seeds

MDPI

Article

The Effects of Fire on California Sage Scrub Germination Assemblages

Bailey Parkhouse [1,*], Hannah Chan [1] and Wallace Martin Meyer III [2]

[1] The Department of Natural Resources, Pitzer & Scripps Colleges, Claremont, CA 91711, USA
[2] Department of Biology, Pomona College, Claremont, CA 91711, USA
* Correspondence: bparkhou@students.pitzer.edu

Abstract

California sage scrub is an endangered, shrub-dominated, southern California ecosystem threatened by increasing fire frequencies and type-conversion to non-native grasslands. Once non-native grasses become established, their presence promotes more frequent fires, perpetuating grass dominance. To better understand how fire influences soil seed bank assemblages, we examined soil seed banks in burned and adjacent unburned sage scrub at the Robert J. Bernard Field Station (BFS) in two areas that burned in September 2013 and May 2017. In contrast to a previous soil seed bank study in California sage scrub, we found that unburned soil seed banks in sage scrub at the BFS were primarily composed of native seeds (88% of sprouts in unburned areas were native), highlighting that soil seed bank dynamics differ among California sage scrub sites. Despite burned areas supporting elevated densities of non-native seeds (the majority of which included *Festuca myuros*, a non-native grass), soil seed banks in our burned areas retained native seeds (21% of sprouts in burned areas were native), including native shrub species, suggesting that not all sage scrub habitats are primed to transition to non-native grasslands following disturbances. However, elevated densities on non-native seedlings in burned areas highlight the vulnerability of sage scrub to fire disturbances and the subsequent establishment of non-native grasses.

Keywords: soil seed bank; fire ecology; invasive ecology; grass–fire cycle; type-conversion; disturbance ecology; seed science

Check for updates

Academic Editor: Alba Cuena Lombraña

Received: 12 December 2025
Revised: 24 January 2026
Accepted: 27 January 2026
Published: 28 January 2026

Copyright: © 2026 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license.

1. Introduction

Soil seed banks include both the dormant and non-dormant seeds stored in the soil. They are a vital predictive tool for ecological restoration, as they may help estimate how plant communities can recover following anthropogenic disturbances such as habitat alteration, human ignitions, and the establishment of invasive species [1–4]. Consequently, a better understanding of soil seedbank dynamics, particularly in Mediterranean ecosystems impacted by changing fire regimes [5], can enhance our ability to provide informed restoration recommendations [4,6–8].

For example, our understanding of soil seed banks in the endangered California sage scrub ecosystem (hereafter sage scrub), one of the most threatened ecosystems in North America [9,10], is limited. Estimates suggest that since 1930, 49% of the remaining sage scrub not converted to urban areas has been type-converted to non-native grasslands, largely because of fire disturbances [11]. Following a fire, non-native annual grasses are known to quickly colonize burned sage scrub areas, increasing ignition probabilities and

fire frequency [5,12,13]. This can result in the development of a grass-fire cycle, a continued cycle of grass colonization and frequent fires that can reduce shrub cover, sometimes leading to type-conversion of native sage scrub to non-native grasslands [1,11,14–16]. Conversely, shrub re-establishment can help control non-native grasses and forbs through shading, allelopathy, nitrogen depletion, herbivory, and granivory, reducing ignition probabilities [13,17–24].

Unfortunately, few studies have examined how fires affect sage scrub soil seed banks. In the one study we know about, Cox and Allen [1] found that soil seed banks in both grassland and invaded sage scrub habitats were dominated by non-native grasses. This suggests that non-native grasses already comprise a significant portion of the soil seed bank in sage scrub and are primed to quickly colonize sage scrub habitats after disturbances. However, non-native grass seed abundances were reduced post-fire [1]. Soil seed bank studies in chaparral, another native California shrub-dominated ecosystem, dominated by evergreen shrubs, suggest that chaparral soil seed banks also experience a similar post-fire vulnerability to non-native grass establishment [25]. Specifically, native soil seed banks in chaparral are most threatened immediately after the fire, with native seed abundances decreasing post-fire and requiring sufficient fire-free periods to recover [25].

Our objective was to further explore post-fire sage scrub soil seed banks in light of grass invasions and increasing fire frequencies. To do this, we examined sage scrub soil seed bank assemblages in burned sage scrub and in adjacent unburned sage scrub (hereafter burned and unburned) areas at the Robert J. Bernard Field Station. We hypothesized that: (1) germination of non-native grasses is high in both burned and unburned sage scrub; (2) germination of native annuals is elevated in burned areas, while (3) germination of native sage scrub shrubs is elevated in unburned areas. By using soil collected across two seasons, we also examined whether seed germination differs between seasons. In addition, we considered soil seed banks from soil at different depths to gain insights as to where germinable seeds are located. While successful germination can be hindered by soil depth for many plant species [26,27], these dynamics have not been addressed in sage scrub.

2. Materials and Methods

2.1. Study Sites

We conducted this study at the Pomona College Greenhouse Facility. Soil was collected from the Robert J. Bernard Field Station (BFS), which is located at the foot of the San Gabriel Mountains in Claremont, California. Annual precipitation in Claremont is highly variable but typically falls around 440 mm [28,29]. Rainfall averaged 473 mm a year in the previous five years at the BFS, and most precipitation occurs from November to May [28–30]. The mean annual temperature for the previous five years was 17.2 °C, with a maximum of 29.9 °C and a minimum of 8.3 °C [30]. BFS soils are derived from the alluvial granite material of the San Antonio Mountains and were classified as mixed, sandy-skeletal Humic Haploxerepts, which are young, weakly developed soils [31].

