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Resilient Plant Communities and Increasing Native Forbs after Wildfire in a Southwestern Oregon Oak Shrubland

Running footer: Oak Shrubland Resilience

3 tables, 4 figures

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Abstract

Fire ecology in oak shrublands is among the least well understood for Pacific Northwest habitats. Following the 2018 Klamathon Fire, we examined the first three years of post-wildfire plant community change and measured soil properties in shrubland dominated by shrub-form Oregon white oak (*Quercus garryana*) in Cascade-Siskiyou National Monument, Oregon. Based on temporal change and comparison with unburned areas, burned oak shrubland communities displayed resiliency and at least transient increases in some native plants apparently benefiting from wildfire. Via oak resprouting and other native plants increasing, total native cover rapidly recovered in burned areas by the second post-fire year to not differ ($P > 0.05$) from unburned areas. Native species richness (25 m^2) did not differ with burning any year while community evenness and diversity were usually highest in burned areas. Native plants associated with burned areas included the perennial grass blue wildrye (*Elymus glaucus*), the shrub Pacific serviceberry (*Amelanchier alnifolia*), and most abundantly forbs, such as the perennial Scouler's hawkweed (*Hieracium scouleri*) and annuals such as slender clarkia (*Clarkia gracilis*). Cover of non-native plants on burned areas was not higher than on unburned areas within any year. After severe burning, the 0–5 cm mineral soil had the finest texture and highest bulk density. Overall, oak shrubland vegetation displayed rapid resilience to wildfire and native forbs at least transiently increased.

Keywords: Annual forbs, Cascade-Siskiyou National Monument, Community composition, Non-native plants, *Quercus garryana*

Introduction

Oak shrublands, dominated by short, shrubby oak (*Quercus*) species or those capable of growing to tree form but that remain in shrub form because of biophysical or disturbance limitations, are a major vegetation type within many climatic regions globally (Tsiouvaras 1987, Tsiourlis et al. 2009, Coulter et al. 2010). For example, oak shrubland extensively occurs in Mediterranean Europe, Israel, and Asia (Naveh and Whittaker 1979, Zhu et al. 2012). In western North America, oak shrublands inhabit areas such as semi-arid Colorado (Abella 2008), the central Arizona chaparral region and desert montane locations (Brown 1978), and southern California to Pacific Northwest Mediterranean and semi-arid climates (White and Sawyer 1994).

In the Pacific Northwest, oak shrubland occurs as part of montane chaparral, post-disturbance communities such as following single or repeated fires that often stimulate resprouting oaks, and as mixed communities of shrub-form oaks with grasses, forbs, and other shrubs such as within mixed conifer landscapes (Detling 1961, Hosten et al. 2006, Duren and Muir 2010, Cocking et al. 2014, Hammett et al. 2017). Several authors have noted that fire history and fire effects in montane shrubland, including shrub-form oaks, are among the least well understood of Pacific Northwest ecosystems (e.g., Agee 1993, Duren and Muir 2010, Bohlman et al. 2021). Montane oak shrublands are hypothesized to have historically experienced a mixed-severity fire regime with patches of lower or higher severity within a burn or temporally among burns (Coulter et al. 2010). It is uncertain whether contemporary wildfires may produce effects in oak shrubland similar to those observed in mixed conifer forest, such as frequently stimulating appearance of forbs and annuals uncommon in unburned forest (e.g., Donato et al. 2009, Abella and Springer 2015, Kerns and Day 2018). Similarly, there is uncertainty whether wildfires result in communities dominated by non-native plants, which have variably increased post-fire in California-Oregon oak chaparral/mixed conifer forest (e.g., Coulter et al. 2010, Franklin 2010) or remained minimal (e.g., Knapp et al. 2007, Webster and Halpern 2010). Further understanding wildfire effects in oak shrublands could aid forecasting effects of fires burning across diverse landscapes containing multiple vegetation types, including oak shrubland, and assist formulating post-fire management strategies.

Here, we examined recovery after wildfire in oak shrubland containing the shrub form of Oregon white oak (*Quercus garryana*; hereafter oak), distinguished as *Q. garryana* var. *breweri* by some taxonomists (Hosten et al. 2006). In these oak shrubland communities, historical fire regimes and contemporary fire effects are less well understood and may differ from those in communities with oak in tree form, such as oak woodlands more extensively studied in the Pacific Northwest (e.g., Maslovat 2002, MacDougall et al. 2004, Christy and Alverson 2011). Many of the oak woodlands have herbaceous-dominated understories and historically experienced frequent, low-severity fires (e.g., Sprenger and Dunwiddie 2011), contrasting with the shorter-statured, woody structure of the oak shrublands hypothesized to have had less frequent, mixed-severity fires (Hosten et al. 2006, Coulter et al. 2010, Bohlman et al. 2021).

