of non-native species of concern including common reed (*Phragmites australis*) and perennial pepperweed (*Lepidium latifolium*), correlating management activities with vegetation changes, providing baseline data for current and future restoration and climate change studies, and much more.

Common reed is a species of concern because it is wide-spread, it displaces native species, and it has rapidly increased in Suisun Marsh since 1999 (Figure 5). When comparing vegetation maps over time, common reed has increased by 216% over the entire marsh, starting with only 863 acres in 1999 and covering 3,142 acres by 2015 (VegCAMP in prep). Vegetation maps are an effective tool to show where species like common reed are increasing rapidly or displacing preferred habitat for the Salt Marsh Harvest Mouse, in order to minimize losses and prioritize control.

Suisun Marsh is an important resource that is owned by several agencies and many private entities but the management is highly regulated and treated as one unit. A comprehensive Suisun Marsh Habitat Management, Preservation, and Restoration Plan was completed in 2014. According to this plan, the next 30 years will bring over 5,000 acres of tidal marsh restoration and over 40,000 acres of managed wetland enhancement across Suisun Marsh. Fine scale vegetation maps are crucial for tracking the progression of the vegetation and channel morphology for these restored and enhanced sites.

SUMMARY

Every member of CNPS knows and appreciates California's great floristic diversity and the sensitivity of our flora to both natural and human agents of change. By following

standard conventions, a vegetation map can be updated and compared to earlier versions, depicting and quantifying changes to the structure, composition, quantity, and quality of the patterns of vegetation. Because vegetation mapping efficiently and accurately represents plant distribution across broad areas it is a very important tool for understanding present, past, or future conditions in larger areas than can be efficiently tracked by traditional individual plant species monitoring methods.

The accessibility of high quality aerial imagery and the availability of vegetation maps online makes comparison over time more feasible now than ever before. A timeline of aerial imagery is currently available online through Google Earth, allowing users to look back in time at various landscapes. Repeat vegetation mapping can show stability, increase, or loss of certain species of plants or plant groups. Taken at face value, these observations may be only interesting to botanists or biogeographers, however, when taken in context of cause and effect, these observations can be strong support for informed conservation or management decisions about individual species, natural communities, or ecoregions.

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Great Valley phacelia (*Phacelia ciliata*), common monolopia (*Monolopia lanceolata*), and California poppy (*Eschscholzia californica*) in the Tehachapi foothills on the Antelope Valley side of Tejon. Photograph by Nick Jensen.

TEJON RANCH—LAND OF CONTRAST, BOTANICAL RICHNESS, AND ONGOING DISCOVERY

by C. Ellery Mayence, Nick Jensen, Neal Kramer, Laura Pavliscak, and Michael D. White

TEJON RANCH— AN INTRODUCTION

Some have heard of it, many have driven past it, but few have experienced the natural wonder of Tejon Ranch. Tejon Ranch, California's largest contiguous private property at 270,000 acres, is located in Kern

and Los Angeles Counties, just over an hour's drive north of the Los Angeles Metropolitan area. Remarkably, this landscape represents 0.25% of California's land area yet supports 13% of the state's native flora. Experiencing Tejon in a year flush with precipitation when wildflowers are in full bloom embodies a landscape indicative of John Muir's words

"when California was wild, it was the floweriest part of the continent." For that matter, experiencing botanical displays on the Ranch even in a so-called 'drought' year can still incite a lengthy list of superlatives.

There is no better way to convey the ecological significance of Tejon than through a discussion of its botanical resources—resources that

have yet to be completely censused as evidenced by a plethora of recent significant botanical discoveries that by all indications will continue as more surveys are conducted. As expressed by Principe and White (2015), Tejon Ranch is one of the most prominent hidden treasures of the Tehachapi region. Our objective here is to comment on how and why Tejon Ranch supports such botanical diversity, convey the overall importance of conducting floristic surveys on the Ranch, and describe how they influence land management. We provide examples of botanical discoveries within interesting ecological contexts and convey the role of the Tejon Ranch Conservancy in ensuring the Ranch's natural resources are appropriately managed.

WHY IS TEJON SO BOTANICALLY RICH?

There are many interconnected reasons as to why Tejon Ranch supports a large fraction of California's botanical diversity. Above all, the Ranch sits at the convergence of several prominent physiographic regions including the San Joaquin Val-



Tejon Ranch is one of the most prominent hidden treasures of the Tehachapi Region—and a significant piece of California's biodiversity conservation puzzle. Map not drawn to scale.

Source: C. Ellery Mayence, Tejon Ranch Conservancy, 2016

ley, Mojave Desert, and the southern Sierra Nevada, Coast, Tehachapi, and Transverse mountain ranges. This equates to the Ranch representing what essentially is one large transition zone between well-defined biomes with distinct floristic associations. Tejon supports at least 45 taxa classified by the California Native Plant Society (CNPS) as species

of special concern (e.g., California jewelflower, *Caulanthus californicus*, Rank 1B.1; San Joaquin adobe sunburst, *Pseudobahia peirsonii*, Rank 1B.1; Fort Tejon woolly sunflower, *Eriophyllum lanatum* var. *hallii*, Rank 1B.1), as well as at least two species endemic to the Ranch, Tehachapi buckwheat (*Eriogonum callistum*, Rank 1B.1) and Comanche Point layia (*Layia leucopappa*, Rank 1B.1). Describing Tejon's rare plant communities in detail is a manuscript in itself and beyond the scope of this piece. Equally as fascinating botanically and an indication of how geography and physiography influence species richness are the number of taxa representing specific genera. Buckwheat (*Eriogonum* spp.), for example, is ubiquitous across the Ranch and represented by an astounding 27 (and counting) taxa. Other genera represented by ten or more native taxa include: *Gilia* (18), *Lupinus* (14), *Clarkia* (14), *Cryptantha* (12), *Phacelia* (12), *Quercus* (12), *Juncus* (10), and *Elymus* (10). More than 40 genera are represented by five to nine native taxa.

The Ranch is a rugged landscape with significant topographical relief,



Grassland habitat, a focus of the Conservancy's land management efforts, comprises more than 100,000 acres of the Ranch and exists in different forms. LEFT: San Joaquin Valley grassland dominated by non-native annual *Bromus* and *Avena* species, and RIGHT: Antelope Valley grassland with a larger fraction of native bunchgrasses including *Stipa speciosa*. Photographs by C. Ellery Mayence.

a diverse geology, and varied soil types, some of which are relatively uncommon elsewhere in the region. Elevation on Tejon ranges from a few hundred feet above sea level to approximately 6,800 feet, rising over a relatively short distance (<10 miles). Situated at the nexus of maritime and desert climates and influenced by topography, slope, and aspect are a multitude of microclimates that, in part, drive plant diversity and community composition. A product of this diverse abiotic environment is the development of unique and diverse soil formations interspersed across the Ranch. Indeed, soil characteristics appear to be one of the single most important drivers of plant diversity on Tejon. Principe and White (2015) nicely describe the variety of special status species that inhabit the alkaline sandy loams and deep clays of the northern and southern Tejon Hills on the San Joaquin Valley side of the Ranch. Perhaps equally as botanically important, though significantly less inventoried, are meta-sedimentary carbonate outcrops on the Antelope Valley side of Tejon laid down in shallow inland seas and uplifted with the Tehachapi Mountains. Well known as the only habitat of *Eriogonum callistum*, it is almost a given that additional noteworthy discoveries await in this area. The volcanic soils straddling the San Andres rift valley are another edaphically unique region of Tejon that has been scantily explored by botanists. As with discoveries elsewhere, extensive surveys will need to be conducted in years with optimum precipitation and temperature regimes—two factors not so easily manipulated. Although unexpected for an area in close proximity to one of the most populous parts of the state, the black box of botanical discovery on Tejon awaits further exploration.