The BFS is primarily composed of intact inland sage scrub (25 ha) [24,32]. Sage scrub at the BFS consists largely of drought-deciduous and low-statured (ca. 1 m in height) evergreen shrubs such as *Artemisia californica*, *Eriogonum fasciculatum*, *Salvia apiana*, and *Eriodictyon trichocalyx* with sparse cover in canopy gaps of non-native annuals such as *Bromus* spp. and *Hirschfelida incanca*, and native annual species, e.g., *Camissoniopsis* spp., *Cryptantha* spp., *Phacelia distans*, and *Crassula connata* [29,33]. The sage scrub habitats at the BFS also feature a mix of large-statured (>2 m in height) evergreen shrub species like *Rhus integrifolia*, *Heteromeles arbutifolia*, and *Malosma laurina*, common in sage scrub in the foothills of the San Gabriel Mountains [32,33].

In addition to sage scrub, the BFS also harbors a smaller transitional area (5.5 ha), where sage scrub shrubs have been recolonizing disturbed areas for decades prior to and following the 2013 human-ignited fire [33,34]. Transitional habitats include recovering areas of sage scrub shrubs, elevated abundances of non-native grasses, and elevated abundances of some native annual species such as *Amsinckia intermedia*, *P. distans*, and *Croton setiger* [29].

The BFS has experienced two human-ignited fires since 2013 [24,34]. In September 2013, a 6.9 ha fire burned the transitional habitat and small portions of adjacent sage scrub habitat [34] (Figure 1). In May 2017, a smaller fire burned 1.96 ha of intact sage scrub [24]. The fire scars of these two fires did not overlap (Figure 1), and there was no previous fire in these areas for the last 40 years. Both fires have modified the composition of above-ground vegetation and have higher densities of non-native grass and native and non-native forbs, as well as reduced cover of *A. californica* relative to the adjacent sage scrub habitat [24,35]. The 2013 burned area has an elevated density of *E. trichocalyx*, and the 2017 burned area has an elevated density of *Acmispon glaber* post-fire [36].

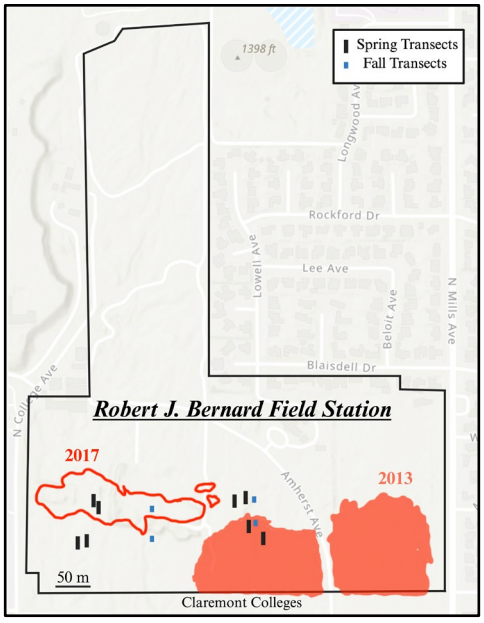


Figure 1. The Bernard Field station with the 2013 burn site (indicated by a filled red area) and the 2017 burn site (indicated with a red outline). Sampling transects are marked with thick black (Spring) or blue (Fall) lines.

2.2. Soil Collection

We collected soil at four locations within the BFS, one within each burn scar (2013 and 2017 fire) and two in unburned sage scrub areas adjacent to the 2013 and 2017 fire scars [1,3]. All transects were started approximately 10 m from the edge of the burn area to effectively sample areas that were or were not directly impacted by the fire. Within each sampling location, sampling was conducted along 20 m transects that ran north to south (Figure 1) [37]. Along each transect, one soil core was collected every two meters. Due to a high concentration of sand and large rocks, instead of traditional soil cores, we used trowels with depth measurements on the face to collect soil from the top 10 cm of soil [1]. If soil sampling to a depth of 10 cm was obstructed by rocks or dense shrub canopies, the soil was sampled as close to the transect while moving directly east. After creating a small hole, trowels were used to collect soil at two depths: shallow (0–5 cm) and deep soil (5–10 cm), hereafter referred to as shallow and deep soil for each location along the transect. Soil sampling was conducted on two occasions: (1) Fall 2023 (30 October 2023), one transect was sampled at each location; and (2) Winter 2024 (26 January 2024), sampling

was repeated using two parallel transects [3,37] (initial transect endpoint was randomly generated 30 m inward of the defined latitude and longitude boundaries, with the second transect randomly positioned to run parallel) at each sampling locations to increase our sample size and attempt to increase the number of seedlings recorded. Thus, we collected 80 samples in Fall 2023 and 160 samples in Winter 2024.

2.3. Greenhouse Germination Experiments

A greenhouse experiment was selected to best compare with the work done by Cox and Allen [1], and to best quantify germinable soil seed bank composition and density by exposing seeds to conditions that should best support germination [1]. Germination experiments began within two days after each soil sampling event using the Pomona College Greenhouse Facility, which maintains temperatures above 20 °C. Rocks and vegetation were removed from the soil using a 2 mm mesh sieve. The soil samples were then homogenized, and 100 cm^3 of sage scrub soil was mixed in 5 × 5 cm planter pots, with 100 cm^3 of Midwest Hearth™ (Sauk Rapids, MN, USA) seed starting soil for the Fall 2023 samples and Midwest Hearth™ potting soil for the winter samples. Each pot received approx. 35 mL of water per day (the Fall 2023 experiment received daily manual watering). For all experiments, no artificial lighting was used, meaning that light cycles were consistent with the daily light cycles of that season. Natural rainfall conditions are not represented.

