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SPECIAL ISSUE ARTICLE

Sequoia and *Sequoiadendron*: Two paleoendemic megatrees with markedly different adaptive responses to recent high-severity fires

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Abstract

Premise: Coast redwood (*Sequoia sempervirens*) and giant sequoia (*Sequoiadendron giganteum*) are two iconic paleoendemic species with limited distributions, well known for their spectacular size. Recently, they have been exposed to high-severity crown fires, with starkly contrasting responses.

Methods: We used all available published literature and field observations to understand the responses to fire in an evolutionary context.

Results: Coast redwoods, found in California's coastal rainforests, were highly resilient to high-severity fires, with most trees surviving due to their ability to resprout from the base and trunk, though seedling regeneration was largely lacking. In contrast, giant sequoias, native to the Sierra Nevada, do not resprout, leading to significant tree mortality after very high-severity fires; they released seeds only in patches where some trees survived moderately high-severity fires.

Conclusions: These high-severity fires were novel events for giant sequoias, but not for coast redwoods. Fire suppression has disrupted the natural fire regime in the giant sequoia ecosystem by preventing frequent lightning-caused surface fires, resulting in high-severity fires that killed a substantial number of these giants. In coast redwood forests, infrequent but high-severity crown fires were the norm before burning by Native Americans. Frequent, low-severity burning by Native Americans over the past few hundred years was localized and 20th-century fire suppression has returned the natural fire regime to these forests. The recent crown fires do not represent a threat to redwood conservation; however, other management goals may require emulating Native American burning practices and in some cases may be best termed cultural restoration.

KEYWORDS

crown fires, Cupressaceae, Mesozoic, Native American burning, resprouting, serotiny

Coast redwood [*Sequoia sempervirens* (Lindl.) Buchholz.], the world's tallest tree (Figure 1), is restricted to central and northern coastal California rainforests. Giant sequoia [*Sequoiadendron giganteum* (Lindl.) Buchholz.] is the world's most massive tree in terms of biomass (Figure 2) and endemic to mid-elevation mixed-conifer forests in the interior Sierra Nevada Mountains of California. These two monotypic species are in the subfamily Sequoioideae of coniferous trees within the family of Cupressaceae. The subfamily includes only one other species, *Metasequoia glyptostroboides* Hu & W.C. Cheng, which is restricted to south central China (Tang et al., 2011). Phylogenetically, *Sequoia* and *Sequoiadendron* are considered sister taxa and *Metasequoia* a more basal taxon in the subfamily (Schulz and Stützel, 2007; Stull et al., 2021) (Figure 3). All three species have very restricted distributions; however, Mesozoic and Cenozoic (Figure 4) fossils are widely distributed across Euro-Asia, making these clear paleoendemics (living fossils). Maximum heights are 115 m for *Sequoia* and 96 m for *Sequoiadendron* (Sillett et al., 2015). Only ~50 species of trees globally are known to reach more than 70 m (Tng et al., 2012), and certainly most tree species are much shorter. Thus, these two majestic species stand out for their size (megatrees).

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FIGURE 1 *Sequoia sempervirens*, coast redwood. Photo credit: Phil van Mantgem.

FIGURE 2 *Sequoiadendron giganteum*, giant sequoia. Photo credit: Nate Stephenson.

Recent lightning-ignited fires subjected stands of these iconic species to high-severity crown fires that destroyed the canopies of many trees. Here we focus on contrasting the radically different impacts and fire responses of these two species (Table 1), which illustrate radically different evolutionary adaptations to fire, and address the question of whether or not these were novel fire events.

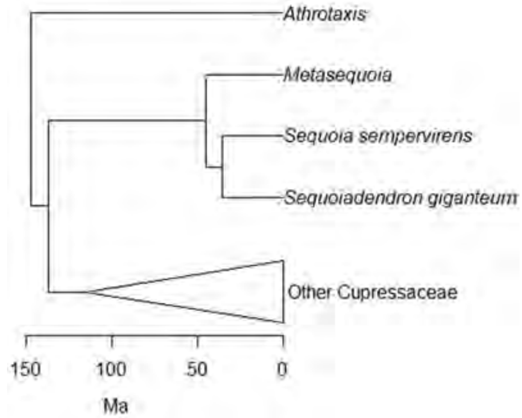

FIGURE 3 Phylogenetic position of *Sequoia sempervirens* and *Sequoiadendron giganteum* within the Cupressaceae family. Ma, million years ago.

