

Article

Post-Fire Succession in an Old-Growth Coast Redwood (*Sequoia sempervirens*) Forest

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Abstract

In 2020, a high-intensity wildfire burned over 35,000 ha in the Santa Cruz Mountains of California, including over 1700 ha of old-growth coast redwood forest. This event created a unique opportunity to evaluate post-fire succession. We compared vegetation recovery in high versus low/moderate severity burned areas using data collected one year and four years following the fire. Random plot sampling was conducted at Big Basin Redwoods State Park to assess the regeneration of trees, shrubs, and herbaceous species. Descriptive and inferential statistical analyses were used to assess recovery over time and across burn severities. Results indicate significant increases in shrub cover and richness over time, with a positive association between shrub recruitment and high-severity fire. Notably, the fire-adapted species blue blossom (*Ceanothus thyrsiflorus* Eschsch.), which was not recorded one year following the fire, dominated the shrub layer after four years, particularly in higher severity areas. Herbaceous species also exhibited an increase in cover and richness over time, though a substantial portion of that increase was based on non-native species recruitment. Analysis did not indicate a significant relationship between fire severity and herbaceous species recovery, however. The regeneration of tree species occurred both through seedling recruitment and basal sprouting. The recruitment of basal sprouts was prolific following the fire, particularly for coast redwood. The number of basal sprouts declined significantly during the time frame of this study, as the sprouts became larger and began to self-thin. Seedling abundance, on the other hand, exhibited an approximately 30-fold increase. Seedling recruitment was primarily driven by coast redwood (*Sequoia sempervirens* [Lamb. ex D. Don] Endl) and Douglas fir (*Pseudotsuga menziesii* [Mirb.] Franco) and was positively correlated with low/moderate fire severity. These findings underscore the complex interactions shaping post-fire forest dynamics and highlight the importance of understanding such patterns to inform management strategies that support the resiliency of coast redwood forests in an era of increasing wildfires.



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Keywords: coast redwood; *Sequoia sempervirens*; succession; old-growth; wildfire

1. Introduction

Fire is a fundamental component of the ecological processes shaping most plant communities in California, including the coast redwood forest. Fire frequency and intensity, which can be influenced by anthropogenic climate change [1–6], can dictate community composition, species distribution, regeneration patterns, and ecological succession [7,8]. Due to complex ecosystem structure and fire unpredictability, however, this dynamic is not fully understood in the coast redwood forest ecosystems.

The dominant species in this forest type, coast redwood (*Sequoia sempervirens* [Lamb. ex D.Don] Endl.), is adapted to withstand fire, with a high crown and thick insulated bark. In addition, coast redwoods produce prolific clonal sprouts following disturbance, including fire. While basal sprouting is a common trait in angiosperms, it is relatively rare in coniferous species, making coast redwood special in its ability to regenerate in this way [9,10]. Another remarkable adaptation of coast redwood is epicormic sprouting, which allows the regeneration of damaged branches along the bole from dormant epicormic buds [11]. The most common tree species associated with coast redwood in the southern part of its range are Douglas fir (*Pseudotsuga menziesii* [Mirb.] Franco), tanoak (*Notholithocarpus densiflorus* [Hook. & Arn.] Manos, Cannon & S.H. Oh), Pacific madrone (*Arbutus menziesii* Pursh), and California bay laurel (*Umbellularia Californica* [Hook. & Arn.] Nutt.) [11]. All of these species are capable of producing basal sprouts following top-kill, except for Douglas fir. Douglas fir only reproduces by seed, and while the thick bark of the mature trees enables it to survive low-to moderate-intensity surface fire, it is highly susceptible to crown fires. As a result, Douglas fir often experiences the highest mortality rates following high-severity fire, while coast redwood exhibits the lowest levels [12,13]. Tanoak, oaks, Pacific madrone, and California bay are common evergreen hardwood trees found in the subcanopy with thin bark and are susceptible to high-intensity fire. Unlike Douglas fir, however, they can reproduce from basal sprouts when top-killed trees and from seed as well [9,14]. For coast redwood, seed germination and survival rates are generally low, particularly in the northern part of the range [11,13]. In the southern part of the range, however, recent research indicates that coast redwood seedling establishment can be prolific, though patchy, following fire [12,15]. The importance of sexual reproduction for maintaining genetic biodiversity should be considered when evaluating the value of fire on the landscape.

The understory of the coast redwood forest is generally dominated by shade-tolerant plants, though canopy gaps can create openings for more broadly adapted species. Shrubs associated with coast redwood forests include California blackberry (*Rubus ursinus* Cham. & Schltdl.), California hazelnut (*Corylus cornuta* Marshall), California huckleberry (*Vaccinium ovatum* Pursh), and poison oak (*Toxicodendron diversilobum* (Torr. & A. Gray) Greene). Several herbaceous species are found in the coast redwood forest as well, including Hooker's fairy bells (*Prosartes hookeri* Torr.), Pacific starflower (*Lysimachia latifolia* [Hook.] Cholewa), Pacific trillium (*Trillium ovatum* Pursh), redwood sorrel (*Oxalis smalliana* R. Knuth), and redwood violet (*Viola sempervirens* Greene), in addition to several species of ferns, including bracken fern (*Pteridium aquilinum* [L.] Kuhn), giant chain fern (*Woodwardia fimbriata* J.E. Sm.), and western sword fern (*Polystichum munitum* [Kaulf.] C. Presl).