It is generally accepted that a positive relationship exists between land area and species diversity (MacArthur and Wilson, 1967)—

that is, the greater the land area the greater the likelihood that more species can be supported. Therefore, size does matter with respect to ecological processes and the provision of habitat, specifically as it pertains to the maintenance of local adaptation, regional genetic diversity, and plant population viability. Globally, as environments become increasingly homogenized through habitat fragmentation, extinction, and the proliferation of well-adapted, non-native species, landscapes such as Tejon take on an increasingly important role in conserving biodiversity. The scale of Tejon Ranch along with minimal outside influence are fundamental to understanding how and why Tejon supports on the order of 1000 plant species.

BOTANICAL DISCOVERY, RARE PLANT REFUGIA, AND SIGNIFICANT RANGE EXTENSIONS

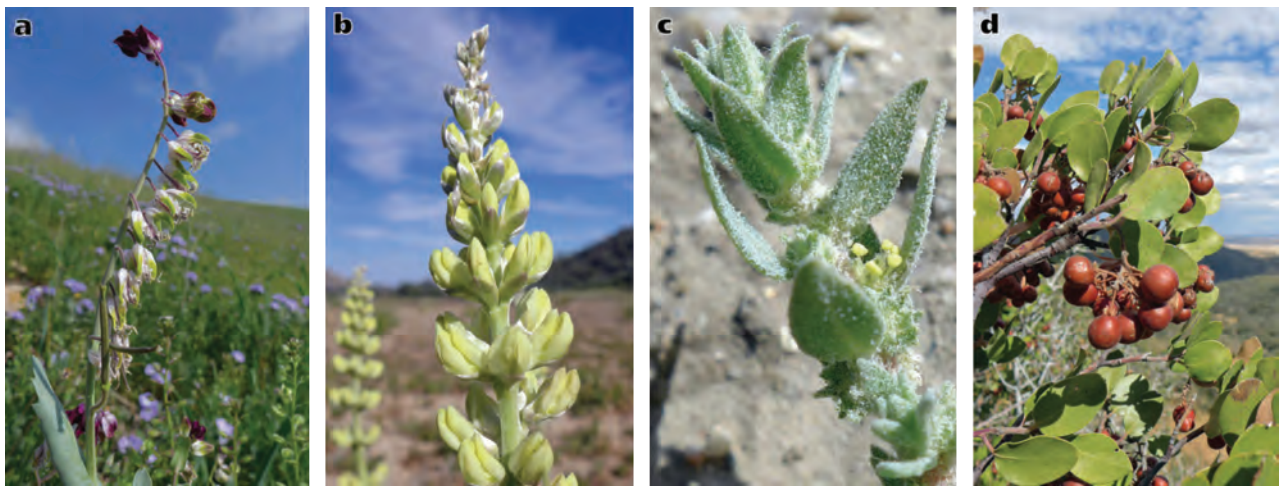
The more time spent afield, the greater the likelihood of new observations and discoveries. This is the essence of botanizing on Tejon. Being private property with restricted public access means that compared to more accessible public and private land, Tejon's botanical resources as a whole have yet to be as thoroughly cataloged. Botanical surveys and discoveries increased significantly eight years ago with the creation of the Tejon Ranch Conservancy who commissioned the work of consulting botanist David Magney, followed by survey work by consulting botanist Neal Kramer and Conservancy employees. Just as significant is botanist Nick Jensen's ongoing, multi-year effort to document and write the first ever flora of Tejon. Prior to the creation of the Conservancy and stemming from surveys associated with proposed development projects, about 1,300 botanical collections were known from the Ranch. This number has increased more



Collections destined for the herbarium—a critical element in documenting and understanding Tejon's flora. Photograph by C. Ellery Mayence.

than five-fold to the 7,000 collections in existence today.

If one factors in yearly and even decadal variation in weather and climate, soil type, specific cues affecting seed germination and plant recruitment, and phenological differences across species, it is easy to not observe certain species in a given year as well as to rarely encounter species that, based on herbarium records, should be present. This could happen for a number of reasons: (1) conditions were not conducive for germination that year, (2) germinants and/or seedlings were predated or died early in development and did not mature, (3) surveys were not conducted in suitable habitat and/or at the appropriate time, or (4) populations were too small and inconspicuous to be readily observed in such a large, topographically complex setting. The



Tejon supports at least 45 special status plant species. Shown are: a) California jewel flower (*Caulanthus californicus*), b) Peirson's lupine (*Lupinus peirsonii*), c) Lost Hills crownscale (*Atriplex coronata* var. *vallicola*), and d) San Gabriel manzanita (*Arctostaphylos glandulosa* subsp. *gabrielensis*). Photographs by Neal Kramer.

Tejon Hills are a hotspot of rare plant occurrences and certainly a major destination for rare plant enthusiasts. Though special status species were known to inhabit the Tejon Hills as early as 2011 if not before, it was not until the winter of 2015-16 when precipitation amount and timing were more typical for the region after several years of drought that numerous rare species were observed in significantly large numbers. Aside from surveying intensity, phenology varies considerably across species so unless target areas are routinely surveyed, it is possible for fast-growing, annual species to complete their life cycle and not be

observed. Whether isolated sites in the Tejon Hills serve as refugia for rare species previously widespread is not known, though it is interesting that other locations with similar characteristics (e.g., elevation, soil type) do not support the same suite of species, or at least have not been observed to do so.

Range extensions add another level of complexity and intrigue to rare plant distributions, especially when over long distances and/or across significant geographical barriers. For example, Peirson's lupine (*Lupinus peirsonii*, Rank 1B.3), San Gabriel manzanita (*Arctostaphylos glandulosa* subsp. *gabrielensis*, Rank

1B.2), and Mount Gleason paintbrush (*Castilleja gleasoni*, Rank 1B.2) are CNPS special status species previously considered endemic to the San Gabriel Mountains or further afield yet now known to occur on Tejon Ranch. Such disjunct distributions bring to light several interesting biogeographical questions, specifically whether such species were more widespread and have retreated to their current distributions as a result of climate change over the past several thousand years. Alternatively, it is possible for seed to disperse over long distances, with the observed individuals representing founder populations. Botanical discovery that results in significant range extensions provides clues into broader biogeographical processes that may not be apparent under current environmental conditions.

PLANT CONSERVATION AND LAND MANAGEMENT

Working landscapes, notably cattle ranches like Tejon, elicit a different conservation and land management framework compared to lands managed solely for low-impact recreation and conservation. Simply identifying a new population of a special status species does



With so many species comes the full spectrum of colors and variants. Shown are: (left) sapphire woollystar (*Eriastrum sapphirinum*) and (right) San Joaquin adobe sunburst (*Pseudobahia peirsonii*). Photographs by Neal Kramer.

not necessarily equate to a change in land management, but rather, at least in the short term, greater devotion to stewardship and monitoring to assess population structure and change over time. This is particularly true on Tejon where cattle have been part of the landscape since the mid-19th Century. Many of the plant species known to occur on the Ranch today, special status species included, have persisted despite consistent grazing and trampling by livestock—though historical distributions for most are poorly understood.

Though it goes without saying that Tejon likely supported greater native botanical diversity prior to European settlement, one could argue that being a working landscape for 100+ years may have actually benefited conservation of species not initially lost as land utilized by native peoples was consumed by intensive agrarian uses. This is not to say that grazing has resulted in an increase in plant diversity or is beneficial in all cases, but rather that persistent grazing has likely helped offset complete transformation by non-native Mediterranean grasses of, for example, the San Joaquin Valley side of the Ranch. These invasive grasses are superior competitors compared to many native California forbs and grasses (Bartolome *et al.*, 2014), and can radically alter landscape-scale ecological processes. When implemented properly, grazing can decrease the competitive edge held by non-native species and minimize thatch accumulation, both of which benefit native plant persistence. However, the benefit of grazing is very much site dependent—and debatable in some cases. For land managers, the question becomes when, where, and at what intensity is grazing beneficial—or not?