Era	Period	Epoch	Began (Ma)
Cenozoic		Holocene	0.01
	Quaternary	Pleistocene	1.8
		Pliocene	5.3
		Miocene	23
		Oligocene	34
		Eocene	54
	Tertiary	Paleocene	65
Mesozoic	Cretaceous		145
	Jurassic		200
	Triassic		251

FIGURE 4 Geological eras (from Keeley et al., 2012). Ma, million years ago.

DISTRIBUTION

Coast redwood grows along a narrow 700 km strip of the U.S. Pacific coast, from central California to barely over the Oregon border, typically less than 50 km from the coast and at low elevations (<900 m a.s.l.) (Figure 5). However, fossils from the La Brea tarpits show it occurred more than 300 km farther south during the Pleistocene (George and MacDonald, 2017). They grow in areas with moderate to heavy winter rain and summer fog; heavy coastal fog provides a humid atmosphere, and since the species grows well at considerable distance from the ocean on plantations in other continents, it seems possible this relationship has as much to do with determining the fire regime as it does tree growth (Olson et al., 1990). Redwood is dominant throughout its range but is generally mixed with other conifers, such as Douglas-fir [*Pseudotsuga menziesii* (Mirb.) Franco], California nutmeg (*Torreya californica* Torr.), and

TABLE 1 Summary of the main characteristics of the two Mesozoic paleoendemic megatrees, based on sources cited in text.

Characteristic	Coast redwood (*Sequoia sempervirens*)	Giant sequoia (*Sequoiadendron giganteum*)
Current distribution	Coastal, California	Sierra Nevada, California
Elevation (m a.s.l.)	<1000	1400–2500
Climate requirements	Winter rain, summer fog	Snowy winters, dry summers
Natural fire regime		
Fire type	Crown fires	Surface fires
Fire severity	High	Low
Human impacts	Native American burning, timber harvesting	Fire suppression, prescription burning
Plant traits		
Maximum age	2200 years	>3200 years
Shade tolerant	Yes	No
Clonal spread	Yes	No
Self-prune branches	No	Yes
Basal bark	Thick up to 35 cm	Thick up to 45 cm
Cones	2–3 cm, infrequent	4–7 cm, abundant
Serotiny	No	Facultative[a]
High severity response		
Survival	Very high	Low
Resprouting	Yes (epicormic, lignotuber)	No
Seedling recruitment	Rare after fire, mostly in gaps between fires	Largely after fires
Origin	Jurassic, Eurasia	Probably Cretaceous, North America

[a]For definition, see section Post-fire responses.

broadleaf hardwood trees such as tanoak [*Notholithocarpus densiflorus* (Hook. & Arn.) Rehd.] and shrubs. Redwoods cover roughly 890,000 ha of landscape; however, 95% of these landscapes have been harvested and comprise second-growth forests. Today, less than a quarter of the primary (old-growth) coastal redwood forests are protected within state or federal reserves (Sillett et al., 2022).

Giant sequoia occurs in scattered groves of the western Sierra Nevada, California, between 1400 and 2150 m a.s.l., comprising a total area of <11,000 ha (Stephanson et al., 2024b) (Figure 5). It is a shade-intolerant species that typically grows in mixed conifer forests, rarely forming pure stands. It is usually found in a climate characterized by dry summers and snowy winters. The species range is restricted to >90 groves varying in size from less than 1 to 1300 ha. Very limited timberharvesting has occurred, so most groves comprise old-growth forests; however, these are only a fraction of the area of old-growth coastal redwood forests still in existence.

EVOLUTIONARY HISTORY

Basal members of the Cupressaceae originated in the Triassic and were well established by the Jurassic (Yao et al., 1997, 1998), and *Sequoia* is the only extant genus reported from the Jurassic (Seward, 1919). *Sequoia sempervirens* is very similar to fossils from the Middle Jurassic of eastern China (Miller, 1977), and these fossils were from a warm humid environment much like the contemporary *S. sempervirens* (Chaney, 1950; Ma et al., 2021). During the Cretaceous, *Sequoia* distribution was cosmopolitan; however, in the later Cenozoic, it became locally extinct in Europe and Asia, and fossils indistinguishable from the contemporary taxa are unknown in North America until the Oligocene or Miocene (Endo, 1951; Zhang et al., 2015).