The fire history of the coast redwood forests is complex, varying across both temporal and spatial scales [16]. The Santa Cruz Mountains are ecologically diverse, consisting of several zones, including coastal scrub, coast redwood mixed evergreen forests, coast redwood-Douglas fir forests, oak woodlands, and chaparral. References [17,18] classified the fire history of the Santa Cruz Mountains into five fire regimes using fire-spread modeling techniques, vegetation type, and historical data. The authors suggested that the lightning-fire regime prior to the Holocene and human settlements had a mean fire interval of 135 years in coast redwood forests and from 30 to 135 years in the mixed evergreen forests. Based on fire scar data and historical evidence, they inferred that indigenous ignitions between 11,000 B.C. and 1792 A.D. reduced the mean fire intervals to 17–82 years. Indigenous burning consisted of low-intensity surface fires near human settlements and in grasslands and woodlands for cultural and subsistence purposes [16].

During the Spanish era (1792–1848), fire frequency in the coast redwoods increased to 20–50 years as a result of logging and conversion of land to pasture or farmland [18]. Between 1847 and 1929, intense logging practices by Anglo-European settlers further

increased fire frequency and intensity. Following a series of large fires, U.S. policies shifted to eliminating all fires in forests across North America [19]. Fire suppression policies substantially reduced fire frequency across all ecological zones of the Santa Cruz Mountains.

In recent decades, perspectives have evolved to recognize the ecological value of low-intensity fires, but the value of moderate- to high-intensity fires is less acknowledged. Some researchers [20] challenge the traditional view that fire regimes in western North America before the fire exclusion years were historically dominated by low- to moderate-severity fires. Instead, their research indicates that high-severity fires driven by weather conditions were unprecedented and included in mixed-severity fire regimes. With climate change and persistent droughts, more intense forest wildfires are projected across the western United States in the coming decades. As a result, fire regimes are likely to shift from predominantly low- and moderate-intensity to high-intensity fires. In large, high-severity burned patches, changes in microclimate and regeneration dynamics can constrain species reestablishment, alter the vegetation types, and facilitate the spread of new species that may create positive feedback loops, further reinforcing changes in fire regimes. The authors observed such changes in stand structure in Douglas fir forests, where post-fire regeneration was constrained due to the species' lack of sprouting ability and limited seed bank reserves. In another post-fire study across the range of coast redwood forests, research indicated that higher-severity fires favored coast redwood trees both in the upper canopy, by showing resistance, and in the subcanopy, by vigorously sprouting, thus outcompeting broadleaved species such as tanoak [9].

Current studies of disturbance regimes point to an increase in fire frequency and intensity in the coast redwood forests [4,6,21], yet little empirical data exists on how severe wildfires impact coast redwood ecosystems. The CZU Lightning Complex Fire of 2020 burned vast areas of Big Basin Redwood State Park, including over 1700 ha of old-growth. While coast redwoods are fire-adapted, the intensity and scale of this fire raised concerns about the capacity of these forests to recover. Initial observations in 2021 documented rapid sprouting and limited seedling generation but highlighted vulnerabilities such as shifts in species composition and the potential spread of non-native species [22]. Forest recovery remains a long-term process shaped by burn severity, regeneration mechanisms, and competition between species. This study revisits the site in 2024 to assess changes in forest recovery trajectories since 2021. By examining the influence of burn severity on forest structure and diversity, through this research we endeavored to provide empirical data on the recovery of coast redwood forest following fire and to establish baseline information to inform management strategies for promoting long-term recovery in the face of increasing severe wildfires.

2. Materials and Methods

Data was gathered in Big Basin Redwoods State Park, in the heart of the Santa Cruz Mountains in California (37.17250° N 122.22250° W). Big Basin, founded in 1902, was the first state park in California. It encompasses 8903 ha (22,500 acres) and contains the largest area of old-growth in the southern range of the coast redwood forests. Coast redwood and Douglas fir are the dominant canopy species, and tanoak, Pacific madrone, and oak commonly make up the sub-canopy. Elevations within the park range from sea level to 609 m. The site has a maritime-Mediterranean climate characterized by cool wet winters, and dry summers that are moderated by coastal fog. The mean daily maximum temperature fluctuates between 23.3 °C in July, August, and September and 12.7 °C in December and January. Annual precipitation has been trending down from a mean of 733 mm in 1979 to 501.9 mm, in 2023.