As new populations of special status species are identified, effort is made, especially for extremely small populations or populations of very rare species, to implement activities

that benefit their persistence, albeit on a small spatial scale. For example, when a population of California jewel flower (*C. californicus*) was discovered in the Tejon Hills, volunteers were organized to physically remove Saharan mustard (*Brassica tournefortii*) from the vicinity. Similarly, when a population of western dog violet (*V. adunca* subsp. *adunca*) was discovered, the first for this species in Kern County, it was determined that to meet its habitat requirements it would be necessary to limit encroachment by nearby willows. As such, conservation and land management approaches will differ based on species requirements and site-specific attributes and should be adaptable to changing conditions.

THE ROLE OF THE CONSERVANCY

The Tejon Ranch Conservancy, a 501c3 not-for-profit accredited land trust, was created in 2008 and works to protect, enhance, and restore the native biodiversity and ecosystem values of Tejon Ranch and the Tehachapi Range for the benefit of California's future generations. In doing so the Conservancy works closely with the land owner, the Tejon Ranch Company, to prioritize and implement conservation and land management activities. To achieve its internal objectives, the Conservancy has established three program areas: Science, Stewardship, and Public Access and Education. These programs operate interactively with university and Conservancy-led research projects, citizen science, stewardship projects, conservation easement monitoring, environmental education and outreach, and private and public outings representing major activities. For native plant enthusiasts, the Conservancy hosts numerous CNPS chapters throughout the year and collaborates with the Jepson Herbarium on at least one multi-day workshop per year. Because much of what the Conser-

vancy does hinges on scientific research, it collaborates with educational institutions on all levels and provides logistical support for numerous Master's and Doctoral research projects.

LOOKING AHEAD

The future is bright for the conservation of botanical resources on Tejon Ranch and it is likely that forthcoming botanical surveys will yield new species, as such discovery shows no sign of slowing. Of the property's 270,000 acres, approximately 88% or 240,000 acres are protected under an extensive network of conservation easements. As has been the case since it was created, the Conservancy will continue to use in-situ research and best available science to achieve conservation goals and enhance land management. As opportunities arise, the condition of degraded habitats will be improved with the restoration of key ecosystem processes and services serving as success criteria.

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An exquisite stand of bigcone Douglas-fir looking toward Mount Markham from the Mount Wilson Toll Road, Angeles National Forest. Photograph by Michael Kauffmann.

BIGCONE DOUGLAS-FIR MAPPING AND INVENTORYING IN THE ANGELES NATIONAL FOREST

by Michael Kauffmann, Julie Evens, and Jaime Ratchford

The genus *Pseudotsuga* has a present-day range that is quite discontinuous. The species within the genus are confined to western North America and eastern Asia. Unlike the extensive, continuous range of the more common Douglas-fir (*Pseudotsuga menziesii*) across the western United States, bigcone Douglas-fir (*Pseudotsuga macrocarpa*) is a Southern California endemic (Figure 1).

PSEUDOTSUGA

The fossil record for the genus begins in the early Tertiary, about 50 million years ago (MA). Bigcone

Douglas-fir appears in the fossil record for the first time in the late Pliocene, about 3 MA (Axelrod 1950). The character of the fossil flora accompanying bigcone Douglas-fir was similar to today's flora in the Transverse Range. This suggests that bigcone Douglas-fir may have always been restricted in range (Hermann 1985). More recent fossil evidence indicates that in the early Pleistocene, a time that was cooler and wetter, the forest flora that included *P. menziesii* extended further south than it does today, possibly into what is now Baja California, and inhabiting the Transverse Ranges concurrently with *P. macro-*

carpa (Axelrod 1961). Undoubtedly, the range of at least *P. menziesii* underwent repeated changes—corresponding to climate trends—throughout the Pleistocene across both the southern Coast Ranges and southern Sierra Nevada. During this time it is possible that the two species repeatedly overlapped in range—though, like today, never hybridized.

Asian *Pseudotsuga* species and *P. macrocarpa* are the more ancient species within the genus while the modern *P. menziesii* most likely evolved during the Pleistocene. Since that time, *P. menziesii* has gone on to establish itself as a major compo-

nent of the forest vegetation in western North America, as well as one of the most important lumber trees in the world, while *P. macrocarpa* continues to survive within a highly restricted range. While considered to have little economic value, ecosystem services include shade creation, forage and habitat for wildlife, and aesthetic beauty.

A NATURAL HISTORY

Bigcone Douglas-fir spans the Transverse and Peninsular ranges—an extent of 135 miles from north to south and 210 miles east to west—across Santa Barbara, Ventura, Kern, Los Angeles, San Bernardino, Orange, Riverside, and San Diego counties. Northern range limits include areas around Mount Pinos in Kern County and the headwaters of La Brea Creek in Santa Barbara County. Western limits include Zaca Peak in the San Rafael Mountains. The southern and eastern limits are east of Julian along Highway 78 in San Diego County.

Across this region the species ranges in elevation from 300-2,100 m (1,000-7,000 ft) where it generally occurs on cooler, north facing slopes at lower elevations shifting to south facing slopes in higher elevations. The most vigorous stands occur on the north slopes, which retain more moisture and lower average temperatures. Habitats include chaparral, riparian canyons, mixed-conifer woodlands, and desert slopes, all of which offer rough terrain and steep aspects that are often very steep (over 50°). The tall stature of the species, compared to many of the shrubs with which it associates, makes it quite distinct, especially large specimens. The two largest documented trees grow in the San Gabriel Mountains. The largest recorded, near Mount Baldy

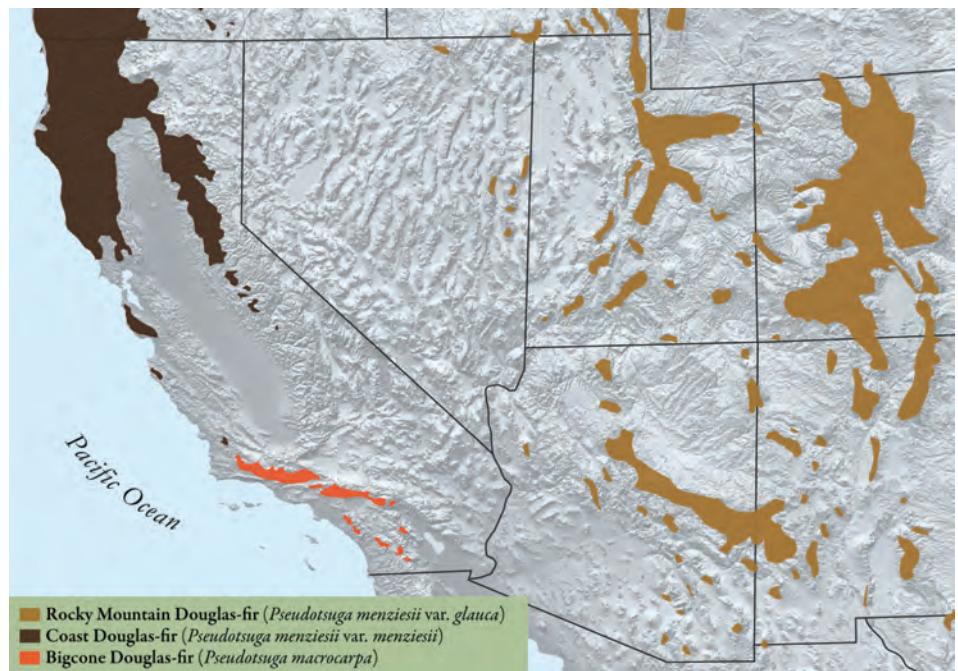


FIGURE 1: Range of *Pseudotsuga* across the southwestern United States. From Kauffmann 2013.