In light of the contemporary disjunct distribution of *Sequoia* and *Sequoiadendron*, it is noteworthy that they have never been found in the same macrofossil flora (Shirley, 1940; Lowe, 2014), suggesting long-standing differences in habitat characteristics and potentially in fire regimes. Although there is a rich fossil history in the Mesozoic and Cenozoic for *Sequoia*, such a history is lacking for *Sequoiadendron*, perhaps due to the preference of the former species for mesic conditions more suitable to fossil deposition. Fossil records are primarily macrofossils of leaves, twigs, and fruits deposited in wetland sediments (Millar, 1996), and these are sites more akin to *Sequoia* than *Sequoiadendron*, not surprising considering there is an inherent bias against fossil deposition in semiarid environments (Keeley et al., 2012: Chapter 10). In short, we know less about the fossil history of *Sequoiadendron* at least in part due to its preference for more arid environments conducive to a frequent fire regime.

Miocene fossils of *Sequoiadendron* are known from sites more southerly and to the interior than those of *Sequoia* (Axelrod, 1986; Lowe, 2014). The earliest fossil record of the genus *Sequoiadendron* comes from the Early Miocene (18.5 million years ago [Ma]) Middlegate Basin of western Nevada (Lowe, 2014), assigned to *Sequoiadendron chaneyi* Axelrod. Giant sequoia had spread throughout the northern hemisphere by the Cretaceous, but ranges contracted owing to climatic change toward colder and drier conditions in the Late Tertiary. The widely disjunct populations are the result of range constriction over the last 2 million years due to the semiarid Mediterranean-type climate (Dodd and DeSilva, 2016) and Pleistocene glaciation (Axelrod, 1986). Pollen records suggest changing climates in the Holocene have contributed to both the expansion and contraction of groves (Anderson, 1994).

FIGURE 5 Current distribution of *Sequoia* and *Sequoiadendron*. Photo credit: Anne Pfaff.

RECENT HIGH-SEVERITY FIRES

In 2020, a lightning storm ignited several large fires in the Central Coast between 16 and 18 August, which burned through extensive stands of coast redwood. These included the 35,000-ha CZU Complex Fire centered in Big Basin State Park, the 22,000-ha Walbridge Fire in Austin Creek State Recreation Area, and the 51,000-ha Dolan Fire in Big Sur and eastern portion of the Ventana Wilderness Area (Cal Fire, 2023). From estimates of fire severity based on remote sensing with the relative difference-normalized burn ratio (RdNBR), area burned by high-severity fires ranged from 41% of the total area burned in the CZU Fire to 29% in the Dolan Fire (Kane and Carrasco, 2024). Here, severity is used as a measure of the ecosystem impact and should not be confused with fire intensity, i.e., the energy output from the fire (Keeley, 2009).

A few days later, lightning ignited fires in the interior mountains in Sequoia National Forest in what was labeled the Sequoia Complex Fire (SQF) and burned over 53,000 ha within nearly two dozen giant sequoia groves in Sequoia National Forest and the adjacent Sequoia National Park. A year later south of the SQF Complex Fire in September 2021, lightning ignited the Windy Fire (39,000 ha) in the

Sequoia National Forest and burned through giant sequoia groves, and at roughly the same time north of the SQF Complex Fire, lightning ignited two fires in Sequoia National Park. This KNP Complex Fire burned more than 35,000 ha in the park, including some of the largest stands of giant sequoia. The SQF Complex fire of 2020 and the KNP Complex fire of 2021 had cumulative burn areas of ~106,000 ha, of which ~47,000 ha were classified as high-severity (Soderberg et al., 2024).

In summary, the two species were subjected to high-severity (crown) fires that generated top-kill. And as we discuss next, these two species have radically different responses that affect their resilience and suggest a different history of fire regimes (Table 1).