On 16 August 2020, a catastrophic wildfire caused by a rare summer lightning storm, followed by dry northeast winds, burned through the Santa Cruz Mountains. The CZU Lightning Fire Complex affected 35,009 hectares in the San Mateo and Santa Cruz counties [23]. Big Basin Redwoods State Park experienced the highest burn severity in the region, as 97% of the park was engulfed. The fire was finally reported as “contained” after 38 days, but spot fires continued for some time.

To evaluate post-fire recovery over time and across burn severity levels, we conducted field sampling at Big Basin in 2021 [22] and 2024. Plots were stratified by burn severity (high versus low-to-moderate) using a burn severity map as a reference [23], with ground truthing based on upper canopy scorch height. In 2021, 30 plots were surveyed ($n = 8$ low-to-moderate, $n = 22$ high), and in 2024, 30 new plots were surveyed ($n = 15$ low-to-moderate, $n = 15$ high). Vegetation data were collected at each plot for individual trees, shrubs, and herbaceous species to assess differences in cover, composition, and regeneration across years and burn severities. Circular 20 m diameter sample plots were randomly located in the central old-growth section of the park. To reduce the impact of edge effects, a 50 m buffer was included between plots and from paved roads, and a 15 m buffer between burn severity patches and other known ecological gradients such as riparian zones [6]. At the center of each plot, percent canopy cover was estimated using a convex spherical densiometer in the four cardinal directions [24]. Additional measurements included slope, aspect, elevation, and GPS coordinates. On each plot, all tree species were recorded, with height and basal area calculated from diameter at breast height (DBH). Trees were categorized into three size classes: mature tree (DBH > 10 cm), sapling (DBH < 10 cm) and height > 1 m. Tree height and char height were measured using a laser rangefinder. The number of basal sprouts per plot was reported in each of the three size classes, and the total number of seedlings for each species was recorded, in addition to tree mortality—defined as the absence of foliage on any part of the tree [9]. Herbaceous species composition and percent cover were estimated using six (0.5 m × 0.5 m) nested quadrats with 2 m intervals alternatively along a randomly selected 15 m transect within each sample plot. Shrub cover was determined using whole-plot ocular estimates. Species identification was accomplished using the Jepson Manual of California Vegetation [25].

SPSS version 29 was used for all statistical analyses. For continuous variables, normality was tested using the Kolmogorov–Smirnov (K-S) and Shapiro–Wilk tests, and homogeneity of variances was assessed using Levene’s test. A Scheire–Ray–Hare test approach was utilized for variables that did not meet the assumption of normality and homogeneity of variances, including shrub cover, herbaceous percent cover, abundance of basal sprouts, seedling abundance, and canopy cover. A General Linear Model (GLM) analysis was then conducted on the ranked data, including year, burn severity, and their interaction as factors. For species richness, the data met parametric assumptions, therefore a two-way ANOVA was utilized to examine the effects of year, burn severity, and their interaction on richness and diversity. Additionally, a Pearson Chi-Square test of independence was used to investigate whether the distribution of basal sprout size classes was independent of sampling years, and Spearman’s rank correlation test was used to investigate the relationship between *Ceanothus* cover and Douglas fir seedling abundance in high-severity plots, as neither variable met parametric assumptions.

3. Results

The results of this study indicate substantial post-fire recruitment of vegetation in both the understory and overstory layers, with variation in patterns of regeneration noted between years and across burn severities.

3.1. Shrub Recruitment

In 2021, total percent shrub cover was minimal ($M = 2.90$, $SE = 1.39$) and was dominated primarily by resprouting California huckleberry (*Vaccinium ovatum* Pursh). In 2024, percent shrub cover increased dramatically across all sampled areas ($M = 33.72$, $SE = 6.34$), with a significant main effect of year noted in the Scheirer–Ray–Hare test ($F(1, 56) = 45.504$, $p < 0.001$). A total of 10 shrub species were identified, with blueblossom (*Ceanothus thyrsiflorus*) being the most abundant (Table 1).

Table 1. Mean percent cover of shrub layer and standard errors recorded in 2021 and 2024 following the CZU Wildfire in Big Basin Redwood State Park in the Santa Cruz Mountains, California.

Species	Mean % Cover ($\pm SE$)	
	2021	2024
All species combined	2.90 (± 1.39)	33.72 (± 6.34)
<i>Ceanothus thyrsiflorus</i> (Blueblossom ceanothus)	-	29.80 (± 6.21)
<i>Vaccinium ovatum</i> (California huckleberry)	2.88 (± 1.39)	2.30 (± 1.15)
<i>Baccharis pilularis</i> (Coyote brush)	-	1.03 (± 0.50)
<i>Eridictyon californicum</i> (Yerba santa)	-	0.37 (± 0.37)
<i>Rubus ursinus</i> (California blackberry)	0.02 (± 0.02)	0.07 (± 0.07)
<i>Rubus armeniacus</i> (Himalayan blackberry)	-	0.03 (± 0.03)
<i>Rosa gymnocarpa</i> (Wood rose)	-	0.03 (± 0.03)
<i>Genista monspessulana</i> (French broom)	-	0.03 (± 0.03)
<i>Diplacus aurantiacus</i> (Sticky monkey flower)	-	0.02 (± 0.02)