Village, was measured in 2005 to 50m tall and 7m in circumference—making it one of the largest trees in the region.

Bigcone Douglas-fir inhabits a zone generally between the lower elevation chaparral and the higher elevation mixed-conifer forest. Within the chaparral zone, the species is often found in small patches. In mature forests, bigcone Douglas-fir forms the upper canopy while canyon

live oak (*Quercus chrysolepis*) forms the mid-canopy. Trees occur on gravelly soils that are usually shallow, often with a sparse understory of Mediterranean-type chaparral species.

Bigcone Douglas-fir is distinct from other species in the genus be-



LEFT: Bigcone Douglas-fir seed cone (left) compared to coast Douglas-fir. • RIGHT: The second largest documented bigcone Douglas-fir was found during our surveys. It is 118' tall, with a 265" circumference, and a 114' crown spread for 412 total points (according to the American Forests Tree Measuring Guidelines). Photo by Michael Kauffmann with Daniel Hastings.



cause it has uniquely large cones and seeds (Table 1). With an increase in cone and seed size, a functional shift in the mode of seed dispersal has occurred. Species that have evolved characteristics such as well-defended cones and larger seeds typically have a closer relationship with animals as seed dispersers (Vander Wall *et al.* 2006). Excluding *Pseudotsuga macrocarpa*, ancestrally and currently all other species in the genus have winged seed for wind dispersal. Although *P. macrocarpa* has a winged seed, the mass of the seed renders this wing largely ineffective for wind dispersal. Animal-dispersed pines live in drier environments and animal-dispersed *P. macrocarpa* lives in drier environments too. Thus we see convergent trends: animal seed dispersal allows occupancy of drier sites.

Bigcone Douglas-fir is one of the most fire resistant and adapted conifers in the world, with the ability to survive frequent fires because of the prolific resprouting of new needles and branches from meristematic tissue on branches and boles. It also

has unusually thick bark—15-20 cm in mature trees. Within one to three years after fire events, buds not killed will typically sprout new shoots (Vander Wall *et al.* 2006). These adaptations suggest bigcone Douglas-fir has evolved to survive multiple fire events that arrive via the surrounding chaparral with a short fire return interval (Lombardo *et al.* 2009). A fire scar chronology on 85 trees from 15 sites dating back to 1600 across Los Padres National Forest suggests that in this region a 400 year old tree would, on average, experience 13 fires in its lifetime (Lombardo *et al.* 2009).

BIGCONE DOUGLAS-FIR IN THE ANGELES NATIONAL FOREST

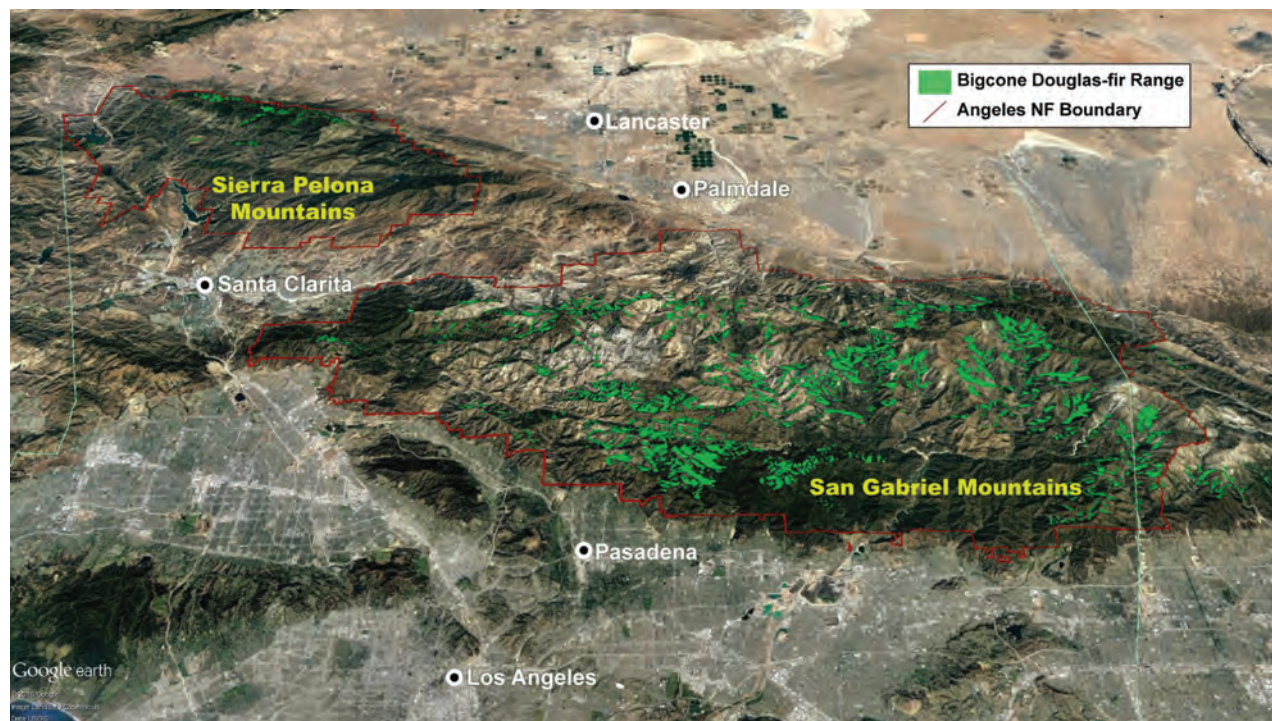
Across the Angeles National Forest, bigcone Douglas-fir occurs in some of the highest densities for anywhere in the species' range (Figure 2). While the heart of this range is in the San Gabriel Mountains, a smaller, disjunct population occurs

in the Sierra Pelona Mountains to the northwest. These two populations have quite distinct ecologies.

Stands in the San Gabriel Mountains are in four general regions classified in a transect from the front range to the Mojave Desert (Figure 3). The lowest elevation sites occur in the front-range, generally in north-facing canyons or on steep slopes. The interior slope sites include river drainages and higher elevation peaks like the San Gabriel River and the Tujunga Canyon regions. The higher elevation sites are mixed conifer stands where the species overlaps with montane conifers. The north-slope, or Mojave slope, stands comprise interesting associations of mixed-evergreen plants like the rare Parry's manzanita (*Arctostaphylos parryana* subsp. *parryana*) and other desert flora.

In the Sierra Pelona Mountains, the species occupies a small percentage of acreage for the entire forest. Here, bigcone Douglas-fir mixes with black oak (*Quercus kelloggii*) in open grasslands on the ridgeline of Liebre Mountain down into the

FIGURE 2: Range of *Pseudotsuga macrocarpa* across the Angeles National Forest. From Kauffmann *et al.* 2017.





Bigcone Douglas-fir stand on the south-facing slopes of the San Gabriel Mountain's front range, overlooking the Inland Empire. Photograph by Michael Kauffmann

the north slope and canyons and into the upper elevations of the Antelope Valley near Neenach. Elsewhere in the Sierra Pelonas, bigcone Douglas-fir persists in small, isolated, relict stands on rocky summits or in sheltered north-facing river canyons. These low density stands persist because stand-replacing fires have not occurred in these small pockets.

MAPPING AND INVENTORYING PROJECT

The California Native Plant Society, working in collaboration with the US Forest Service (USFS), initiated field surveys in the summer/fall of 2015 to assess the extent and status of the California endemic bigcone Douglas-fir in the Angeles National Forest. Goals in the field

included verifying distribution and status of bigcone Douglas-fir, ground-truthing polygons designated by US Forest Service Remote Sensing Lab's California Vegetation (CALVEG) system as "Bigcone Douglas-fir" Regional Dominant, and conducting 370

rapid assessments on bigcone Douglas-fir stands. The data collected during field assessments were used to develop both an updated distribution map via heads-up digitizing and a vegetation classification to better define bigcone Douglas-fir stands for the area.