POST-FIRE RESPONSES

Sequoia sempervirens

After the three 2020 Central Coast fires, coast redwood mortality was 5% because the vast majority of trees resprouted; even the 43% that were top-killed (Kane and Carrasco, 2024), consistent with results from an earlier fire (Mahdizadeh and Russell 2021). Resprouting was from the base and epicormically along the entire length of the stem (Figure 6). Resprouting is a rare trait in gymnosperms (Keeley and Pausas, 2022), and it is of particular note that one of its conifer associates, *Torreya californica*, is also a resprouter (Keeley et al., 2012: Chapter 9). In the redwood populations, even the smallest saplings resprouted, and resprouting was positively correlated with increasing burn severity, whereas high-severity fires killed many Douglas-fir and tanoak (Ramage et al., 2010; Woodward et al., 2020). Basal resprouting in redwood derives from true lignotubers (Del Tredici 1998), defined as an ontogenetic trait produced early in seedling growth, and is only found in a small subset of all resprouting species (Keeley and Pausas, 2022). Lignotuber resprouting and epicormic resprouting are considered adaptations to high-severity fires as they occur only in ecosystems with this fire regime (Pausas et al., 2018). In the vast majority of conifer forests, crown fires typically are described as stand-replacing fires, but such is not the case with coast redwood; thanks to their remarkable resprouting capacity, redwoods persist through high-severity fire regimes. Resprouts contain carbon that was fixed decades earlier and emerge from buds dormant for centuries (Peltier et al., 2023). Over very long periods, resprouting may lead to clonal spread with between-ramet spread up to 40 m (Douhovnikoff et al., 2004).

FIGURE 6 Post-fire resprouting basally and epicormically in *Sequoia sempervirens*. Photo credit: Jon Keeley.

Redwood seedling recruitment was rare across the three fires mentioned above, being absent in over 80% of the plots sampled in the first year by Kane and Carrasco (2024). Woodward et al. (2020) also reported no seedlings in the first year in the CZU Fire perimeter. CZU sites were investigated 4 years after fire and still no seedling recruitment was found (J. E. Keeley, personal observations). Even in previous studies where post-fire seedlings were recorded, recruitment was highly variable. For instance, Lazzeri-Aerts and Russell (2014) investigated three burned sites and found no seedlings at one, fewer than 1 per 20-m^2 at another, and at their site with the highest average, recruitment was extremely variable with many plots having no seedlings. They found no correlation between seedlings and slope, aspect, or canopy cover. One possible explanation for low seedling recruitment is that high-severity fires incinerate cones, preventing seedling recruitment (Cowman and Russell, 2021). Cones are common on 5-year-old resprouts, but in some areas, cones are absent for many years (Olson et al., 1990), although reportedly abundant on older dominant trees (Boe, 1968). Soon after maturity cones disperse seeds in December and January, though seed viability is low and germination is typically less than 1% (Becking, 1996). Successful seedling recruitment requires bare mineral soil and years of significant moisture, and growth is best in full sunlight, which occurs in response to disturbances other than fire such as trails, treefalls, landslides or flooding events (Stone and Vasey, 1968; Veirs, 1996; Busing and Fujimori, 2002). Lack of post-fire seed fall is consistent with the fact that post-fire redwood forests do not present safe sites for redwood seedling establishment. In this post-fire community, space is rapidly preempted by post-fire resprouters and seeders. For instance, redwood, nutmeg, and tanoak resprout vigorously. In addition, there are shrub species that maintain long-lived dormant seedbanks, which are triggered by fire to germinate (seeders) that quickly occupied the space and resources. For example, after the CZU Fire in Big Basin, our studies have shown that the redwood understory had as many as 100,000 *Ceanothus thyrsiflorus* Esch. seedlings/ha, which formed an extremely dense 2-m high thicket that was still going strong 4 years after fire (J. E. Keeley, personal observations). Redwood seedling recruitment under these circumstances of high cover would not likely result in successful establishment.

Sequoiadendron giganteum

In contrast, to the coast redwood, the Sierra Nevada giant sequoia trees that had severe top-kill ultimately died because this species has no capacity for resprouting. Within the 2020 SQF Fire area, more than 40% of large sequoias were killed, overall representing more than 7500 large (DBH > 1.2 m) sequoias (Stephenson and Brigham, 2021), and the Windy Fire caused a a similar outcome (Shive et al., 2022). In total, the SQF, KNP, and Windy fires caused a loss of ~19% of the global population of this species (Soderberg et al., 2024; Stephenson et al., 2024a). Giant sequoia seedling recruitment has been documented and shows that after fires, where tree crowns were not consumed, there was copious seed fall followed by seedling recruitment (Soderberg et al., 2024). This species has what here is defined as facultative serotiny (i.e., capable but not restricted to this function). For the vast majority of serotinous species, seed dispersal is limited to post-fire conditions (Lamont et al. 2020), which we suggest is best termed obligate serotiny. In the case of giant sequoia, because cones last only a few years, there is some annual seed fall (averaging about 1–2 million seeds per ha over the past 20 years), but after fire, seed fall jumped an order of magnitude or more (D. Soderberg, U.S. Geological Survey Sequoia Field Station, personal communication). Facultative serotiny is the best term for this behavior since with a typical natural fire interval of 20 years in giant sequoia (Swetnam et al., 2009), there may be roughly the same total seed fall without fire as with fire. However, long-term studies have shown that seedling recruitment in the absence of fire is rare (Rundel, 1971; Meyer and Safford, 2011), and even fires of very low severity may be insufficient to stimulate high seed fall and seedling recruitment (Soderberg et al., 2024; Stephenson et al., 2024a). Thus, facultative serotiny functions much like it does in obligately serotinous species, largely producing a single even-aged cohort after a fire (Table 1).