We focused on variation in plant community diversity measures in oak shrubland in the post-fire habitat, which we also assessed through analysis of substrate, soil, and soil seed bank characteristics to associate with vegetation diversity. Plant diversity was of interest because wildfire could homogenize vegetation by serving as a filter to species composition such as through species' resistance-resilience to fire and colonization processes (Richter et al. 2019). Conversely, wildfire could diversify within- or among-site plant communities, such as by reducing competitive, dominant species and enabling or directly stimulating species colonization (Doyle et al. 1998, Donato et al. 2009, Abella and Springer 2015, Strand et al. 2019). We examined three questions: 1) How do plant community cover, diversity, and species compositional variables differ across burn severities (two burn severities and as compared with unburned areas) through time? 2) Does heterogeneity in plant community variables differ among burn severities? and 3) How do post-fire soil properties vary among burn severities?

Methods

Study Area

We conducted the study within Cascade-Siskiyou National Monument, a 46,000-ha public preserve administered by the Bureau of Land Management in southwestern Oregon. The monument was established in 2000 to conserve the area's unique biodiversity and habitats at the confluence of the Siskiyou Mountains and Cascade Range (Bureau of Land Management 2008). Our specific study area was within the Klamathon Fire within the Klamath River Ridges level 4 ecoregion, which has a warm summer Mediterranean climate and contains mixed conifer forest and oak-dominated montane shrubland (Thorson et al. 2003). The human-ignited Klamathon Fire began in July 2018 and had a burn perimeter covering 15,382 ha in southwestern Oregon and northern California, including 4,500 ha within the monument. A weather station just east of the burn perimeter at an elevation of 823 m reported the following climatic averages from 1960–2021: 50 cm year^{-1} of precipitation (including 44 cm year^{-1} of snow), daily high temperatures of 9 °C in January and 35 °C in July, and daily low temperatures of -3 °C in January and 14 °C in July (Copco #1 Dam, California; Western Regional Climate Center, Reno, NV). In the burn year and during our post-fire sampling years, precipitation was 75% of average in 2018, 106% in 2019, 69% in 2020, and 78% in 2021. Livestock grazing was not authorized in the study area for at least 10 years before our study. Large native herbivores present include mule deer (*Odocoileus hemionus hemionus*) and black-tailed deer (*Odocoileus hemionus columbianus*).

Plot Establishment and Plant Community and Substrate Sampling

In August 2018 immediately after the fire, we used random geographic coordinates to establish 30 permanent plots (each 5 m × 5 m) in a 40-ha area containing a diversity of burn severities in close proximity within the burn perimeter in oak shrubland vegetation. While on site, we classified each plot into one of three burn-severity categories, with 10 plots per category (Figure 1; Supplemental Figure S1, available online only). High-severity plots had 90–100% of the ground charred and no leaves remaining on any still-standing oak stems. Moderate-severity plots had 50–90% of the ground charred and at least some leaves attached to still-standing oak stems. None of the burned plots had less than 50% of the ground charred, as the fire burned at moderate to high severity across the study area, so there was no low-severity category. Unburned plots were interspersed with burned plots within the burn perimeter and had no evidence of char on the ground surface nor on oak stems. Pairwise distances between plots ranged from 20–620 m and averaged 254 m apart (Supplemental Figure S2, available online only). Plots were in the Skookum-rock outcrop-McMullin soil taxonomic complex, classified as Ultic Argixerolls and Haploxerolls (Johnson et al. 1993). Parent material consisted of colluvium and residuum derived from tuff breccia and andesite and colluvium derived from metasedimentary and igneous rock (Johnson et al. 1993). All plots had an eastern- to southeastern-facing slope aspect, slope gradients ranging from 5–35%, and elevations from 1300–1400 m. Plots were oriented along the slope using randomly selected compass bearings.