TABLE 1. CHARACTERISTICS OF CONES AND SEEDS OF DOUGLAS-FIR (*PSUEDOTSUGA MENZIESII*) AND BIGCONE DOUGLAS-FIR (*P. MACROCARPA*)*

Cone or seed trait	<i>P. menziesii</i>	<i>P. macrocarpa</i>
Seed mass (mg)	24.8 ± 3.7	132.6 ± 23.8
Seed length (mm)	7.3 ± 0.7	10.9 ± 1.0
Wing area (mm ²)	52.0 ± 14.1	97.3 ± 32.0
Descent velocity (m/s)	1.28 ± 0.22	2.47 ± 0.62
*Adapted from Vander Wall <i>et al.</i> 2006		



Bigcone Douglas-fir and Parry's manzanita vegetation type on calcareous soil at the edge of the Mojave Desert, San Gabriel Mountains. Photograph by Michael Kauffmann.

GENERAL PATTERNS

Several patterns emerged in our survey data. Of the 35,300 acres of bigcone Douglas-fir on the Angeles National Forest, over 94% of those stands occur in the San Gabriel

Mountains with just under 6% in the Sierra Pelona Range (Table 2). No stand-replacing fires were documented via heads-up digitizing or ground truthing in the Sierra Pelonas while 10% of the acreage in the San Gabriel Mountains appears to

have been impacted by stand-replacing fires within the last ten years. Across both ranges we found some evidence (i.e. char on bark) of fire in 77% of the surveys.

Mortality between 10 and 90% was strikingly high, with 19% of

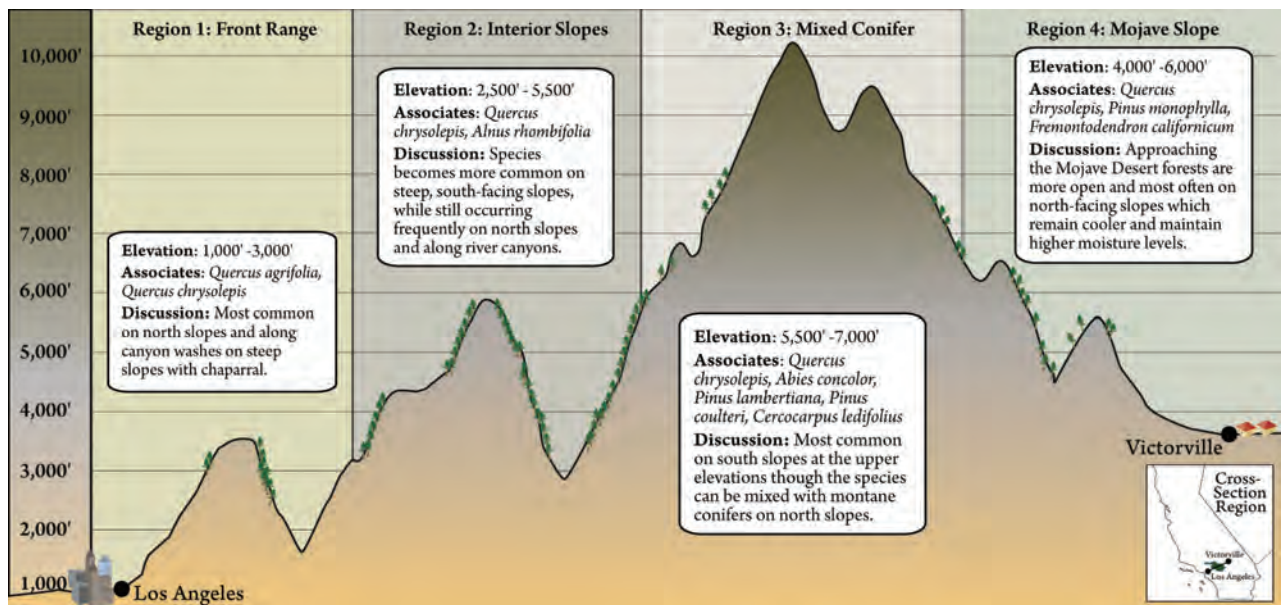


FIGURE 3: Ecological cross-section of the San Gabriel Mountains featuring Bigcone Douglas-fir distribution. From Kauffmann *et al.* 2017.



stands exhibiting mortality (generally between 10 and 20%). This mortality is occurring at lower elevations on both the south slopes of the San Gabriel Mountains and the north-slopes of the Sierra Pelonas. Most likely this mortality is due to xerification.

VEGETATION PATTERNS

A classification analysis for this project resulted in 21 alliances and 39 associations where bigcone Douglas-fir exists in the Angeles NF. An alliance is a hierarchical classification unit of vegetation defined by the diagnostic species of the uppermost canopy layer and contains one or more associations. Associations define the vegetation in finer detail and reflect the variation of the vegetation at a more local level. Eleven new associations were classified in the Bigcone Douglas-fir Forest Alliance (indicated by an asterisk in Table 3) as a result of the fieldwork.

Of the 35,300 acres mapped in

TABLE 2: AREA OF BIGCONE DOUGLAS-FIR POPULATIONS BY FOREST REGION.

Range	Region	Acres	Hectares	%
San Gabriel Mountains	Healthy stands	23,504	9,512	70.6%
	Mortality present (>10%)	6,046	2,447	18.2%
	Stand-replacing fire event (>90%)	3,728	1,509	11.2%
	Total within Angeles NF	33,278	13,468	94.2%
Sierra Pelona Range	Healthy stands	1,396	565	68%
	Mortality present (>10%)	656	265	32%
	Stand-replacing fire event (>90%)	--	--	0%
	Total within Angeles NF	2,052	830	5.8%
Total acreage in the Angeles National Forest		35,330	14,298	

TABLE 3. THE FLORISTIC CLASSIFICATION OF ALLIANCES AND ASSOCIATIONS ORGANIZED ALPHABETICALLY BY LIFEFORM.

Newly defined associations are designated with an asterisk (*). Complete table available at <http://cnps.org/cnps/vegetation/pseudotsuga-macrocarpa>.

ASSOCIATION	# SURVEYS
<i>Pseudotsuga macrocarpa</i> (Alliance)	7
<i>Pseudotsuga macrocarpa</i> – <i>Quercus agrifolia</i>	3
<i>Pseudotsuga macrocarpa</i> – <i>Quercus chrysolepis</i>	54
<i>Pseudotsuga macrocarpa</i> – <i>Quercus chrysolepis</i> – (<i>Acer macrophyllum</i>)*	14
<i>Pseudotsuga macrocarpa</i> – <i>Quercus chrysolepis</i> – <i>Abies concolor</i> – <i>Pinus</i> spp. (<i>P. lambertiana</i> , <i>jeffreyi</i> , <i>ponderosa</i>)*	17
<i>Pseudotsuga macrocarpa</i> – <i>Quercus chrysolepis</i> – mixed conifer / <i>Cercocarpus ledifolius</i> *	4
<i>Pseudotsuga macrocarpa</i> – <i>Quercus chrysolepis</i> – <i>Pinus coulteri</i> * 25	
<i>Pseudotsuga macrocarpa</i> – <i>Quercus chrysolepis</i> – <i>Pinus monophylla</i> / <i>Fremontodendron californicum</i> * 14	
<i>Pseudotsuga macrocarpa</i> – <i>Quercus chrysolepis</i> – <i>Quercus wislizeni</i> / <i>Arctostaphylos glandulosa</i> * 6	
<i>Pseudotsuga macrocarpa</i> – <i>Quercus chrysolepis</i> / <i>Bromus diandrus</i> * 14	
<i>Pseudotsuga macrocarpa</i> – <i>Quercus chrysolepis</i> / <i>Ceanothus integerrimus</i> * 35	
<i>Pseudotsuga macrocarpa</i> – <i>Quercus chrysolepis</i> / <i>Cercocarpus montanus</i> * 17	
<i>Pseudotsuga macrocarpa</i> – <i>Quercus chrysolepis</i> / <i>Hesperoyucca whipplei</i> * 14	
<i>Pseudotsuga macrocarpa</i> – <i>Quercus kelloggii</i> * 5	