Another difference between facultative serotiny in giant sequoia and obligate serotiny in other species is that sequoia seedling recruitment occurs after moderate-severity fires where the canopy survives, thanks to their thick bark and the self-pruning of lower branches. In contrast, seedling recruitment in obligately serotinous species largely occurs only after high-severity crown fires, which cause total top-kill. After the SQF and KNP fires, seedling recruitment averaged from 2000 to 20,000 seedlings per ha, with a few sites having upward of 40,000 seedlings/ha, primarily in stands subjected to low- to moderate-severity burning, and was almost completely absent after high-severity burning (Soderberg et al., 2024). This lack of seedling recruitment after high-severity crown fires is thought to be due to the cones hanging from long, thin peduncles, which are burned during crown fires; most cones drop into the fire, which kills the seeds (Stephenson et al., 2024a). Other cone traits could also be responsible (Greene et al., 2024). In contrast to the effects of high-severity fires, the convective heat pulse during surface fires causes cones that remain attached high in the tree to dry and release their seeds (Harvey et al., 1980). In general, there is a negative relationship between fire severity and seedling recruitment in giant sequoia (Soderberg et al., 2024). Other studies of giant sequoia have also found seedling recruitment is fire-dependent, although the response to fire severity varies (Meyer and Safford, 2011; Hanson et al., 2024), and these differences are apparently due to different definitions of high severity and to different post-fire climates; however, the evidence is clear that groves subject to extreme fire severity typically lack seedling recruitment (York et al., 2013; Stephenson et al., 2024b; see Stephenson et al., 2024a for a detailed review).

In summary, high-severity fires had very different impacts on coast redwood than on the Sierra Nevada giant sequoia. Coast redwood seems well-adapted to such fires, with nearly complete survival by resprouting. In contrast, giant sequoia is adapted to frequent low- to moderate-severity surface fires, where resilience is ensured by copious seedling recruitment. For these two species, fire-adaptive traits have evolved in response to a long history of very different fire regimes.

WERE THESE RECENT DISTURBANCES NOVEL FIRE EVENTS?

Novel disturbance regimes are those to which ecosystems are not adapted (Turner and Seidl, 2023), or in this case, regimes to which particular species are not adapted. The response of giant sequoia to these recent high-severity crown fires suggests these were novel fire events; however, the adaptive response of coast redwood suggests otherwise.

A fuller explanation of redwood and giant sequoia fire regimes must consider the drivers behind fire regimes. While much has been written on the "proximal" causes of fire regimes (i.e., the phenomena that are immediately responsible and how something is affected), very little has been written on the "ultimate" factors that determine a fire regime (i.e., why a fire regime develops; Pausas et al. (2025) discuss proximal vs ultimate factors in fire regimes). One of the few models proposed for ultimate causes of fire regimes is that they are driven by a combination of site productivity and ignition frequency (Keeley and Zedler, 1998). The model predicts that coast redwood forests, which have very high productivity and a naturally low frequency of ignition, would have a fire regime of infrequent high-severity fires. In contrast, Sierra Nevada mixed conifer forests with moderate-high productivity coupled with a natural high fire frequency, are predicted to have a frequent surface fire regime.

Sequoia sempervirens

Coast redwood fire regime is complex due to topographic variation, weather patterns, and anthropogenic disturbances.

Differences in fire frequency are apparently a function of the steep climatic gradient extending from the cool, moist coastal sites to the relatively warm, dry inland sites. Veirs (1980) estimated the most mesic sites burned at >250-yr intervals in high-severity fires and noted that in no observed case has a natural redwood stand been decimated by one of these long-interval fires.