After a 4-week (Fall experiment) or 7-week (Winter experiment) incubation period, germinating seedlings were identified to the lowest taxonomic level possible. For the Winter experiment, unidentified species were potted in separate pots, allowing them to continue growing for later identification. To allow remaining seeds to germinate, soil samples were churned and allowed to grow for an additional 5 weeks.

Early in the Winter 2024 experiment, we observed reduced abundances of non-native grass seedlings. To confirm that this pattern was not influenced by the use of potting versus seed starting soil, we conducted a post hoc experiment using soil we collected on 9 February 2024 from only the 2013 fire scar and adjacent sage scrub areas (see Table A1). For these samples, we used seed starting soil to eliminate the possibility that the soil may suppress grass germination. After 8 weeks, seedlings were identified to the lowest taxonomic level possible.

2.4. Statistical Analysis

We performed multiple chi-squared tests. First, to determine whether the number of germinated seedlings differed between burned and adjacent unburned areas, we ran a Chi-squared test for each plant species comparing seedling abundances between burned and unburned shallow soils for the 2013 and 2017 burned areas separately. We did not run similar analyses for deep soils, as seedling abundances were low. Second, to examine if the number of seedlings differed between deep and shallow soils, we ran chi-squared tests comparing abundances in shallow and deep soils for unburned sage scrub soils from the 2013 and 2017 fire areas and shallow and deep soils from the two burned areas. Finally, we ran chi-squared tests to examine differences in seedling abundances between Fall and Winter collections. To standardize the effort between seasons, we divided the Winter abundances in half. Chi-squared tests were only run when we recorded ≥16 seedlings for each plant species for each comparison. We used a Bonferroni correction to account for multiple testing (α-value = 0.005 for all chi-squared tests).

To provide the reader with the ability to compare results between our study and those of Cox and Allen [1], we also converted our numbers of seedlings per 100 cm^3 to sprouts per m^2 (see Table A2).

3. Results

In our study, we recorded 659 total seedlings, 344 in the Fall, but only 222 in the winter, despite doubling the sample effort. We recorded 93 seedlings in the post hoc sample collection.

3.1. Native and Non-Native Composition

The number of native and non-native seedlings differed among burned and unburned areas (Table 1). The number of native shrubs was elevated in the unburned area (Table 1). These patterns were primarily driven by elevated abundances of *A. califonica* in unburned soils, as the two other native shrub species recorded were rare. Similarly, native annual seedlings had elevated abundances in the unburned areas. Again, patterns for native annuals were driven by one species, *Pseudognaphalium* spp., which was elevated in unburned areas.

Table 1. Number of seedlings of each plant species germinated from soil collected in burned and unburned areas and from shallow and deep soils in each habitat for Fall and Winter soil collections (n = 240). Uppercase letters denote significant differences between deep and shallow soils, while lowercase letters denote differences between burned and unburned sage scrub habitats.

Plant Species	**2013**				**2017**			
	Shallow		**Deep**		**Shallow**		**Deep**	
	Burn	**Unburned**	**Burn**	**Unburned**	**Burn**	**Unburned**	**Burn**	**Unburned**
Native Shrubs								
Artemisia californica	1 ^{a}	13 ^{b}	0	5	2 ^{Aa}	19 ^{Ab}	0 ^{B}	2 ^{B}
Acmispon glaber	0	0	0	0	1	1	0	0
Malosma laurina	0	0	1	0	0	0	0	0
Total	1 ^{a}	13 ^{b}	1	5	3 ^{Aa}	20 ^{Ab}	0 ^{B}	2 ^{B}
Non-native Annual								
Festuca myuros	49 ^{Aa}	2 ^{Ab}	10 ^{B}	0 ^{B}	82 ^{Aa}	5 ^{Ab}	4 ^{B}	4 ^{B}
Bromus spp.	6	0	1	0	4	0	0	1
Hirschfeldia incana	3	0	0	0	3	4	0	0
Brassica spp.	3	2	0	0	1	0	0	0
Erodium spp.	1	0	0	0	1	0	0	0
Crassula tillaea	0	0	0	0	7	4	1	3
Total	62 ^{Aa}	4 ^{Ab}	11 ^{B}	0 ^{B}	98 ^{Aa}	13 ^{Ab}	5 ^{B}	8 ^{B}
Native Annuals								
Cardamine sp.	6	15	2	6	2	9	1	3
Camissoniopsis spp.	2	2	0	0	1	3	0	0
Crassula connata	0	0	0	0	25 ^{A}	43 ^{A}	13 ^{B}	7 ^{B}
Cryptantha spp.	1	1	2	0	3	0	1	0
Phacelia distans	0	0	0	0	1	0	1	0
Pseudognphalium spp.	1 ^{Aa}	43 ^{Ab}	0 ^{B}	8 ^{B}	2	0	1	0
Apiastrum angustifolium	0	1	0	0	0	0	0	0
Total	10 ^{Aa}	62 ^{Ab}	4 ^{B}	14 ^{B}	34 ^{A}	55 ^{A}	17 ^{B}	10 ^{B}
Native Perennials								
Dipterostemon capitatus	0	0	0	0	0	0	0	1
Total	0	0	0	0	0	0	0	1
Unidentified Taxa								
Unidentified 1	4 ^{Aa}	6 ^{Ab}	1 ^{B}	2 ^{B}	63 ^{Aa}	14 ^{Ab}	16 ^{B}	6 ^{B}
Unidentified 2	2	0	1	0	0	0	0	0
Total	4	6	2	2	63 ^{aA}	14 ^{aA}	16 ^{B}	6 ^{B}
Total Seedlings	77 ^{A}	85 ^{A}	18 ^{B}	21 ^{B}	198 ^{aA}	102 ^{bA}	38 ^{B}	27 ^{B}

In contrast, non-native annual seedlings had elevated abundances in burned areas (Table 1). While many common invasive annuals had elevated seedling abundances in burned areas (e.g., *Bromus* spp., and *Hirschfeldia incana*), only the non-native grass, *F. myuros*, was abundant enough to run statistical analyses.