the Angeles NF, 18,573 acres were mapped as Bigcone Douglas-fir Forest Alliance. In contrast, the CALVEG map had 34,055 acres attributed as bigcone Douglas-fir dominant stands (USDA 2014). The difference between these two maps appears partially as an error of omission in the CALVEG map, since the

alliance map identified 9,236 acres as Bigcone Douglas-fir Forest that were not mapped previously in the CALVEG map. We suppose that the resulting alliance map benefited from significant ground-truthing during the project, and from using more detailed aerial imagery than was used in the existing CALVEG map of the

region. Conversely, there were 24,766 acres mapped in the CALVEG map as bigcone Douglas-fir dominant stands that were not mapped as such in the new alliance map—this difference in acreage is likely due in part to the CALVEG map being produced be-

fore the 2009 Station Fire, which resulted in some stand-replacement of conifer vegetation in the landscape (e.g., canyon live oak, grassland, and chaparral vegetation).

MANAGEMENT RECOMMENDATIONS

Because bigcone Douglas-fir grow in two ecologically distinct regions of the Angeles NF we provide recommendations for each region. See Kauffmann *et al.* (2017) for a more detailed account of recommendations; below are some highlights.

Sierra Pelona Mountains

Thickets of conifers, predominantly bigcone Douglas-fir and some Coulter pine (*Pinus coulteri*),



LEFT: Fuels management may have saved this stand of PSMA after the 2009 Sheep Fire in Lone Pine Canyon. Photograph by Michael Kauffmann.

• BELOW: The Station Fire footprint extends up the slopes of Bear Canyon (near Mount Wilson) toward Tom Sloane Saddle where the fire stopped, leaving unburned forest on the left (NE facing) side of the picture. Photo by Michael Kauffmann.





Bigcone Douglas-fir encroaching into a black oak woodland in the Sierra Pelona Mountains. View is to the north toward the Tehachapi Mountains. Photograph by Michael Kauffmann.



have been recruiting in open spaces of black oak woodlands that were formerly managed by the Serrano Indians (Yuhaviatam) as a food source for acorns as well as open hunting grounds (Keeley 2002). We recommend using targeted prescribed fire or conifer sapling removal by hand within the upper elevation oak woodland habitat to ensure this habitat does not type-convert to conifer forest.

San Gabriel Mountains

The San Gabriel Mountains have proportionately less low-level mortality than the Sierra Pelonas but higher incidence of stand-replacing (last 10 years) fire events—mostly due to the Station Fire. Fire fre-

quency increases with proximity to roads—many of which were easier to construct through this western region of the mountains as compared to the steeper, central and eastern portions. In addition, roads vector invasive species that are ignitable.

While roads may increase fire frequency, they may benefit bigcone Douglas-fir recruitment by creating open space for seedling establishment. Recruitment was high on naturally and anthropogenically disturbed slopes where there is newly-exposed mineral soil with little to no competition from other plant species (Figure 4). We recommend the Forest Service disperse locally collected seeds in roadcuts or on new landslides between 1,200-





FACING PAGE, TOP: Bigcone Douglas-fir in the San Gabriel Wilderness. Photos by Michael Kauffmann. • INSET: Daniel Hastings and Joslyn Curtis surveying for trees near Wrightwood, California. • FACING PAGE, BOTTOM: Low elevation mortality in bigcone Douglas-fir stands in the San Dimas Experimental Forest. • ABOVE: Bigcone Douglas-fir growing along the San Gabriel River on rocky slopes approaching 90 degrees.

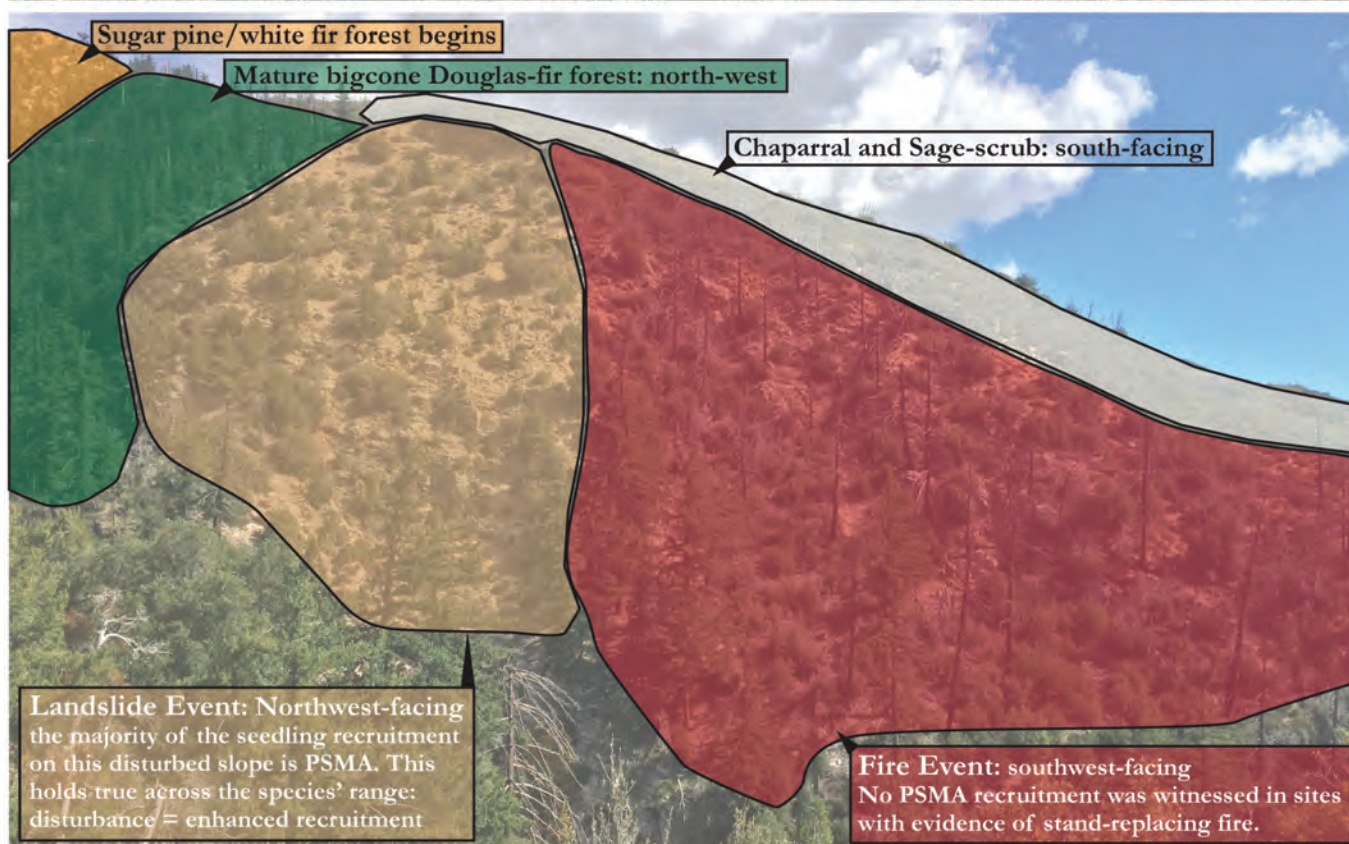


FIGURE 4: Landscape-scale patterns in bigcone Douglas-fir seedling recruitment can be seen in this unique location near Crystal Lake. Graphic by Michael Kauffmann.