We sampled plots near peak phenology in mid-May to early June annually from 2019–2021, from the first to the third growing seasons post-fire. Each plot contained 15, 20 cm × 50 cm quadrats. The 15 quadrats included five each along the southern and northern plot lines, starting at 0 m and spaced every 1 m, and along the plot diagonal starting at 1 m. We categorized aerial cover of each vascular plant species to the nearest percent in each quadrat from 1–5%, then at 5% intervals up to 100%, the maximum cover a species could attain. Cover of all species within quadrats could exceed 100% if foliage of multiple species overlapped. In the first post-fire year, when it was possible to readily observe resprouting, we subdivided oak cover into resprout/not resprout based on whether foliage or new stems originated from the base of a dead stem or epicormically (Nemens et al. 2019). We then surveyed remaining areas of plots for vascular plant species not already recorded in quadrats and assigned cover of these species on a plot basis. Final cover of each species occurring in plots was the average cover in the 15 quadrats plot^{-1} or the whole plot cover. Nomenclature and classification of growth form (e.g., shrub), potential longevity (annual, biennial, or perennial), and nativity to the U.S. follow Natural Resources Conservation Service (2023).

We also characterized substrates on each plot and collected a supplemental soil seed bank dataset. In each quadrat in each plot every year, we used the same cover classes as for vascular plants to categorize surface cover of litter (including leaves, needles, diaspores, dead shoots, and twigs < 2 cm in diameter), wood (woody pieces ≥ 2 cm in diameter), and bare ground. We collected soil seed bank samples in March 2021, three years post-fire, and report methods, results, and interpretation mainly in Supplemental Appendix S1 (available online only). We then use this supplemental dataset in the main paper to aid interpretation of vegetation changes.

Soil Property Characterization

In March 2021, three years post-fire, we sampled the 0–5 cm mineral soil in a random subset of half the plots of each burn-severity category. We collected 15 subsamples (totaling 1000 cm^3 and combined on a plot basis) from equally spaced locations along the perimeter of each plot just outside the plot. After air drying and passing samples through a 2-mm sieve, we analyzed the < 2 mm fraction for texture (hydrometer method), pH (1:1 slurry:extract), and electrical conductivity. Using the sieved > 2 mm fraction, we calculated coarse fragment content by weight and volume (water displacement) and bulk density (105 °C oven dry weight of the < 2 mm fraction in a 200-mL subsample).

Data Analysis

We conducted univariate repeated measures analyses in SAS 9.4 (SAS Institute 1999), community compositional analyses (ordination, permutation tests, and indicator species analysis) in PC-ORD 7.10 (McCune and Mefford 1999), and univariate (for 2021 soil data) and heterogeneity analyses in PAST 4.12 (Hammer 2022). First, we computed 20 univariate substrate (cover of bare ground, litter, and wood) and plant community variables each year for each plot (Table 1; data in Supplemental Table S1, available online only). Univariate plant community variables included cover and species richness (25 m^{-2}) of native and non-native plants, grasses, forbs, shrubs, trees, and annuals; cover of oak; Shannon diversity index (calculated using species frequency of occurrence in the 15 quadrats $plot^{-1}$ or assigned a frequency of one for whole plot occurrence), and evenness. Evenness was also based on frequency and calculated as Shannon diversity / ln(species richness). After Box-Cox-transforming these variables to improve normality and equality of variance, we analyzed each variable in a two-factor, repeated measures analysis of variance including burn severity (severe, moderate, and unburned) and year (2019, 2020, and 2021 spanning 1–3 years after fire) implemented using PROC GLIMMIX with autoregressive structure in SAS. When main effects or interactions had $P < 0.05$, we separated means using Tukey tests. We compared 2021 soil properties among burn-severity categories using one-way analysis of variance followed by Tukey tests.

After preparing a plot × species matrix containing species % frequencies (from the 15 quadrats $plot^{-1}$ or whole plot occurrence) each year and for all years combined, we ordinated community composition using non-metric multidimensional scaling in PC-ORD 7.10 (Sørensen distance, random starting coordinates, and 250 runs each with real and randomized data). In secondary matrices, we included cover and frequency of substrate variables (e.g., litter) and individual species and community variables (e.g., annual plant cover) to display as potential correlates ($r^2 \geq 0.40$ to qualify) with community patterns in ordinations each year. We then tested if community composition (species frequencies) varied among burn-severity categories within years using multi-response permutation procedures (Sørensen distance and n_i/Σ n group weighting in PC-ORD 7.10). When overall tests were significant at $P < 0.05$, we compared burn severities using Bonferroni-corrected pairwise tests. To compare burn severities across all years simultaneously, we used blocked multi-response permutation procedures by incorporating repeated measures blocked by plot (Euclidean distance, no median alignment).