3.2. Seasonal Variation in Germination Rates

Differences in germination rates among seasons were species-specific (Table 2). For example, *F. myuros*, the most abundant grass in our study, had elevated germination in soil collected during the Fall. In contrast, native and non-native *Crassula* species had elevated germination rates in winter soils. In addition, Unidentified 2 had elevated abundance in the Winter.

Table 2. Number of seedlings for soil collected in the Fall of 2023 and Winter of 2024 (n = 240). The number of seedlings for the Winter samples was divided in half to standardize for the doubled sampling effort. Uppercase letters indicate differences between seasons.

Plant Species	Fall Soil Collection	Winter Soil Collection
Native Shrubs		
Artemisia californica	14	14
Acmispon glaber	1	0.5
Malosma laurina	1	0
Total	16	14.5
Non-native Annuals		
Festuca myuros	146 ^{A}	5 ^{B}
Bromus spp.	8	2
Hirschfeldia incana	9	0.5
Brassica spp.	3	1.5
Erodium spp.	2	0
Crassula tillaea	0	7.5
Total	168 ^{A}	16.5 ^{B}
Native Annuals		
Cardamine sp.	25	9.5
Cryptantha spp.	4	2
Camissoniopsis spp.	3	2.5
Crassula connata	0 $^{\mathbf{A}}$	44 ^{B}
Phacelia distans	2	0
Pseudognaphalium spp.	22	16.5
Apiastrum angustifolium	1	0
Total	57	74.5
Native Perennials		
Dipterostemon capitatus	1	0
Total	1	0
Unidentified Taxa		
Unidentified 1	102 $^{\mathbf{A}}$	3.5 ^{B}
Unidentified 2	0	1.5
Total	102 ^{A}	5 ^{B}
Total Seedlings	344 ^{A}	111 ^{B}

3.3. Soil Depth

Soil depth was a significant factor, with shallow soils routinely harboring higher seedling densities (Table 1). The number of seedlings was elevated in shallow soils for native shrubs in the 2017 burn area (82% of germinated seedlings were from shallow soils; 92% from the 2017 burn area), non-native annuals (88% of germinated seedlings) from both

burn areas, native annuals (78% of seedlings) from both burn areas, and unidentified taxa (77% of seedlings) from the 2017 burn area. Total seedling density was elevated in both the 2013 burn (80% seedlings) and the 2017 burn area (82% seedlings). Similarly, *A. californica*, *F. myuros*, *C. connata*, *Pseudognphalium* spp., and Unidentified 1 had elevated abundances in shallow soils. The only species that had more seedlings in deep soil was *M. laurina*, though only one seedling was recorded for this plant species.

4. Discussion

Our findings provide new insights into sage scrub soil seed banks. While Cox and Allen [1] found that exotic grass seedlings were numerous in all soils, including what they referred to as invaded sage scrub, we found low abundances of non-native grasses and forbs in intact sage scrub soil seed banks. This finding suggests that not all sage scrub soil seed banks contain high densities of non-native seeds and are primed for non-natives to quickly colonize sage scrub areas following disturbances. For example, in our study, 94% of germinated *F. myuros* seeds, the most abundant non-native grass, were from burned habitats. Similarly, germination of non-native *Bromus* spp., less common in our soil seed bank study (0 seedlings per m^2 in unburned sage scrub areas at the BFS), was also elevated in burned areas (>66 seedlings per m^2). In contrast, native shrubs and forbs had elevated densities in the unburned areas (e.g., >200 *A. californica* seedlings per m^2 in unburned areas at the BFS; <6 per m^2 in invaded sage scrub). Therefore, while Cox and Allen [1] noted that non-native seed densities were high despite the presence of native shrubs and suggested that sage scrub habitats are particularly susceptible to rapid non-native colonization following fire disturbances, our findings suggest that some intact sage scrub habitats, like the BFS, retain native seed assemblages for post-fire-disturbance regeneration [35]. Consequently, soil seed bank dynamics vary across sage scrub sites.

Differences between our study and Cox and Allen's [1] may be predicated on differences in invasion resistance in sage scrub between the two study sites. Cox and Allen [1] described their sage scrub habitat as "heavily invaded" by non-native grasses and forbs. In contrast, we referred to our sage scrub as intact with sparse densities of non-native grass and forbs in some shrub interspaces. For example, *Bromus* spp. seedling densities were >3000 per m^2 in sage scrub in Cox and Allen's [1] study, while we did not record one *Bromus* spp. seedling in our unburned sage scrub samples. While this does not suggest that *Bromus* spp. is absent from our intact sage scrub area, it highlights that densities are low. Predicting resistance to invasion is difficult and influenced by a multitude of biotic and abiotic factors [38]. In sage scrub, invasion resistance may be associated with sage scrub soil conditions (chemical and microbial) [17,37,39,40], herbivory [19,23,24], and seed predation [41], all of which can restrict the abundance of some common invasive plants. Therefore, while predicting invasion resistance in sage scrub is complex and can be influenced by many factors at both the species and community levels, it may be possible to predict soil seed bank assemblages from above-ground densities of non-native grasses and forbs in shrub interspaces.