In coastal redwood forests, natural ignitions due to lightning are rare due to high moisture content of vegetation and rarity of lightning (Brown et al., 1999; Brown and Baxter, 2003; Stephens and Fry, 2005). The markedly lower lightning fire frequency in the Central Coast, which is 5–10 times lower than in the Sierra Nevada (Keeley and Syphard, 2018), is largely the result of fewer lightning strikes (Van Wagtendonk and Cayan 2008) and fewer ignitions due to the mesic conditions in coastal redwood forests. Farther north in the North Coast region lightning strikes are more common, but due to the more mesic coastal forest conditions, suitable fire weather is more limited; for example, the number of summer hours/day of fog is an order of magnitude greater than in the Central Coast, which would inhibit fires (Sillett et al., 2022). Historically, factors inhibiting fire activity may have been even greater in the past because there has been a 33% reduction in fog frequency since the early 20th century (Johnstone and Dawson, 2010). Consistent with the role of summer mesic conditions inhibiting fires, Oneal et al. (2006) found that fire rotations were an order of magnitude longer on coastal mesic sites than on drier interior sites.

Although charred trunks are evidence of past fires, Veirs (1980) and Brown (2007) found that fire scars are rare in coastal redwoods. However, several investigators have provided fire scar evidence of localized sites with frequent historical fires. Due to the rarity of fire scars, coupled with discontinuities in rings (as much as a 100-year difference from one side of a tree to another; Brown and Swetnam, 1994), fire scar studies have mostly not relied on cores, but rather have focused on sampling stumps from cut-over forests. Typically, trees with many scars were preferentially selected (Stephens and Fry, 2005); thus, this highly biased sample selection cannot be used to draw conclusions about fire history for coast redwood forests in general.

However, these fire scar studies of coast redwood do illustrate the importance of Native American influence on localized sites. In the southern part of the redwood range at Salt Point State Park, Finney and Martin (1989) reported historical fires at less than 30-year intervals back many centuries. They contended that these were most likely all ignited by Native Americans, who frequented the area for salt collecting. Further reflecting the human source of ignitions, they noted a significant increase in fire frequency following Euro-American settlement. In the Central Coast reserves and parks, Stephens and Fry (2005) reported median ranges from 2 to 43 years and concluded these were likely all due to the dense population of Ohlone Native Americans in the area. Others have reported similar results from this region (Jacobs et al., 1985; Jones and Russell, 2015), and there is general agreement these are the result of human ignitions (Lorimer et al., 2009). In the northern part of the redwood range, Brown and Swetnam (1994), working in Redwood National/State Park on second-growth forests, selected stumps with fire scars and reported fire intervals of less than 10 years since 1714. In rectifying their short fire intervals with Veirs' conclusion of very long intervals, they admitted that short intervals might be due to anthropogenic burning. Varner and Jules (2017) called this an enigmatic fire regime, asking how did frequent fires burn in these wet forests? As pointed out by Stephens et al. (2018), it was not just that humans subsidized the natural ignition source but they also had the capacity for burning over a much wider range of climatic conditions. The role of Native American burning in the fire scar record seen in these north coast forests seems very likely considering the high density of Native Americans at the time of contact (Milliken, 2009), reflected in the fact that the Yurok Tribe (whose land is west of the confluence of the Trinity and Klamath rivers) today is the largest tribe in California, and is actively involved in restoring traditional burning practices (Halpern, 2016).

We conclude that in an evolutionary context the coast redwood evolved under the long-interval crown-fire regime described by Veirs (1980, 1982). Its resilience to such fires is consistent with that conclusion, coupled with the fact that resprouting in conifers is globally rare except in high-severity crown-fire regimes (Keeley and Pausas, 2022). Unlike many western forests where fuel accumulation leading to crown-fires is the result of a century of fire suppression, in mesic redwood rainforests this regime is the result of infrequent fires due to summer moisture and few lightning ignitions (Stuart, 1987). Indeed, Greenlee and Langenheim (1990) contended that the fire regime since fires have been actively suppressed (~1930) was the closest approximation to the natural fire regime relative to the prior centuries dominated by Native American management. In general, post-fire resprouting, particularly lignotuber resprouting and epicormic resprouting, is generally associated with crown-fire regimes (Keeley and Pausas, 2022). In this context, the recent 2020 fires were not novel fire events. Preventing such fires through prescription burning is apparently not needed to maintain dominance of this iconic species (Mahdizadeh and Russell, 2021). However, ecosystem and societal needs, as discussed below, may provide other reasons for prescription burning in the understory of redwood forests.