To identify if individual species (frequency data) were associated with burn-severity categories, we performed indicator species analysis (Dufrêne and Legendre 1997) for all combinations of burn severities (i.e. all three categories and each combination of two of the three categories; De Cáceres et al. 2010) in PC-ORD 7.10. We identified species significantly associated with a burn-severity category based on having an indicator value ≥ 50 with $P < 0.05$ determined via 4,999 permutations (McCune and Mefford 1999).

We examined if heterogeneity among plots varied across burn severities within years for vegetation variables by computing pairwise, Bonferroni-corrected Fligner-Killeen tests (Donnelly and Kramer 1999) to compare coefficients of variation. For community composition (species frequencies), we tested for equality of multivariate dispersion (Anderson 2006) using pairwise tests (Bonferroni-corrected) between burn severities within years.

Results

Plant Community

In the three post-fire years, we detected 147 vascular plant species, of which 125 (85%) were native and 22 (15%) were non-native. Severely and moderately burned plots each in total contained 98 species while unburned plots contained 86 species. There were 89 total species in the first post-fire year (2019), 100 in the second (2020), and 95 in the third (2021).

Average cover of native plants in severely and moderately burned plots increased after the first post-fire year to reach levels not differing ($P > 0.05$) from those in unburned plots by the second year (Table 1, Figure 2). Oak increased in post-fire years to reach cover on burned plots not differing from on unburned plots by the third year. In 2019 (post-fire year 1), resprouts comprised 49% of the total oak cover in severely burned plots and 31% in moderately burned plots. Cover of native species other than oak more than tripled (18 to 54%, severely burned plots) or quadrupled (18 to 71%, moderately burned plots) from the first to the second year after fire. Average cover of non-native plants did not differ significantly among burn severities any year.

Considering plant growth forms, cover of forbs increased in the second post-fire year, then declined in the third year on burned plots (Figure 2). Specifically considering native forbs in burned areas, cover rose from an average of 15% (16% in moderately and 15% in severely burned plots) in 2019 to 41% (42% in moderately and 41% in severely burned plots) in 2020, before declining to 22% in 2021 (20% in moderately and 24% in severely burned plots; Supplementary Table S2, available online only). Annuals comprised most (proportionally 0.63–0.88 on average from 2019–2021 for burned and 0.73–0.94 for unburned plots) of the native forb cover. Cover of grasses and shrubs did not vary significantly with burn severity (Table 1).

Species richness (25 m^2) of native plants did not vary significantly with burn status (Figure 3). However, community evenness and Shannon diversity were higher in both burn severities than in unburned plots for the first two post-fire years and remained higher in moderately burned plots the third year. Non-native species richness increased only during the second post-fire year with severe burning and remained elevated (compared to the first post-fire year and compared to unburned plots) with moderate burning. Species richness of annual plants was highest in severely and moderately burned plots in the second post-fire year (Table 1).

Multivariate analyses of community composition showed that differences among burn severities were greatest in the first post-fire year before weakening to non-significance by the third year (Figure 4, Supplemental Table S3, available online only). In ordinations, variables correlated with community compositional patterns differed among years (Figure 4). Covers of bare ground and perennial plants were only correlated with community variation in the first year.

Of 17 indicator species significantly associated with a burn-severity category in one or more years, two (12%) were native shrubs, one (6% each) was a native perennial grass, three (18%) were native perennial forbs, six (35%) were native annual forbs, and five (29%) were non-native, all of which were annuals (Table 2). For the nine native forb indicator species, all were associated with severe or moderate burning (or both), except for the annual cleavers (*Galium aparine*) associated with unburned plots. Native annual forbs most strongly and consistently associated with burning from most to least were slender clarkia (*Clarkia gracilis*), miner's lettuce (*Claytonia parviflora*), clearwater cryptantha (*Cryptantha intermedia*), diamond clarkia (*Clarkia rhomboidea*), and basin cryptantha (*Cryptantha ambigua*). All native perennial forbs that were indicator species, including Scouler's hawkweed (*Hieracium scouleri*), purplehead (*Dichelostemma capitatum*), and American vetch (*Vicia americana*), were associated with moderate or severe burning or both. The native perennial grass blue wildrye (*Elymus glaucus*) was associated with moderate burning. Considering the two woody species, oak was associated with unburned plots, but only in the first year as the species showed resilience to burning, and the shrub Pacific serviceberry (*Amelanchier alnifolia*) was associated with moderate burning.