Despite the soil seed bank in our sage scrub habitat being composed primarily of natives, we found that burned areas support elevated densities of non-native seeds. Elevated germination of non-native annuals in our burned habitats supports previous research that fires promote the establishment of non-native grasses [1,11,12] and suggest that densities of non-natives can remain elevated more than a decade into post-fire recovery. However, it is unclear if post-fire non-native grass establishment in sage scrub is associated with seed densities prior to fire. Cox and Allen [1] demonstrated that seed densities of non-native grasses were extremely low immediately after a fire. However, they were able to quickly recover the following year, suggesting that either dispersal of non-natives or germination

of the remaining but significantly reduced non-native grass seeds was enough to quickly re-establish non-native soil seed banks. Thomson et al. [35] found that cover of non-natives in the 2013 burn area increased from 18% the first year after the fire to 60% the third year following the fire. Non-natives had low cover in adjacent unburned areas (W. M. Meyer, personal observation). The BFS has a non-native grassland and transitional area with higher densities of non-natives nearby, and these could have been the sources of recruitment in our burned area. Though our study did not examine the soil seed banks in burned areas until multiple years following a fire, and did not incorporate pre-fire soil seed bank data, our results comparing data from burned to adjacent unburned areas support the shift from a native shrub and forb-dominated soil seed bank to an invasive grass-dominated soil seed bank following fire. Unfortunately, increased grass cover can limit the recovery of native shrubs and reduce native shrub canopy cover in burned areas [35]. Combined, this can slow recovery of native shrubs and native soil seed banks, limit the influence of native shrubs on non-native grass and forb cover, and enhance ignition probabilities, further threatening the recovery of the sage scrub ecosystem.

Season also impacted plant germination assemblages. For example, *F. myuros* and total non-native annual germination rates were elevated in the Fall and over six times higher than those in the Winter. These results suggest that non-native grasses may exhaust their soil seed bank at the beginning of each growing season, with most germinable seeds sprouting at the beginning of the season, though dormancy needs to be examined further [42]. Consequently, by late Winter or early Spring, it is possible that few viable seeds remain in the soil. In contrast, germination of native shrubs and annuals was similar across seasons, except for elevated germination of *C. connata* in the winter.

Understanding that germination rates can vary according to when you collect soil for soil seed bank studies is important, as it can provide key management insights and highlight that some caution is required when interpreting the results of these studies. The main issue is that the seasonality of germination, particularly following fire, is often unknown [43]. If non-native annuals have higher germination rates in Fall, at the beginning of the cool-moist growing season in southern California, then targeted removal, especially right after the fire when densities are low, could have a significant impact on non-native seed densities while minimizing management effort, though sustained effort will be required [1,35]. Reductions in non-native annual densities support the establishment of native forbs and shrubs [35], which could create a positive feedback loop as these shrubs could create conditions that further restrict non-natives [13,18–23,41]. Cox and Allen [1] suggested that the late Fall immediately following a fire may be an opportune time to potentially reseed areas with natives in places where non-native seed densities are low. However, the success of this strategy will likely depend on temperature and humidity conditions in the growing season following the fire and will likely be improved by some effort to keep non-native cover low [35].

In addition to providing some important management insights, differences in germination across seasons suggest that some caution must be applied to the interpretation of any soil seed bank study. For example, how would you effectively interpret a study where seeds were only collected during one season? In southern California, it seems that sampling early in the growing season (beginning of cool-moist Mediterranean season) before rains initiate germination may be the best approach if you intend to quantify densities of non-native grasses, but you may miss the diversity of some natives (e.g., *C. connata* in this study) and other common non-natives that sprout late in the cool-moist season (March–April). For example, *Centaurea melitensis*, a species that is widespread in both our burned and native areas, was never recorded in this study. What sampling effort is required to effectively capture the diversity of plants in the soil seed bank and understand the timing

of germination for most plant species using soil seed bank studies? Our rarefaction curves suggest that more sampling effort is required to inventory all the species in one season in one habitat, suggesting that even more effort would be required to effectively inventory soil seed bank assemblages.

Soil depth is also an important consideration for any soil seed bank study. Here, we demonstrate that germination rates are elevated in soil from the top 5 cm. However, we did find viable *A. californica* and other native shrub seeds in deep soils, suggesting that viable seeds are not only found in shallow soils. Similarly, *M. laurina*, a native shrub, germinated from deep soil only. We are unsure what this may imply about the viability and persistence of these seeds in the seedbank, though it may suggest that seeds remain viable for long periods of time. Despite deeper soils providing interesting insights into sage scrub soil seed bank dynamics, we recommend using the top 5 cm of the soil and increasing your sample size among treatments as a better use of effort in sage scrub soil seed bank experiments.

5. Conclusions

Our study highlights that soil seed bank dynamics vary across sage scrub sites. In a previous study, sage scrub soil seed banks were dominated by non-native grasses, suggesting that they may be primed for non-natives to quickly colonize sage scrub areas following disturbance [1]. Instead, we found that soil seed banks in sage scrub at the BFS were primarily composed of native seeds. Despite both sites supporting elevated densities of non-native seeds in burned areas, highlighting the vulnerability of sage scrub to fire disturbances and the subsequent establishment of non-native grasses, soil seed banks in our burned areas retained native shrub seeds, suggesting that not all sage scrub habitats are primed to transition to non-native grasslands following disturbances. Consequently, it may be possible to understand the threat of type conversion in sage scrub habitats by sampling soil seed banks and/or making pre-fire observations of the presence and abundance of non-native grasses and forbs in sage scrub areas prior to the fire.