A significant main effect of burn severity was also discovered ($F(1, 56) = 5.85$, $p = 0.019$), suggesting that shrub cover differed between low/moderate and high severity burn plots. The overall model was statistically significant ($F(3, 56) = 24.618$, $p < 0.001$), explaining approximately 57% of the variance in shrub cover ranks ($R^2 = 0.568$). In addition, a significant interaction between year and burn severity was detected ($F(1, 56) = 10.789$, $p = 0.002$), indicating that the effect of burn severity on shrub cover varied across years. These results suggest that shrub cover increased over time following the fire and that the difference in shrub cover between burn severities became more pronounced from 2021 to 2024 (Figure 1).

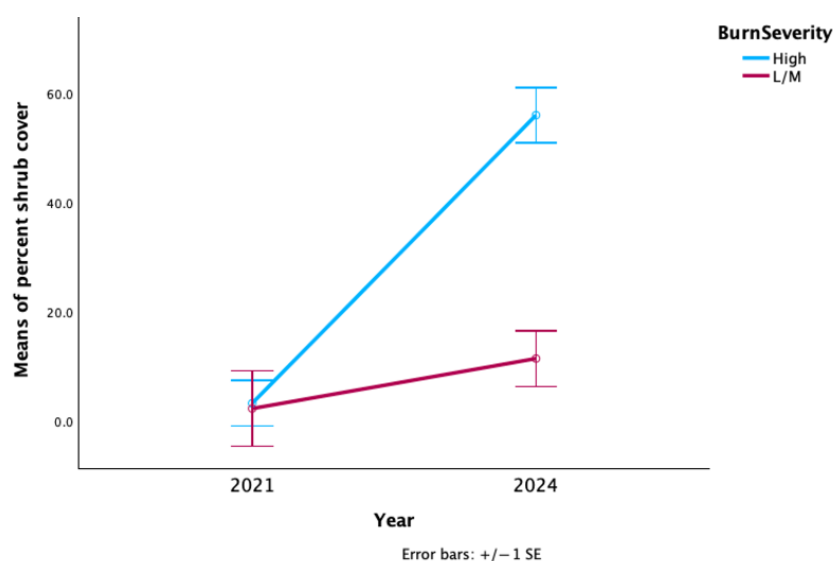


Figure 1. Comparison of shrub layer percent cover between years and burn severities with ± 1 standard error around the mean.

3.2. Herbaceous Species Recruitment

Variation in herbaceous cover and composition was also detected. A Scheirer–Ray–Hare test revealed a significant main effect of year ($F(1, 56) = 50.892, p < 0.001$), indicating that the percent cover of herbaceous species differed significantly between 2021 and 2024 (Table 2; Figure 2). However, there was no significant effect of burn severity on herbaceous percent cover ($F(1, 56) = 2.647, p = 0.109$), and no significant year and burn severity interaction was detected ($F(1, 56) = 0.119, p = 0.731$), suggesting that the change in herbaceous cover over time was consistent across burn severity levels. The overall model was statistically significant ($F(3, 56) = 18.722, p < 0.001$), accounting for approximately 50% of the variability in ranked herbaceous percent cover ($R^2 = 0.501$).

Table 2. Mean percent cover of herbaceous species and standard errors recorded in 2021 and 2024 following the CZU Wildfire in Big Basin Redwood State Park in the Santa Cruz Mountains, California.

Species	Mean % Cover ($\pm$ SE)	
	2021	2024
All species combined	1.47 (± 0.90)	20.45 (± 4.43)
Native herbaceous cover	1.47 (± 0.90)	15.14 (± 3.46)
Non-native herbaceous cover	-	5.32 (± 1.68)