The non-native indicator species displayed a range of associations with burning. Cheatgrass (*Bromus tectorum*) was associated with unburned plots in 2019, while the annual forbs prickly lettuce (*Lactuca serriola*), spiny sowthistle (*Sonchus asper*), and pennycress (*Thlaspi arvense*) were associated with severe or moderate burning in 2020 or 2021.

Conifer tree species were absent in burned and infrequent in unburned plots. The two conifers recorded during the study inhabited only one unburned plot (incense cedar [*Calocedrus decurrens*]) and 1–2 unburned plots (western juniper [*Juniperus occidentalis*]) among years, with all occurrences as small individuals < 1 m tall.

Comparing coefficients of variation for univariate plant community variables revealed that covers of native plants and oak were more heterogeneous among burned plots for both severities than for unburned plots in the first post-fire year (Supplemental Table S4, available online only). Subsequently, covers of non-native plants and forbs and Shannon diversity were more heterogeneous in unburned plots than in at least one of the burn severities in the second post-fire year. In testing multivariate dispersion for variability in community composition among plots, dispersion was similar among all burn-severity categories with one exception. Composition was more variable for moderately burned, compared with unburned, plots in the second post-fire year (Supplemental Table S5, available online only).

Soil Properties

The main difference among burn severities in soil properties (0–5 cm mineral soil) analyzed in the third post-fire year (2021) was that soil in severely burned plots was finer-textured, with high clay and low coarse fragment concentrations by weight (Table 3). Severely burned plots also exhibited high bulk density associated with lower coarse fragment content.

Discussion

Vegetation Change

With unburned plots serving as a benchmark, post-fire plant community variables displayed a mixture of resistance (lack of significant change with burning; e.g., species richness), resilience (conditions on burned and unburned plots converging through time; e.g., oak cover), or apparently transient increases or temporary compositional change (e.g., forb cover). Overall, there was a brief (one year) post-fire reduction in native plant cover, followed by rapid recovery via oak resprouting and increases in other native plants; no significant change in native species richness; increased evenness and Shannon diversity and no consistent loss of heterogeneity in plant communities; and at least transient increases in species apparently benefiting from fire.

Only two native species (oak and cleavers) were significantly associated with unburned plots and only in the first year. Oak cover rebounded rapidly on burned plots and may be expected to benefit from fire given the species' resprouting capacity compared with most competing conifer trees (Regan and Agee 2004). Oak's resilience in our study occurred despite most individuals being top-killed (Figure S1), much more prevalently than the minimal 7% top-kill reported for oaks in tree form after prescribed fires in oak woodlands where oak also showed high resilience (Nemens et al. 2019). Oaks in shrub form experiencing higher severity fire in oak shrubland may sustain more damage but nevertheless also appear to display rapid resilience. Regarding the annual forb cleavers, the only other native species associated with unburned plots the first year, a prior study found that its germination was reduced or eliminated by 75–100 °C heating treatments (Pratt et al. 1984). This species may be among the few presently in the oak shrubland community negatively responding to fire.

Forbs and Annuals—Exemplifying potential transient change in species benefiting from fire, cover of forbs and species richness of forbs and annual plants were higher in burned than unburned plots in one or two years before declining three years post-fire. An increase in forbs and short-lived plants has occurred soon after wild or prescribed fires in some prior studies in western mixed conifer forests (e.g., Abella and Springer 2015, Kerns and Day 2018, Goodwin et al. 2018) and in Pacific West oak woodland-chaparral (e.g., Sugihara and Reed 1987, Coulter et al. 2010, Franklin 2010). Although continued monitoring would be needed in our study to ascertain longer-term trends, some other studies that assessed post-fire changes for longer than five years in mixed conifer forests found that forbs and annuals-biennials remained elevated for 5–10+ years after burning (Webster and Halpern 2010, Jang 2021). Additionally, our soil seed bank assessment indicated that forbs dominated seed banks three years post-fire, suggesting a readily available *in situ* seed supply of these species for at least the near term (e.g., ~ 3 years) based on their longevities in soil (Appendix S1).

Several mechanisms have been proposed as to why forbs and short-lived plants have increased after fire. The species may respond to post-fire reductions in litter thickness and increased bare ground, enabling seedling emergence in open microsites (Wayman and North 2007). Our results seemed to support this, as we found that bare ground was correlated with species compositional gradients. Fire-related germination cues, such as smoke, heat, and charred wood, could stimulate emergence from soil seed banks (Keeley and Keeley 1987, Abella et al. 2007). Thermophilization, whereby post-fire environments become more well-lit and warmer after fire, could facilitate forbs and short-lived plants (Stevens et al. 2015, Springer et al. 2018). Reduced tree/tall shrub canopy cover and reduced competition from shrubs, at least temporarily before woody plants resprout, has also been related to transient increases in forbs and short-lived plants (Anderson and Bailey 1979, Bohlman et al. 2016, Richter et al. 2019).