Author Contributions: Conceptualization, B.P., H.C. and W.M.M.III; methodology, B.P. and H.C.; formal analysis, B.P. and H.C.; investigation, B.P. and H.C., resources, W.M.M.III; data Curation, B.P. and H.C.; writing—original draft preparation, B.P. and H.C., writing—review and editing, B.P., H.C. and W.M.M.III; visualization, B.P. and H.C.; supervision, B.P., H.C. and W.M.M.III; project administration, W.M.M.III; funding acquisition, W.M.M.III. All authors have read and agreed to the published version of the manuscript.

Funding: Research was supported by funds from Pomona College.

Data Availability Statement: The original contributions presented in this study are included in the article. For example, Table 1 provides all the raw data. Further inquiries can be directed to the corresponding author(s).

Acknowledgments: We would like to thank the Pomona College Greenhouse and the Robert J. Bernard Field Station for access to resources and our study sites. Special thanks to Sadie Heckman, Cira Seyer-Ochi, Nina Karnovsky, Frances Hanzawa, Ross Pringle, and Ramona Werner for help in multiple aspects of the project.

Conflicts of Interest: The authors declare no conflicts of interest.

Appendix A

Table A1. Number of seedlings for soil collected in a post hoc experiment done in the Winter of 2024 (n = 20). This experiment examined whether patterns observed, specifically the low abundances of *F. myuros*, were potentially due to the use of potting soil used in the Winter experiment and not seed starting soil used during the Fall experiment. In this study, we used seed-starting soil and also found low presence of *Bromus* spp. and *F. myuros* in shallow soils (0–5 cm), suggesting that patterns are associated with seasons and not due to the use of different soil types.

Plant Species	Burned	Unburned
Native Shrubs		
Artemisia californica	4	14
Total	4	14
Non-native Annuals		
Festuca myuros	1	2
Bromus spp.	1	2
Hirschfeldia incana	4	0
Centaurea melitensis	1	0
Total	7	4
Native Annuals		
Cardamine spp.	0	4
Camissoniopsis spp.	2	0
Pseudognaphalium spp.	3	39
Apiastrum angustifolium	0	1
Total	5	44
Unidentified Taxa		
Unidentified 1	1	12
Unidentified 2	0	1
Unidentified 3	1	0
Total	2	13
Total Seedlings	18	75

Table A2. Seedling densities (per m^2) across habitat types and soil depths, calculated from 100 cm^3 soil samples. Uppercase letters indicate significant differences between soil depths, while lowercase letters indicate differences between burned and unburned habitats within each depth.

Plant Species	2013				2017			
	Shallow		Deep		Shallow		Deep	
	Burn	Unburned	Burn	Unburned	Burn	Unburned	Burn	Unburned
Native Shrubs								
Artemisia californica	16.7	216.7	0^B	83.3	33.3	316.7	0	33.3
Acmispon glaber	0	0	0	0	16.7	16.7	0	0
Malosma laurina	0	0	16.7	0	0	0	0	0
Total	16.7	216.7	16.7	83.3	50	333.3	0^B	33.3
Non-native Annual								
Festuca myuros	816.7	33.3	166.7	0	1366.7	83.3	66.7	66.7
Bromus spp.	100	0	16.7	0	66.7	0	0	16.7
Hirschfeldia incana	50	0	0	0	50	66.7	0	0
Brassica spp.	50	33.3	0	0	16.7	0	0	0
Erodium spp.	16.7	0	0	0	16.7	0	0	0
Crassula tillaea	0	0	0	0	116.7	66.7	16.7	50
Total	1049.7	66.7	182.4	0	1332.4	216.7	82.4	133.3
Native Annuals								
Cardamine sp.	100	250	33.3	100	33.3	150	16.7	50

Table A2. *Cont.*

Plant Species	2013				2017			
	Shallow		Deep		Shallow		Deep	
	Burn	Unburned	Burn	Unburned	Burn	Unburned	Burn	Unburned
Camissoniopsis spp.	33.3	33.3	0	0	16.7	50	0	0
Crassula connata	0	0	0	0	416.7	716.7	216.7	116.7
Cryptantha spp.	16.7	16.7	33.3	0	50	0	16.7	0
Phacelia distans	0	0	0	0	16.7	0	16.7	0
Pseudognphalium spp.	16.7	716.7	0	133.3	33.3	0	16.7	0
Apiastrum angustifolium	0	16.7	0	0	0	0	0	0
Total	166.7	1033.4	66.6	233.3	566.7	916.7	266.8	166.7
Native Perennials								
Dipterostemon capitatus	0	0	0	0	0	0	0	16.7
Total	0	0	0	0	0	0	0	16.7
Unidentified Taxa								
Unidentified 1	66.7	100	16.7	33.3	1050	233.3	266.7	100
Unidentified 2	0	0	16.7	0	0	0	0	0
Total	66.7	100	33.3	33.3	1050	233.3	266.7	100
Total Seedlings	1299.7	1416.7	298.7	349.9	3049.1	1466.7	615.9	433.3