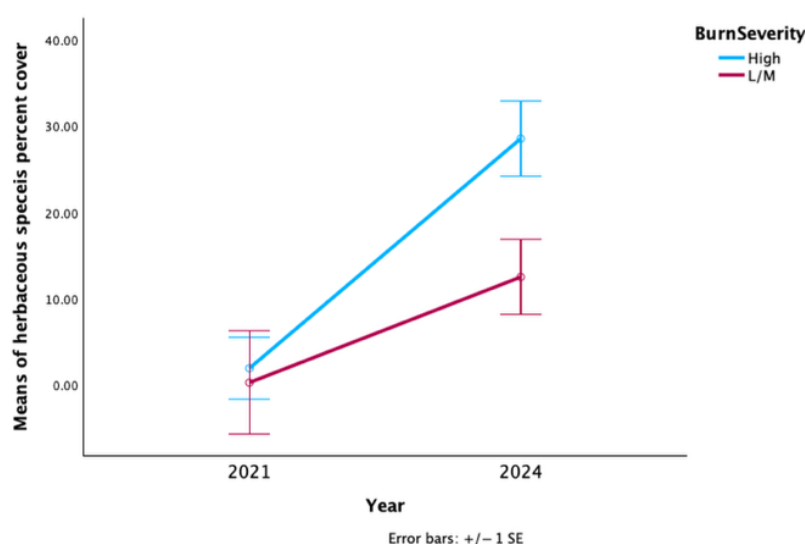
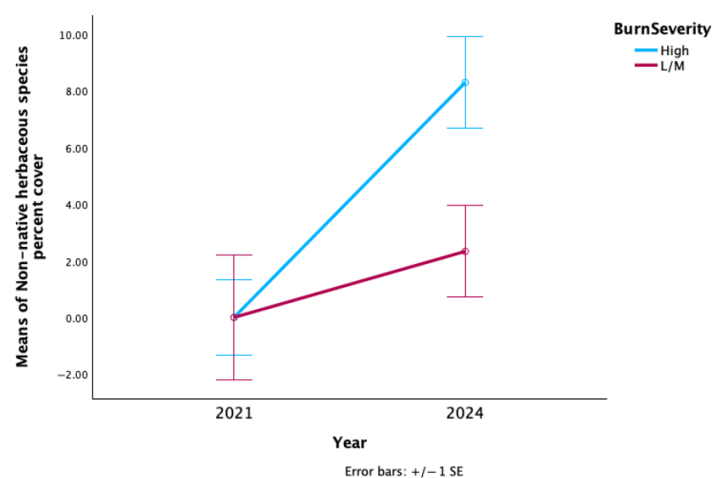


Figure 2. Comparison of herbaceous percent cover between years and burn severities with ± 1 standard error around the mean.

A total of 22 native herbaceous plants were identified, with California hedgenettle (*Stachys bullata* Benth.) being the most prevalent (Table 3; Figure 3). In addition, eight non-native species were recorded, with spreading hedgeparsley (*Torilis arvensis* [Huds.] Link) and Italian thistle (*Carduus pycnocephalus* L.) being the most common. A Scheirer–Ray–Hare test showed a significant increase in non-native herbaceous plant cover from 2021 to 2024 ($F(1, 56) = 39.006, p < 0.001$). While this increase was observed more in high-severity burned plots, the effect of burn severity was not statistically significant ($F(1, 56) = 5.852, p = 0.827$). In addition, no significant interaction between years and burn severity was detected ($F(1, 56) = 5.852, p = 0.827$).

Table 3. Mean percent cover of herbaceous species and standard errors recorded following the CZU Wildfire in Big Basin Redwood State Park in the Santa Cruz Mountains, California.

Native Species	Mean % Cover ($\pm$ SE)	
	2021	2024
<i>Stachys bullata</i> (California hedgenettle)	0.03 ($\pm$ 0.02)	2.79 ($\pm$ 1.76)
<i>Festuca californica</i> (California fescue)	-	2.36 ($\pm$ 0.93)
<i>Erigeron canadensis</i> (Canada horseweed)	-	2.05 ($\pm$ 0.92)
<i>Lonicera hispidula</i> (Pink honeysuckle)	-	1.45 ($\pm$ 1.43)
<i>Galium aparine</i> (Common bedstraw)	0.20 ($\pm$ 0.17)	1.33 ($\pm$ 0.80)
<i>Oxalis smalliana</i> (Redwood sorrel)	0.20 ($\pm$ 0.17)	1.21 ($\pm$ 0.69)
<i>Lysimachia latifolia</i> (Pacific starflower)	0.02 ($\pm$ 0.02)	0.67 ($\pm$ 0.38)
<i>Galium californicum</i> (California bedstraw)	-	0.57 ($\pm$ 0.32)
<i>Wipplea modesta</i> (Yerba de selva)	-	0.50 ($\pm$ 0.50)
<i>Fragaria vesca</i> (Wild strawberry)	-	0.43 ($\pm$ 0.43)
<i>Viola sempervirens</i> (Redwood violet)	0.03 ($\pm$ 0.02)	0.36 ($\pm$ 0.36)
<i>Juncus effusus</i> (Common rush)	-	0.36 ($\pm$ 0.36)
<i>Pseudognaphalium californicum</i> (Ladies' tobacco)	-	0.22 ($\pm$ 0.20)
<i>Polystichum munitum</i> (Western swordfern)	0.02 ($\pm$ 0.02)	0.21 ($\pm$ 0.13)
<i>Epilobium ciliatum</i> (Slender willow herb)	-	0.20 ($\pm$ 0.13)
<i>Koeleria macrantha</i> (Prairie junegrass)	-	0.14 ($\pm$ 0.14)
<i>Calystegia purpurata</i> (Morning glory)	-	0.11 ($\pm$ 0.11)
<i>Pteridium aquilinum</i> (Western brackenfern)	0.07 ($\pm$ 0.03)	0.09 ($\pm$ 0.83)
<i>Viola ocellata</i> (Two-eyed violet)	0.02 ($\pm$ 0.02)	0.03 ($\pm$ 0.03)
<i>Solanum americanum</i> (American black nightshade)	-	0.03 ($\pm$ 0.03)
<i>Trillium ovatum</i> (Pacific ovatum)	0.07 ($\pm$ 0.03)	0.01 ($\pm$ 0.01)
<i>California brome</i> (<i>Bromus sitchensis</i>)	-	0.01 ($\pm$ 0.01)
<i>Equisetum arvense</i> (Common horsetail)	0.67 ($\pm$ 0.67)	-
<i>Cardamine californica</i> (milkmaids)	0.07 ($\pm$ 0.04)	-
<i>Adenocaulon bicolor</i> (trail plant)	0.02 ($\pm$ 0.02)	-
<i>Toxicoscordion fremontii</i> (Fremont's star lily)	0.03 ($\pm$ 0.02)	-
<i>Prosartens hookeri</i> (Hooker's fairy bell)	0.02 ($\pm$ 0.02)	-
Non-Native Species		
<i>Torilis arvensis</i> (Hedge parsley)	-	2.44 ($\pm$ 1.06)
<i>Carduus pycnocephalus</i> (Italian thistle)	-	1.42 ($\pm$ 1.17)
<i>Vicia villosa</i> (Hairy vetch)	-	0.67 ($\pm$ 0.43)
<i>Cirsium vulgare</i> (Bull thistle)	-	0.63 ($\pm$ 0.34)
<i>Erigeron bonariensis</i> (Flax-leaved horseweed)	-	0.06 ($\pm$ 0.56)
<i>Epipacis helleborine</i> (Broadleaf helleborine)	-	0.05 ($\pm$ 0.03)
<i>Crepis capillaris</i> (Hawk's beard)	-	0.03 ($\pm$ 0.03)
<i>Hordeum murinum</i> (Foxtail barley)	-	0.02 ($\pm$ 0.02)