Complementing the inference of at least temporary fire benefits to native forbs and annuals at the community level, half of the individual native species that were significant indicators for burned plots were forbs, and over half of these were annuals. Furthermore, many forbs were associated with the severest burning with the most bare ground. One of the species, slender clarkia, was described by Dunwiddie et al. (2014) as having high fidelity to prairie and oak woodlands and is thought to have declined with loss of open habitats during fire-free periods in the Pacific Northwest. Clearwater cryptantha, also burn-associated in our study, maintained 55% germination in a prior study when seeds were exposed to 120 °C dry heat for five minutes, and germination increased to 72% when exposed to charred wood (Keeley and Keeley 1987).

This suggests the possibility that fire may not harm and could promote germination of seeds in soil insulated from lethal temperatures (Keeley and Keeley 1987). A native perennial forb associated with burned plots in our study, Scouler's hawkweed, was associated with open meadows within a conifer forest landscape in a prior Oregon study (Halpern et al. 2019). Collectively, the limited autecology literature for the burned-plot indicator species supports an interpretation that they benefit from open conditions including bare soil, potentially fire-related germination cues, and perhaps other features in post-fire environments.

Grasses—Grasses are another plant group of unique interest because they are thought to have been a characteristic component of historical oak ecosystems in the Pacific Northwest but may have declined during intensive livestock grazing and other changes beginning in the late 1800s and early 1900s (Christy and Alverson 2011). Although we did not find significant variation in cover or species richness of grasses as a group with burning, two major species showed notable patterns. First, Lemmon's needlegrass (*Achnatherum lemmonii*) attained its highest cover and frequency with severe burning. Maslovat (2002) conjectured that the species benefits from fire by having hygroscopic awns enabling seeds to move along open soil surfaces to favorable microsites and by forming at least short-term persistent soil seed banks available to germinate after fires. Second, blue wildrye in our study was abundant in moderately burned plots, especially 2–3 years post-fire. In a Wyoming conifer forest, Doyle et al. (1998) reported that blue wildrye exhibited colonization delayed for 2–3 years after fire, then was abundant for multiple years. In a mixed conifer-hardwood forest in northern California, Hanson and Stuart (2005) found that blue wildrye was present only in burned areas with sparse tree canopy cover and was absent under dense canopy cover. The species can have readily germinable seeds (Hoffman

1985) but can also form at least short-term persistent soil seed banks (Pratt et al. 1984, Lang and Halpern 2007, Buonopane et al. 2013). Further untangling what may limit recruitment of grasses in post-fire environments may assist identifying how grass populations could have changed in the past and whether restoration actions are appropriate for increasing native grass populations.

Non-Native Plants—Cover and species richness of non-native plants displayed minimal difference among burn severities throughout the study. Our results augment the highly variable post-fire changes in non-native plants reported by prior studies in habitats embedded within mixed conifer landscapes. For example, non-native plants after fire increased in chaparral in Oregon (Coulter et al. 2010) and mixed conifer forest in California (Franklin 2010). They increased temporarily then decreased in conifer forest in Montana (Jang et al. 2021) and Oregon (Kerns and Day 2018). In contrast, non-native plants did not increase or remained sparse after fire in mixed conifer forest in California (Knapp et al. 2007, Webster and Halpern 2010), Arizona (Springer et al. 2018), and in Idaho, Montana, and Washington (Morgan et al. 2015, Strand et al. 2019). It is possible that much of the variation among studies relates to seed supply and whether non-native species were already present pre-fire or nearby (Donato et al. 2009). We found that at least half of the taxa we detected three years post-fire in soil seed banks were non-native to North America, suggesting at least *in situ* seed availability in the soil for a subset of the non-native species that were detected in the vegetation (Appendix S1).