References

1. Cox, R.D.; Allen, E.B. Composition of soil seed banks in southern California coastal sage scrub and adjacent exotic grassland. *Plant Ecol.* **2008**, *198*, 37–46. [CrossRef]
2. Gioria, M.; Pyšek, P. The legacy of plant invasions: Changes in the soil seed bank of invaded plant communities. *BioScience* **2016**, *66*, 40–53. [CrossRef]
3. Holl, K.D.; Steele, H.N.; Fusari, M.H.; Fox, L.R. Soil seed banks of maritime chaparral and abandoned roads: Potential for vegetation recovery. *J. Torrey Bot. Soc.* **2000**, *127*, 207–220. [CrossRef]
4. Shi, Y.F.; Shi, S.H.; Jiang, Y.S.; Liu, J. A global synthesis of fire effects on soil seed banks. *Glob. Ecol. Conserv.* **2022**, *36*, e02132. [CrossRef]
5. Safford, H.D.; Van De Water, K.M. *Using Fire Return Interval Departure (FRID) Analysis to Map Spatial and Temporal Changes in Fire Frequency on National Forest Lands in California*; No. PSW-RP-266; USDA Forest Service, Pacific Southwest Research Station: Albany, CA, USA, 2014. [CrossRef]
6. Maia, P.; Vasques, A.; Pausas, J.G.; Viegas, D.X.; Keizer, J.J. Fire effects on the seed bank of three Mediterranean shrubs: Implications for fire management. *Plant Ecol.* **2016**, *217*, 1235–1246. [CrossRef]
7. Céspedes, B.; Torres, I.; Luna, B.; Pérez, B.; Moreno, J.M. Soil seed bank, fire season, and temporal patterns of germination in a seeder-dominated Mediterranean shrubland. *Plant Ecol.* **2012**, *213*, 383–393. [CrossRef]
8. Santana, V.M.; Alday, J.G.; Baeza, M.J. Effects of fire regime shift in Mediterranean Basin ecosystems: Changes in soil seed bank composition among functional types. *Plant Ecol.* **2014**, *215*, 555–566. [CrossRef]
9. Noss, R.F.; Scott, J.M. *Endangered Ecosystems of the United States: A Preliminary Assessment of Loss and Degradation*; Biological Report 28; U.S. Department of the Interior, National Biological Service: Washington, DC, USA, 1995.
10. Riordan, E.C.; Rundel, P.W. Land use compounds habitat losses under projected climate change in a threatened California ecosystem. *PLoS ONE* **2014**, *9*, e86487. [CrossRef]
11. Talluto, M.V.; Suding, K.N. Historical change in coastal sage scrub in southern California, USA, in relation to fire frequency and air pollution. *Landsc. Ecol.* **2008**, *23*, 803–815. [CrossRef]
12. Keeley, J.E.; Baer-Keeley, M.; Fotheringham, C.J. Alien plant dynamics following fire in Mediterranean-climate California shrublands. *Ecol. Appl.* **2005**, *15*, 2109–2125. [CrossRef]
13. Pausas, J.G.; Keeley, J.E. Abrupt climate-independent fire regime changes. *Ecosystems* **2014**, *17*, 1109–1120. [CrossRef]
14. D'Antonio, C.M.; Vitousek, P.M. Biological invasions by exotic grasses, the grass-fire cycle, and global change. *Annu. Rev. Ecol. Syst.* **1992**, *23*, 63–87. [CrossRef]
15. Cione, N.K.; Padgett, P.E.; Allen, E.B. Restoration of a native shrubland impacted by exotic grasses, frequent fire, and nitrogen deposition in southern California. *Restor. Ecol.* **2002**, *10*, 376–384. [CrossRef]