**Figure 3.** Comparison of non-native herbaceous species percent cover between years and burn severities with ± 1 standard error around the mean.

Measures of diversity were also low, with an average species richness of approximately one species per plot in 2021, increasing to four species per plot by 2024. Similarly, the Shannon diversity index (H), while quite low across all samples, exhibited a significant increase within the time frame of this study, from 0.197 in 2021 to 0.804 in 2024. A parametric two-way ANOVA analysis indicated a significant main effect of year for both species' richness and Shannon diversity ($F(1, 56) = 24.087, p < 0.001$); ($F(1, 56) = 91.147, p < 0.001$). However, there was no significant difference detected between herbaceous species richness or Shannon diversity across burn severity levels ($F(1, 56) = 1.458, p = 0.232$) ($F(1, 56) = 5.341, p = 0.509$), and no significant interaction detected ($F(1, 56) = 0.001, p = 0.978$), suggesting that the increase in species diversity over time occurred regardless of burn severity.

3.3. Tree Recruitment

Tree recruitment, both through basal sprouting and seedling establishment, varied across time and burn severity. Basal sprouting was prolific following the fire, with sprouts recorded for coast redwood, tanoak, oak, and Pacific madrone. However, the average number of sprouts across species and across all height sizes declined over time, from $M = 349$ ($SE = 60.58$) in 2021 to $M = 157$ ($SE = 18.30$) in 2024 (Figure 4). A Scheirer–Ray–Hare test revealed a significant main effect of year ($F(1, 56) = 4.010, p = 0.050$), indicating a statistically significant difference in sprouting between 2021 and 2024. In contrast, burn severity had no significant effect on sprout abundance ($F(1, 56) = 3.087, p = 0.084$), nor was there a significant interaction between year and burn severity ($F(1, 56) = 3.167, p = 0.081$). The decline in the number of basal sprouts coincided with a distinct shift in the height distribution of sprouts. In 2021, most sprouts were in the small height class (0.0–0.5 m), whereas in 2024, a greater proportion had grown into the medium (>0.5–1 m) and large (>1 m) size classes. The results of Pearson's Chi-Square test indicated that there was an association between sampled year and sprout size ($\chi^2 = 281.137, df = 2, p < 0.001$).

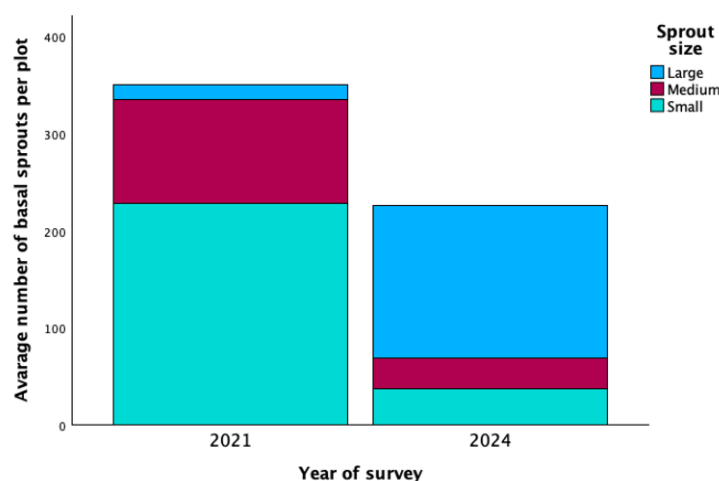


Figure 4. Distribution of basal sprouts by size class (small: 0.0–0.5 m, medium: >0.5–1 m, large: >1 m) in 2021 and 2024. Bars represent the average number of sprouts for all trees recorded in each category.