Soil Properties

Three years post-fire, severely burned plots had the finest textured soil with the highest bulk density. It is not clear whether soil differences among burn severities existed before fire (a possibility we sought to minimize by sampling severities in close proximity, at similar elevation, on the same landform, and within the same soil taxonomic mapping unit), were caused during fire, or developed after fire through processes such as erosion. Although we instead recorded fine-textured soil, severe burning is often predicted to make soil coarser in texture by fusing clay into sand particles at temperatures exceeding 100–500 °C (Giovannini and Lucchesi 1997, Alcañiz et al. 2018) and by post-fire erosion mobilizing fine soil particles (Certini 2005). Across a variety of studies, soil bulk density has variably decreased, not changed, and increased after fires (Alcañiz et al. 2018). Bulk density could increase via processes such as fire destroying soil pore spaces and reducing organic matter concentration (Hubbert et al. 2006). In other properties we measured, such as pH, it is possible transient post-fire changes did occur but dissipated by three years post-fire when we sampled (e.g., Graham et al. 2016). Potentially one of the more ecologically important soil differences we observed in burned plots was the reduction in the O horizon, as this surficial layer can contain many seeds, filter seedling emergence, and influence soil temperature (Hubbert et al. 2006, Buonopane et al. 2013).

Ecological Conservation and Management Implications

The oak shrubland community generally displayed high resilience to wildfire within three years, and some key plant groups (native forbs and annuals) characteristic of historically open oak ecosystems (Dunwiddie et al. 2014) at least transiently increased. Resilience by the dominant oak and the overall plant community even after severe burning could be interpreted as consistent with ecosystems with an evolutionary history of mixed-severity wildfires and an idea that effects of the current wildfire might not be atypical of those historically (Bohlman et al. 2021). The post-wildfire plant community was dominated by native plants. Non-native plants contributed a relatively small portion of vegetation cover, although they were frequent in soil seed banks three years after fire. Monitoring and strategic treatment may be useful to keep cover of non-native plants low. Overall, the mixed-severity wildfire had mainly transient effects on the oak shrubland plant community and at least temporarily benefited native annual and perennial forbs.

While our study focused on plant diversity, other organismal groups could benefit from the observed increases in forbs. For example, forbs provide floral resources to pollinators and other invertebrates in Pacific Northwest oak woodlands (Parachnowitsch and Elle 2005). Potentially related to increases in floral resources and other post-fire environmental changes such as in temperature, several studies have reported increases in pollinators after wildfires in western North American shrublands and mixed conifer forests. A decade after mixed-severity wildfire in montane chaparral in central California, the species richness of bumble bees (*Bombus* spp.) was most strongly positively correlated with herbaceous plant cover (Loffland et al. 2017). Also within the Klamath-Siskiyou ecoregion in southern Oregon like our study, Galbraith et al. (2019) found that the density of flowering plants and the density and species richness of bees in mixed conifer forest increased with increasing fire severity by three years after wildfire. In total, 20× more bee individuals and 11× more species were detected in areas that burned at high severity compared with low severity (Galbraith et al. 2019). Our results and these observations suggest that periodic, mixed-severity wildfires at least temporarily increase some groups of native plants and perhaps certain faunal groups as well in oak shrublands.

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Tables

TABLE 1. Variation in univariate plant community and substrate variables among burn severities through time after the 2018 Klamathon Fire, Cascade-Siskiyou National Monument, Oregon. Two-way, repeated measures analyses of variance with $P < 0.05$ are in bold for the interaction or main effects if the interaction was not significant.

	Burn severity (B)	Year (Y)	B × Y	
Cover	$F_{2,27}$ (P)	$F_{2,54}$ (P)	$F_{4,54}$ (P)	Conclusion[1]
Native	7.1 (0.003)	93.6 (<0.001)	**9.4 (<0.001)**	Lowest in S-M in 2019
Non-native	0.7 (0.507)	37.4 (<0.001)	**4.5 (0.003)**	Lowest in 2019 and declining in U in 2021
Quercus garryana	18.6 (<0.001)	27.8 (<0.001)	**12.6 (<0.001)**	Highest in U, increased in burned through time
Forbs	7.9 (0.002)	56.0 (<0.001)	**6.3 (<0.001)**	Lowest in 2019, highest in S and M in 2020
Grasses	2.8 (0.076)	**75.7 (<0.001)**	2.0 (0.105)	Lowest in 2019
Shrubs	0.2 (0.801)	**25.8 (<0.001)**	1.8 (0.153)	Lowest in 2019
Trees	19.8 (<0.001)	28.2 (<0.001)	**12.7 (<0.001)**	Highest in U, lowest in S-M in 2019
Annual plants	1.9 (0.167)	**42.1 (<0.001)**	2.3 (0.074)	Highest in 2020
Bare ground	91.7 (<0.001)	23.3 (<0.001)	**5.7 (<0.001)**	Lowest in U, highest in S-M and in 2019
Litter	47.5 (<0.001)	47.2 (<0.001)	**9.4 (<0.001)**	Highest in U, lowest in S