16. Keeley, J.E. Resilience of Mediterranean shrub communities to fires. In *Resilience in Mediterranean-Type Ecosystems*; Dell, B., Hopkins, A.J.M., Lamont, B.B., Eds.; Tasks for Vegetation Science; Springer: Berlin/Heidelberg, Germany, 1986; Volume 16. [CrossRef]
17. Halsey, R.W. In search of allelopathy: An eco-historical view of the investigation of chemical inhibition in California coastal sage scrub and chamise chaparral. *J. Torrey Bot. Soc.* **2004**, *131*, 343–359. [CrossRef]
18. Williams, K.; Hobbs, R.J.; Hamburg, S.P. Invasion of an annual grassland in northern California by *Baccharis pilularis* ssp. *consanguinea*. *Oecologia* **1987**, *72*, 461–465. [CrossRef]
19. DeSimone, S.A.; Zedler, P.H. Shrub seedling recruitment in unburned Californian coastal sage scrub and adjacent grassland. *Ecology* **1999**, *80*, 2018–2032. [CrossRef]
20. Vourlitis, G.L. Chronic N enrichment and drought alter plant cover and community composition in a Mediterranean-type semi-arid shrubland. *Oecologia* **2017**, *184*, 267–277. [CrossRef]
21. Keeley, J.E.; Fotheringham, C.J.; Baer-Keeley, M. Factors affecting plant diversity during post-fire recovery and succession of mediterranean-climate shrublands in California, USA. *Divers. Distrib.* **2005**, *11*, 525–537. [CrossRef]
22. Keeley, J.E.; Fotheringham, C.J.; Baer-Keeley, M. Demographic patterns of postfire regeneration in Mediterranean-climate shrublands of California. *Ecol. Monogr.* **2006**, *76*, 235–255. [CrossRef]
23. Quon, L.H.; Bobich, E.G.; Questad, E.J. Facilitation and herbivory during restoration of California coastal sage scrub. *Restor. Ecol.* **2019**, *27*, 1041–1052. [CrossRef]
24. Meyer, W.M., III; Halligan, C.; Thomey, L.; Madunich-Arévalo, K.; Parry, C.; Scaff, R.; Macy, R.; Jones, I.; Halligan, E.; Jaramillo, A.; et al. Herbivore influence on post-fire California sage scrub plant and soil microbial assemblages. *Diversity* **2022**, *14*, 1110. [CrossRef]
25. Zammit, C.A.; Zedler, P.H. The influence of dominant shrubs, fire, and time since fire on soil seed banks in mixed chaparral. *Vegetatio* **1988**, *75*, 175–187. [CrossRef]
26. Tangney, R.; Merritt, D.J.; Callow, J.N.; Fontaine, J.B.; Miller, B.P. Seed traits determine species' responses to fire under varying soil heating scenarios. *Funct. Ecol.* **2020**, *34*, 1967–1978. [CrossRef]
27. Tangney, R.; Paroissien, R.; Le Breton, T.D.; Thomsen, A.; Doyle, C.A.T.; Ondik, M.; Miller, R.G.; Miller, B.P.; Ooi, M.K.J. Success of post-fire plant recovery strategies varies with shifting fire seasonality. *Commun. Earth Environ.* **2022**, *3*, 126. [CrossRef]
28. Thomson, D.M.; Kwok, J.W.; Schultz, E.L. Extreme drought alters growth and interactions with exotic grasses, but not survival, for a California annual forb. *Plant Ecol.* **2018**, *219*, 705–717. [CrossRef]
29. Dartnell, S.; Cavalcanti, A.R.O.; Misaki Bluebell, A.; Hamlett, N.V.; Crane, E.J., III; Meyer, W.M., III. Flower-visiting insect assemblages on fall-blooming native California sage scrub shrubs. *Diversity* **2022**, *14*, 958. [CrossRef]
30. Bernard, R.J. Biological Field Station. In *Environment*; Robert J. Bernard Biological Field Station: Claremont, CA, USA, 2024; Available online: https://bfs.sites.pomona.edu/about/environment/ (accessed on 8 December 2025).
31. Wheeler, M.M.; Dipman, M.M.; Adams, T.A.; Ruina, A.V.; Robins, C.R.; Meyer, W.M., III. Carbon and nitrogen storage in California sage scrub and non-native grassland habitats. *J. Arid. Environ.* **2016**, *129*, 119–125. [CrossRef]
32. Rundel, P.W. Sage scrub. In *Terrestrial Vegetation of California*, 3rd ed.; Barbour, M., Ed.; University of California Press: Oakland, CA, USA, 2007; pp. 208–228. [CrossRef]
33. Staubus, W.J.; Boyd, E.S.; Adams, T.A.; Spear, D.M.; Dipman, M.M.; Meyer, W.M., III. Ant communities in native sage scrub, non-native grassland, and suburban habitats in Los Angeles County, USA: Conservation implications. *J. Insect. Conserv.* **2015**, *19*, 669–680. [CrossRef]
34. Adams, T.A.; Staubus, W.J.; Meyer, W.M., III. Fire impacts on ant assemblages in California sage scrub. *Southwest. Entomol.* **2018**, *43*, 323–334. [CrossRef]
35. Thomson, D.M.; Meyer, W.M., III; Whitcomb, I.F. Non-native plant removal and high rainfall years promote post-fire recovery of *Artemisia californica* in southern California sage scrub. *PLoS ONE* **2021**, *16*, e0254398. [CrossRef]
36. Jones, I.; Meyer, W.M., III. *Acmispon glaber* shrub canopies facilitate *Bromus madritensis* establishment after fire in California sage scrub. *Bull. South. Calif. Acad. Sci.* **2023**, *122*, 158–163.
37. Bozzolo, F.H.; Lipson, D.A. Differential responses of native and exotic coastal sage scrub plant species to N additions and the soil microbial community. *Plant Soil.* **2013**, *371*, 37–51. [CrossRef]
38. Kimball, S.; Nguyen, M.A.; Funk, J.L.; Lulow, M.; Vose, G.; Huxman, T.E. Plant traits reveal that biotic resistance to invasibility is shaped by slope aspect. *Ecol. Appl.* **2025**, *35*, e70048. [CrossRef]
39. Pickett, B.; Irvine, I.C.; Bullock, E.; Arogyaswamy, K.; Aronson, E. Legacy effects of invasive grass impact soil microbes and native shrub growth. *Invas. Plant Sci. Manag.* **2019**, *12*, 22–35. [CrossRef]
40. Singh, M.; Meyer, W.M., III. Plant-soil feedback effects on germination and growth of native and non-native species common across southern California. *Diversity* **2020**, *12*, 217. [CrossRef]
41. Loesberg, J.A.; Meyer, W.M., III. Granivory in California sage scrub: Implications for common plant invaders and ecosystem conservation. *Plant Ecol.* **2021**, *222*, 1089–1100. [CrossRef]

42. Mackenzie, B.D.E.; Auld, T.D.; Keith, D.A.; Ooi, M.K.J. Fire seasonality, seasonal temperature cues, dormancy cycling, and moisture availability mediate post-fire germination of species with physiological dormancy. *Front. Plant Sci.* **2021**, *12*, 795711. [CrossRef]
43. Luna, B.; Piñas-Bonilla, P.; Zavala, G.; Pérez, B. Timing of fire during summer determines seed germination in Mediterranean *Cistaceae*. *Fire Ecol.* **2023**, *19*, 52. [CrossRef]

Disclaimer/Publisher's Note: The statements, opinions and data contained in all publications are solely those of the individual author(s) and contributor(s) and not of MDPI and/or the editor(s). MDPI and/or the editor(s) disclaim responsibility for any injury to people or property resulting from any ideas, methods, instructions or products referred to in the content.