3,100 m (4,000-7,000 feet). This management approach will repopulate and stabilize slopes and promote persistence of bigcone Douglas-fir. Other recommendations include environmental education and public outreach to promote fire safety and noxious weed awareness.

Away from roads, recruitment appears to be most common in wilderness areas that have not been managed due to their remote nature. With lack of management, fires have remained unconfined, of generally low-intensity, and frequent. These historical fire regimes are important to maintain because they are the conditions to which this species has adapted over the past five million years. Steep slopes in the interior mountains have offered long-term refugia from high-intensity stand-replacing fire. Recommendations in remote areas of the forest include adding wilderness designation and eliminating roads where possible.

THE FUTURE

Across the forests of the Transverse and Peninsular Ranges, high potentials for stress are imminent in certain portions of the species range due to climate-water deficits and large-scale fires. Bigcone Douglas-fir is likely to find refugia along the higher, north facing elevations in the Angeles NF and potentially further north through the Tehachapi Mountains, Sierra Nevada, and Coast Range over the next 85+ years.

Even before the current human-induced climate changes, fossil evidence suggests that the range of the species has been in decline. The species is highly valued across the mountains of southern California as an endemic species, for its aesthetic beauty, wildlife habitat, and influence on regional biodiversity with the habitat it creates. These are relict habitats where high severity fires have been rare but other disturbances like landslides and lower intensity fires have remained a com-



View down Lone Pine Canyon toward Victorville, California. Photo by Michael Kauffmann.

mon part of the species' ecology, allowing them to continue to flourish, for now, across the Angeles National Forest.

ACKNOWLEDGMENTS

CNPS fieldwork staff included Daniel Hastings and Joslyn Curtis. Angeles National Forest Fuels Planner Diane Travis, Southern Province Ecologist Nicole Molinari, Humboldt State University professor Lucy Kerhoulas, and Anton Jackson with TEAMS Enterprise Unit. Their support in project funding and review of the article are greatly appreciated.

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BOOK REVIEWS

Gathering Moss: A Natural and Cultural History of Mosses by Robin Wall Kimmerer. Oregon State University Press. \$18.95. ISBN: 978-0870714993

Robin Wall Kimmerer's *Gathering Moss: A Natural and Cultural History of Mosses* guides readers through a shift in perspective towards what is overlooked, under-valued or—at the extreme—the completely unseen. The book is a natural history guide to mosses, brimming with contextualized anatomical definitions and clearly presented ecological principles that incite a sense of wonder for this small-scaled world. Woven throughout the narrative, however, Kimmerer gently nudges readers towards a more substantial shift in perspective, from nature-as-simple object to nature-as-intelligent teacher.

Each chapter is arranged as a vignette-length personal narrative and tackles various aspects of moss biology and ecology, showing the reader there is always more than meets the eye. In one such vignette, Kimmerer takes time to explain the importance of the boundary layer—the meeting point of air and land—to mosses existence and relationship to water, all to levels of detail that will satisfy avid naturalists.

Other chapters look into mosses' roles in ecological succession and restoration, variations in moss reproductive strategies, and moss communities. The author also introduces many of her favorite moss genera such as *Dicranum*, *Dendroalsia*, *Tetraphis*, *Bryum*, and *Sphagnum*—many of which have figured into her experiments.

Yet Kimmerer is not content to keep the subject-object lines clear and one of the main ways she confounds those lines is by turning the lens onto herself. In the very first chapter, we accompany her on a dreamy passage into a mossy clearing within a boulder pile, which she pointedly recounts, she has never seen before despite having walked past this section of land hundreds of times. As such, Kimmerer de-

stabilizes her position as an unseen and unbiased observer-guide and introduces the importance of a change in attention, something she invites the reader to do as well. Throughout the book, she situates some of her important research questions in bryology into the story of her life. By revealing the personal side of scientific inquiry, she makes the questions all the more vivid for the reader. This personalized element of the book lends it to being a great read for young adults with an interest in biology, plants, and/or natural history.

The blurriness of subject-object lines is itself, ultimately, the shift Kimmerer asks her readers to make. While Kimmerer may impose such clearly defined roles in the process of scientific inquiry, in the other realms of her life as a mother, a neighbor, an indigenous woman, and a human being on an ecologically-threatened planet, mosses and nature have powerful agency and wisdom from which we can learn essential principles. A beautiful chapter entitled “The Forest Gives Thanks to the Mosses” tracks how, in myriad ways, mosses are intricately connected to the thriving of the forest ecosystem and its many members. If Nature is our teacher, the main lesson is one of reciprocity and interconnectedness.

Gathering Moss is a look at overlooked worlds: mosses, indigenous ways of knowing, and Nature, to name but a few. It merits more than a glance.

—Catherine Curley

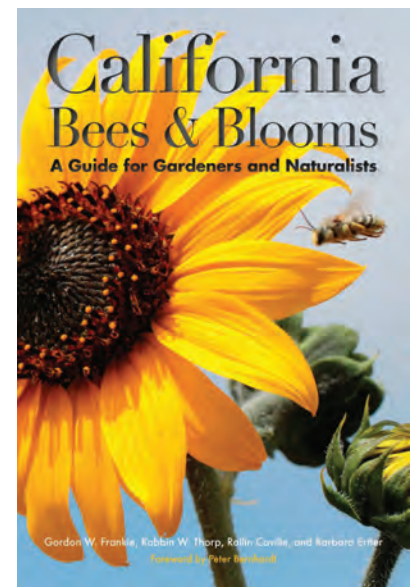
California Bees and Blooms: A Guide for Gardeners and Naturalists by Gordon W. Frankie, Robbin W. Thorp, Rollin E. Coville, and Barbara Ertter. Heyday. \$28.00. ISBN: 978-1597142946

California Bees and Blooms opens in homage to the return of John Muir's ‘bee pastures’ and an introduction to pollinator decline. Acknowledging we can no longer rely on honeybees for agricultural pollination services—we look to the wild pollinators. One well-

planted urban bee garden can attract 40 to 50 species of bees.

As a beekeeper, this book is for the beekeeper and bee enthusiast alike, with reference to the social honeybee and world of solitary native bee species. It's a book for the avid gardener and flower enthusiast. I was interested to learn more about specific bee-plant interactions—for example the female squash bee (in the family Apidae) visits squash flowers in the early morning before sunrise, followed by a later honeybee visit. When the flower closes in late morning you can peek inside and often times find one or more male squash bees fast asleep—where it will stay until the following morning!

Early chapters are loaded with detailed information ranging from the sophisticated lifecycle and bee identification characteristics to equally so-



phisticated bee mimicry and anatomical disparities. Here we're offered an in-depth look at bee identification by wing characteristics or other ways such as host plants visited, seasonality, foraging behavior and geographic distribution. Chapters are then divided up into bee families grouped by descriptors such as “sweat bees” (those that lap up our perspiration!), mason bees (the architects) and mining bees. Within the chapters, bee profiles and

close-up color photography detail the 22 most common genera found in urban California. Each genus is further described by general appearance, special features, similar looking insects, distribution and abundance, flight season and behavior, preferred flowers, and nest habitat. We also learn about natural enemies of bees—that little white crab spider we see in our flowers is not so innocent!

Cultivators of gardens will enjoy the chapter about pollination syndromes—a set of flower characteristics that can be used to identify its most likely pollinator. Another chapter is dedicated to the plants that consistently attract native bees. Each plant profile includes descriptive information, flowering season, what resource it offers bees, the most frequent bee visitors, bee ecology and behavior, and gardening tips. You can read up on that lavender bush or western redbud you have growing in your yard to find out more about its particular pollinators. Knowing the Latin names and families of plants goes a long way in navigating through this section.

After reading this book I am excited to see the bee world with new eyes, and challenge myself to look beyond my social honeybees. What I might have passed off as a bumblebee, I may now see is a carpenter bee. And now I'm on the lookout for one of those many metallic-colored bees. The book closes with 'recipes' for designing bee habitats that serve diverse purposes, and lastly, ways to take action to protect native bees. It is a well-organized and informative body of work. You, too, will undoubtedly see the bee world with new eyes after reading through this thoughtful and descriptive guidebook.