Sequoiadendron giganteum

In striking contrast, the Sierra Nevada giant sequoia evolved in an environment of frequent low-severity fires. Swetnam (1993) developed a 2000-year chronology of fire events showing sequoias can persist in the face of very high fire frequencies, and these were surface fires (Swetnam et al., 2009). Historically, the severity of Sierra Nevada wildfires tended to be low to moderate, with small patches

(<0.1 ha to a few hectares) of high-severity fire interspersed (Stephenson et al., 1991), with a mean fire-return interval at the scale of an individual tree of 15–20 years (Kilgore and Taylor, 1979; Swetnam et al., 2009). Further, while Native American burning occurred in groves near villages, the majority of giant sequoia groves were largely burned by very frequent natural lightning ignited fires (Van Wagtendonk and Cayan 2008). These conditions are consistent with a surface-fire regime driven by moderately high productivity coupled with high ignition frequency (Keeley and Zedler, 1998).

In brief, the natural fire regime for giant sequoia was one of frequent surface fires, driven by moderate productivity, contributing to rapid fuel accumulation coupled with high lightning-fire frequency. However, 20th and 21st century fire suppression has grossly altered the natural fire regime by eliminating frequent surface fires, which historically kept surface fuels too low to generate high-severity crown fires (Safford et al., 2022; Stephens et al., 2022). The 2020 and 2021 crown fires described above were the result of human interference in the natural fire regime that allowed anomalous fuel accumulation, resulting in these novel fire events.

ECOSYSTEM MANAGEMENT

Under a fire regime of infrequent high-severity fires, coastal redwood has the advantage because it performs better than other community associates and, in particular, is more resilient than the coexisting Douglas-fir (Mahdizadeh and Russell, 2021). Veirs (1980) contended that redwood is best developed under 250- to 600-year fire-return intervals, which are common near the coast. However, further inland, the natural fire frequency is shorter, and redwood persists, although on these drier sites, Douglas-fir dominates. It is likely that at localized sites with Native American burning, redwood was resilient to this fire regime, but that regime likely favored Douglas-fir seedling recruitment. Some suggest restoring Native American burning through prescription burning should be used to ensure persistence of Douglas-fir and hardwoods such as tanoak (Ramage et al., 2010) and prevent conifer recolonization of open grasslands that were likely created by Native American burning practices (van Mantgem et al., 2021). Studies show that the use of prescribed burning in old-growth redwood forests can beneficially reduce live and dead surface fuels, with minimal impacts to overstory trees and understory herbaceous species (Cowman and Russell, 2021); however, it is not a requisite for redwood resilience (Mahdizadeh and Russell, 2021). In trying to restore Native American fire regimes in redwood forests, we need to recognize that prescription burning may best be viewed as cultural restoration rather than ecological restoration.

Of course, management needs differ depending on the goal, e.g., conservation vs economic or other societal goals (Russell, 2000; Valachovic and Standiford, 2017). For example, although redwood does well under high-severity crown fires, the human infrastructure throughout its range does not fare well. Further complicating these issues is that that most redwood forests have previously been logged and thus mostly comprise second-growth forests of different ages, creating very unnatural fuel conditions, with potentially different responses to restoration treatments. In Redwood National/State Park, the goal of restoration treatments is to alter the balance of redwood to Douglas-fir in favor of redwood (van Mantgem et al., 2017). However, another complication is that many of the second-growth stands were initiated via aerial seeding of Douglas-fir at high densities, and now Douglas-fir dominates and impedes redwood dominance (Teraoka et al., 2017). For commercial lands, such stands might be appropriate but perhaps not for conservation lands focused on redwood conservation. Russell et al. (2014) found that secondary forests recovered similar to old-growth stands without post-harvest management techniques of thinning and planting, and natural recovery toward old-growth conditions occurred within a century after timber harvesting (Russell and Michels, 2011). Since redwood forests are among Earth's fastest growing unmanaged secondary forests, they seem to be on a trajectory toward old-growth conditions. However, they are still far from old-growth conditions (Iberle et al., 2020), and requirements for restoration of old-growth redwood forests still require management actions (van Mantgem et al., 2017).

Thus, in an evolutionary context, these high-severity crown fires were not novel events for the long-term conservation of coast redwood, but in terms of some management goals, they were very much novel events outside the range of desired conditions. That is, they are an example where ecologically sustainable fire regimes differ from societally sustainable fire regimes.