A Scheirer–Ray–Hare test revealed a significant main effect of year on seedling abundance across plots ($F(1, 56) = 64.507, p < 0.001$). The average number of seedlings exhibited an increase from approximately two seedlings per plot in 2021 ($SE = 2$) to 61 seedlings per plot in 2024 ($SE = 18$), indicating a substantial post-fire recruitment over time. While there was an observable difference in mean seedling counts across burn severity categories, burn severity alone did not have a significant main effect on seedling abundance ($F(1, 56) = 0.592, p = 0.445$). However, the test result showed a significant interaction between burn severity and year ($F(1, 56) = 6.148, p = 0.016$). This interaction sug-

gests that the magnitude of seedling recruitment over time differed depending on burn severity (Figure 5).

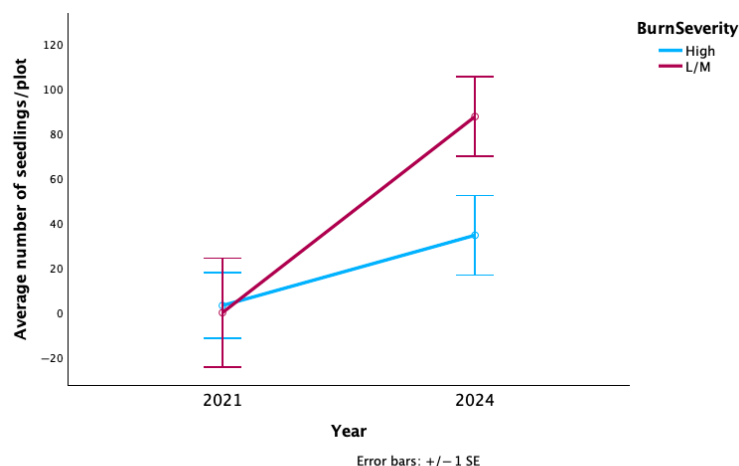


Figure 5. Comparison of the average number of common tree seedlings between years and burn severities with ± 1 standard error around the mean.

In general, there was a larger spread and higher variability in seedling counts under low-to-moderate burn severity, while high-burn severity areas had a much narrower distribution with a few outliers indicating the patchiness of their distribution. A Spearman correlation to assess the relationship between Douglas fir seedling abundance and *Ceanothus* cover revealed a moderate negative correlation ($n = 15$, $r = -0.509$, $p = 0.050$), suggesting that higher *Ceanothus* cover may be associated with reduced Douglas fir regeneration.

3.4. Canopy Cover

While there was an apparent slight increase in percent canopy cover from 87.07% in 2021 (SE = 1.13) to 89.20% in 2024 (SE = 8.54), results from a Scheirer–Ray–Hare test revealed no significant difference in canopy cover within the three years $F(1, 56) = 0.030$, $p < 0.863$). However, burn severity had a significant effect on canopy cover ($F(1, 56) = 32.816$, $p < 0.001$). Areas that experienced low-to-moderate severity burns had significantly higher canopy cover (M = 91.8%, SE = 0.60) compared to areas that experienced high-severity burns (M = 86.6%, SE = 1.3). In addition, no interaction between year and burn severity was detected $F(1, 56) = 1.986$, $p < 0.184$).

4. Discussion

Four years after an intense crown fire in an old-growth coast redwood, significant recovery of vegetation was observed. Four years post-fire, shrub cover increased substantially from just 2.9% in 2021 to 33.7% in 2024, with ten shrub species observed. This increase was largely driven by the dominance of blueblossom (*Ceanothus thyrsiflorus*), a fire-dependent nitrogen-fixing obligate seeder, which comprised nearly 30% of total shrub cover in 2024. This aligns with previous work highlighting *Ceanothus*'s fire-adapted traits and deep soil seedbank longevity [1]. The interaction between year and burn severity indicates that *Ceanothus* cover increased in a greater magnitude in high-severity burned plots over time, likely due to greater canopy opening and higher soil temperatures that favor germination.

A near-significant negative correlation between *Ceanothus* cover and Douglas fir seedling abundance in high-severity burned areas suggests competitive inhibition. This mirrors findings from [26], who documented *Ceanothus*'s capacity to hinder conifer regeneration, particularly Douglas fir, which relies on seedling post-fire. While *Ceanothus* can

enrich soils with nitrogen, its proliferation may delay or suppress Douglas fir seedling establishment by competing for space and light that can potentially outcompete Douglas fir seedlings and alter the forest composition in the short to medium term. Given these findings, further research is needed to better understand the long-term dynamics of this relationship, particularly in evaluating whether the ecological benefits of *Ceanothus*, such as nitrogen enrichment, outweigh its competitive effects on conifer regeneration.