—Denise Newman

A Naturalist's Guide to the Hidden World of Pacific Northwest Dunes
by George Poinar Jr. Oregon State University Press. \$24.95. ISBN 978-0-87071-854-0

Finally, a field guide to dune habitats along the Pacific Coast that is based on wildlife relationships rather than taxonomy. Rather than having sections on plants, birds, lizards, insects, etc.,

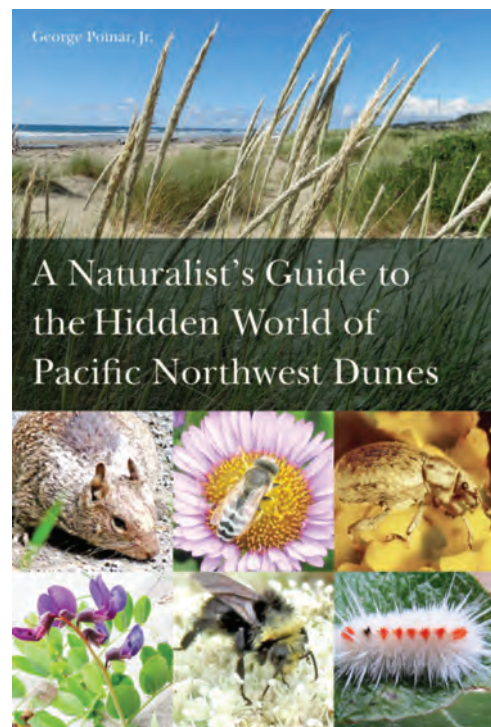
George Poinar has organized the chapters based on habitat types, starting with the kelp and driftwood communities, and for the strand and dune community, describes 58 plant species and their associated organisms.

Each species, from microscopic nematodes to trees, has an informative photograph (or two or three). George took all the photos, and because of that I feel there is a consistency in presentation that allows better understanding. Fifty-eight species of plants form chapters with a text introduction that describes the life styles of the various creatures that are associated with that plant. Insect species with multiple life forms will often have an image of both larvae and adults. For each community, a table is provided showing the detritivores, herbivores, predators, omnivores, parasites, and symbionts among the species described.

In general, little is known about the organisms that coexist with plants. But George tells us that "The presence of ants explains why most insect herbivores on giant vetch are concealed in plant tissue." He is graphic in his description of the events of the natural

world: "At night many [sand fleas] fall victim to...rove beetles that crush them in their mandibles and suck up their body liquids." We learn that carrion beetles eat strawberries, ergot is a fungus that infects dunes grasses, and which insects pollinate dune orchids.

The writing is poetic at times, very descriptive and packed with details. His in-depth knowledge of this hidden



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world is unsurpassed, and his enthusiasm for it is infectious. Each animal species account includes common name and scientific name, order and family; plants are named by common name, scientific name and family. The characteristics, habitat and range are described for each species, along with a comment. Both native and non-native species are described.

The book is fully indexed and includes a glossary of terms. You'll need the index if you want to find anything because the plants are listed in no particular order and by common name.

If I have anything to complain about, it is the title. There was no reason to limit it to the "Northwest" dunes. Of the 432 species listings, 83% occur anywhere along the Pacific coast between Washington and California. This book will be very useful to anyone who visits coastal dunes in California.

George Poinar Jr. is a truly modern naturalist. He understood wildlife relationships when he was a professor at UC Berkeley and I was a student illustrating scientific books and papers for him back in the 1970s. His work with amber (*The Quest for Life in Amber*, Addison Wesley, 1994 and *The Amber Forest: A Reconstructions of a Vanished World*, Princeton, 1999, both by George Poinar Jr. and Roberta Poinar) required that he studied many forms of life—trying to identify prehistoric life trapped in rocks. But George is even more, he is a naturalist-educator, with a strong sense of conservation and the understanding

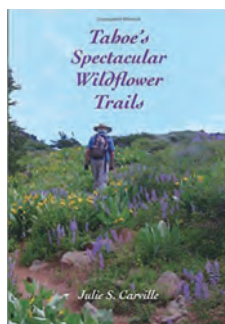
that for the public to understand and care about wildlife, they have to have a vehicle to understand it. This book is the first of its kind and I hope other authors start publishing guides in this format.

—Steve Hartman

Tahoe's Spectacular Wildflower Trails
by Julie S. Carville. Mountain Gypsy Press. \$29.95 ISBN: 978-0-692-69818-1

This wildflower guide is a delightful book with many very good photographs and lots of interesting information about the wildflowers of the Lake Tahoe region. This well-written book is 277 pages long and chock full of photographs, 877 to be exact.

It is arranged in four basic sections: background types of information, trees, wildflowers (arranged by flower color), and the plants by selected trails in the broad Tahoe region. This guide identifies the plants covered by common names, with reference to a plant's scientific name infrequently (but at least once). The photographs of the plants by flower color uses only common names; however, there is a complete list of both common and sci-



entific names in the index as a useful cross-reference.

It is small enough to carry along on a hike of any of the 21 trails highlighted, but of sturdy enough paper to handle such use for many years. You could even drop it in a stream and probably not damage it too much, but I don't recommend that.

If you read and use this book, you will indeed learn a lot about plants, and if you hike the trails with this book in hand, you will be rewarded and enriched in the process.

—David Magney

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ACKNOWLEDGMENTS

The time and effort by all authors and co-authors reviewing and re-reviewing their manuscripts was invaluable in making this issue into what it has become. I would also like to thank all the reviewers including Lucy Kerhoulas, Nicole Molinari, Steve Sillett, Tom Carlberg, and a few anonymous folks for graciously volunteering their time as editorial consultants.

SUBMISSION INSTRUCTIONS

CNPS members and others are invited to submit articles for publication in *Fremontia*. If interested, please first send a short summary or outline of what you'd like to cover in your article to the *Fremontia* editor at fremontia@cnps.org. Instructions for contributors can be found on the CNPS website, www.cnps.org, under Publications/Fremontia.

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FROM THE EDITOR

The first three articles in this issue take us on a journey into the small and beautiful world of lichens and bryophytes. Mosses, liverworts, and lichens are significant components of ecosystems across the state but are often overlooked because of our eye-level connection to vascular plants. A closer look (and a hand lens) reveals a window into the wonderful world of charismatic cryptograms. Shelly Benson, Rikke Reese Næsborg, and Marie Antoine have contributed exquisite stories sharing their love and passion for these often-overlooked critters—taking us on a journey to better understand them.

Todd Keeler-Wolf, Rachelle Boul, Jennifer Buck-Diaz, and John Menke tell the story of how vegetation mapping is changing using data and imagery from the past at various intervals. Their analysis is depicting and quantifying changes of patterns of vegetation across the state to better understand past, present, and future conditions.

C. Ellery Mayence, Nick Jensen, Neal Kramer, Laura Pavliscak, and Michael D. White revisit Tejon Ranch—a place many of us at CNPS hope becomes a National Park. The crossroads of the Sierra Nevada, Tehachapi Mountains, and Transverse Ranges is 0.25% of the state's land area supporting 13% of the species in our native flora. They share that diversity with us and the role of the Tejon Ranch Conservancy in protecting those resources.

Lastly, Julie Evens, Jaime Ratchford and I share a CNPS vegetation program collaboration with the Angeles National Forest. For two years we mapped and inventoried the California endemic bigcone Douglas-fir and in the process broadened our understanding of the health and distribution of this stunning conifer in the San Gabriel and Sierra Pelona mountains of southern California.

It is truly a pleasure to be guiding *Fremontia*—enjoy!

—Michael Kauffmann

(continued on inside back cover)