Recent crown fires in the Sierra Nevada giant sequoia were novel fire events in an ecosystem that historically burned in frequent low-severity surface fires, which was clearly the result of a century of highly effective fire suppression, exacerbated by global warming (Safford et al., 2022; Stephens et al., 2022). Pre-fire fuel treatments have long been recognized as the solution to reducing the threat of these novel high-severity crown fires. Prescription burning was advocated by foresters and conservationists in the early 20th century, but their arguments were largely ignored by state and federal land managers until later in the century when the giant sequoia national parks, Sequoia, Kings Canyon and Yosemite, initiated prescription burning in the late 1960s (Keeley et al., 2021). The recent losses of giant sequoias in high-severity crown fires illustrate that we are far from preventing such events in the future, particularly in light of climate changes projected for these forests (Millar and Stephenson, 2015).

Under these circumstances, we need management actions that are focused on preventing plant community reorganization as predicted by Falk et al. (2022) when forests are exposed to fires outside their historical range. Replanting forests that failed to reseed due to the impacts of high-severity fire is the only means of offsetting the loss of giant sequoias resulting from these recent fires. However, in the case of giant sequoia restoration, some have opposed any action on the grounds that they are in wilderness areas protected by the 1964 Wilderness Act, which sets a very high bar for justifying human interference in ecosystem processes (Park and Van Vranken, 2023). However, the Wilderness Act presumed that these wilderness areas were pristine environments without human impacts (McCloskey, 1966), and apparently had not considered the 1963 Leopold Report (Leopold, 1963) that described the widespread impact of fire suppression on forest fuel structure in the Sierra Nevada, even in wilderness areas. In short, due to human activities (primarily fire suppression), wilderness areas have had a deficit of burning, which has created anomalous fuel loads that now are contributing to anomalously high-severity fires. The Wilderness Act failed to acknowledge these impacts, and now, many believe there is reason for management actions that attempt to prevent further loss of giant sequoia.

WHY MEGATREES?

Lastly, most who visit these two iconic species ask "Why are they so huge?" They are substantially larger in height and girth than other trees in their community. In light of their Mesozoic origins, were conditions so very different than current conditions in a way that favored large size? Currently, these two species are the only ones exceeding 90 m height and 2000 years of age (Sillett et al., 2015). Gigantism, i.e., very large body size, has been explored in extinct and extant fauna (megafauna) (Smith et al., 2010; Vermeij, 2016), but very little about it in plants has been discussed (megatrees). Why did *Sequoia* and *Sequoiadendron* reached such large sizes? Here we suggest several non-exclusive hypotheses.

Plant competition provides strong selection pressure for rapid growth. Thus, megatrees may have evolved in multi-strata forests where high-severity fires had a differential impact on lower and upper strata species. This possibility is supported by studies showing that giant sequoia survives high-severity fires due to its larger stature, while associated smaller conifers are eliminated (Stephenson et al., 1991 and references therein). Other potential hypotheses are that the high atmospheric CO_2 concentration and moist conditions of the Eocene–Miocene period (Hönisch et al., 2023) would enable conifers to reach those sizes. With the reduction in CO_2 concentration and changes in climate and fire regimes, the growth rate may have slowed drastically, but the capacity to grow tall and support large sizes may have remained. Also, contrary to conventional wisdom, the growth rate of trees increases continuously with tree size (Stephenson et al., 2014). Another possibility is that large size preempts space for competitors, as happened with dinosaurs during the Jurassic and Cretaceous, which limited the size and dominance of mammals. Seidel et al. (2015) examined the growing space and neighborhood structure of the China-endemic *Metasequoia glyptostroboides* and found that tree size translated into space-filling against competing tree species.

CONCLUDING REMARKS

Coast redwood survives high-severity crown fire by resprouting. It is an obligate resprouter with no reliance on post-fire seedling recruitment. Giant sequoia, on the other hand, lost a substantial portion of its population due to high-severity burning because it does not resprout; however, under certain conditions, trees dropped a substantial number of seeds that produced copious seedling populations. Coast redwood recovery is positively associated with high fire severity, whereas tree survival and seedling recruitment of giant sequoia are negatively associated with fire severity. Thus, we conclude that the recent high-severity fires were novel fire events for giant sequoias but not for coast redwoods.

AUTHOR CONTRIBUTIONS

J.E.K. conceptualized this paper and collected published data and figures cited in the paper. J.G.P. contributed ideas related to megatrees and prescription burning. J.E.K. and J.G.P. contributed to writing and the bibliography.

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