Herbaceous plant cover also demonstrated robust recovery, increasing from negligible levels in 2021 to over 20% in 2024. Species richness and Shannon diversity followed a similar trajectory, increasing notably with time. Among native herbaceous plants, California hedgenettle (*Stachys bulluta*) emerged as the most abundant species. Other species, such as California fescue (*Festuca californica* Vasey) and Canada horseweed (*Erigeron canadensis* L.), also contributed notably to the overall herbaceous abundance. Although not statistically significant, high-severity burned plots tended to exhibit greater herbaceous cover and species richness. This increase was largely composed of weedy annuals and non-native species that thrive in disturbed environments. In 2024, non-native invasive species accounted for over 5% of total herbaceous cover. The most common non-native species were spreading hedge parsley (*Torilis arvensis*) and Italian thistle (*Carduus pycnocephalus*), both known for their fast colonization in disturbed sites. This pattern aligns with previous research indicating that post-fire soil changes, such as declines in mycorrhizal fungi and increases in bacterial dominance, can create conditions that favor non-native establishment [27–29]. While some native herbaceous species recovered quickly, they may face increasing competition from non-native species over time. Continued monitoring is recommended to understand how long these species persist and what their impacts are.

Tree regeneration occurred via two distinct pathways: basal sprouting and seedling recruitment. Basal sprouting was prolific immediately after the CZU wildfire, with significant contributions from coast redwood, tanoak, oak species, and Pacific madrone. However, the overall abundance of basal sprouts declined significantly over time with a corresponding significant shift toward larger-sized sprouts, which suggests trees are undergoing a self-thinning process. This pattern aligns with research that indicated that basal sprout mortality increases after an initial recruitment pulse following disturbance [10]. The abundance of basal sprouts did not differ significantly by burn severity, emphasizing that over time, tree species traits such as size and age play a more dominant role in the abundance of basal sprouts than fire intensity alone.

Seedling recruitment, in contrast, followed a delayed but upward trend, with a 30-fold increase in mean counts from 2021 to 2024. The increase highlights a delayed yet robust regeneration response among common tree species in the years following fire disturbance. While burn severity had no significant main effect, the significant interaction between year and burn severity indicates that seedling establishment increased more over time in areas that experienced low to moderate burn severity, suggesting that greater canopy retention and less abundance of *Ceanothus* cover and reduced soil heating may have created more favorable microsites for seedling establishment. In high-burn severity plots, tanoak seedlings were absent, and coast redwood and Douglas fir seedlings displayed a narrower range of seedling counts, except for a few plots that had very high numbers of seedlings. In low-to-moderate burn severity areas, seedling recruitment was more consistent and widespread.

Although overall canopy cover increased slightly from 2021 to 2024, the change was not statistically significant, likely due to the inherently slow growth of upper canopy trees and stressors such as drought. Burn severity had a strong and expected impact on canopy cover, reflecting the extensive damage caused by high-intensity crown fire to the overstory. The absence of a significant year and burn severity interaction suggests

that differences in canopy recovery were established early and have persisted over time. Continued monitoring is recommended to better track long-term canopy recovery.

Fire is a natural disturbance process in coast redwood forests; therefore, management practices aimed at rehabilitating burned forests should align with the ecological integrity of these ecosystems. As forests mature post-fire, they naturally develop self-regulating mechanisms that reduce future fire risk. For example, increasing canopy cover creates a cooling effect, retains higher moisture levels, and buffers against strong wind, thus reducing the likelihood of extreme fire spread. Additionally, greater shade suppresses the growth of shade-intolerant understory shrubs, which could otherwise serve as a fuel ladder [30].

Many post-fire interventions, such as salvage logging, seeding, or shrub removal, are intended to restore burned landscapes to their pre-fire condition more rapidly than the natural processes would allow. However, in some cases, these efforts can interfere with the natural successional process, preventing early successional plants from maturing and reaching their full ecological potential. Caution is advised when considering active post-fire vegetation management, as opportunities to study natural recovery following crown fire are exceedingly rare.

5. Conclusions

In summary, the impact of lightning-induced crown fire on the structure and composition of an old-growth coast redwood forest has been followed by rapid successional changes, even within the brief four-year time span of this study. Increases in understory cover and diversity were dramatic, and the re-establishment of tree species through clonal sprouting and seedling recruitment was encouraging. The post-fire establishment of invasive and non-native species is a cause for some concern, though most of these species are shade-intolerant and will likely decline as the forest canopy increases. Continued monitoring of post-fire recovery is recommended, as the successional time frame of a forest dominated by a species whose life span can exceed 1000 years can be significant.

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