Wood	**11.4 (<0.001)**	3.0 (0.061)	0.8 (0.557)	Lowest in S
Species richness				
Native	2.1 (0.142)	**8.3 (<0.001)**	2.5 (0.053)	Highest in 2021
Non-native	2.6 (0.093)	32.1 (<0.001)	**6.3 (<0.001)**	Lowest in 2019, increasing in M through time
Forbs	2.8 (0.076)	18.3 (<0.001)	**5.2 (0.001)**	Generally highest in S-M
Grasses	0.1 (0.909)	**16.9 (<0.001)**	0.4 (0.815)	Lowest in 2019 and 2021, highest in 2020
Shrubs	3.1 (0.060)	1.0 (0.381)	1.8 (0.140)	No significant variation
Trees	7.5 (0.003)	0.5 (0.634)	**3.1 (0.024)**	Highest in U, generally lowest in S-M
Annual plants	0.3 (0.748)	0.6 (0.582)	**8.1 (<0.001)**	Generally highest in S-M in 2020
Diversity measures				
Evenness	33.5 (<0.001)	18.0 (<0.001)	**5.8 (<0.001)**	Lowest in U and declining in 2021 in M-S
Shannon diversity	27.6 (<0.001)	41.4 (<0.004)	**6.3 (<0.001)**	Lowest in U and declining in 2021 in M-S

[1]S, severely burned; M, moderately burned; U, unburned.

TABLE 2. Indicator species analysis of associations with burn-severity combinations from one (2019) to three (2021) years after the 2018 Klamathon Fire, Cascade-Siskiyou National Monument, Oregon. Indicator values in bold have $P < 0.05$.

	Comparisons								
	Severe	Moderate	Unburned	Severe	Moderate	Severe	Unburned	Moderate	Unburned
Species[1]									
2019	Indicator values								
Bromus tectorum (AG)*	5	15	49	12	38	7	**69**	16	54
Claytonia parviflora (AF)	48	27	3	52	30	**78**	5	**58**	7
Clarkia rhomboidea (AF)	47	5	15	**62**	7	56	18	12	36
Cryptantha ambigua (AF)	40	6	0	40	6	**50**	0	30	0
Dichelostemma capitatum (PF)	39	36	19	49	45	61	29	**63**	33
Galium aparine (AF)	25	32	43	43	57	36	**64**	43	57
Quercus garryana (T)	25	26	49	49	51	34	**66**	35	**65**
Vicia americana (PF)	12	45	21	19	**69**	22	38	57	26
2020									
Amelanchier alnifolia (S)	28	38	9	34	46	49	15	**64**	15
Anthriscus caucalis (AF)*	1	20	38	2	**54**	1	**57**	21	39
Clarkia gracilis (AF)	44	33	15	54	41	**70**	24	60	27
Claytonia parviflora (AF)	29	42	10	35	51	55	19	**66**	16
Cryptantha intermedia (AF)	**61**	23	1	65	25	**82**	1	**72**	2
Elymus glaucus (PG)	**7**	**50**	31	11	**82**	13	63	56	35
Hieracium scouleri (PF)	26	44	2	28	48	**58**	5	**70**	4
Lactuca serriola (AF)*	44	8	0	44	8	**60**	0	30	0
Sonchus asper (AF)*	23	31	0	23	32	48	0	**58**	0
2021									
Clarkia gracilis (AF)	37	41	12	45	50	**68**	22	**65**	19
Elymus glaucus (PG)	12	**50**	26	18	**74**	24	52	60	32
Thlaspi arvense (AF)*	0	34	10	0	**50**	0	30	34	10

[1]A, annual; P, perennial; F, forb; G, grass; S, shrub, T, tree; *, non-native to the U.S.

TABLE 3. Soil properties among burn severities in 2021, three years after the 2018 Klamathon Fire, Cascade-Siskiyou National Monument, Oregon. For each soil variable when analysis of variance (ANOVA) had $P < 0.05$, means without shared letters differ.

	Severe	Moderate	Unburned	ANOVA	
	Mean±SEM			$F_{2,14}$	*P*
Sand (%)[1]	39±5	45±8	46±9	0.27	0.771
Silt (%)	32±1	36±5	40±8	0.18	0.839
Clay (%)	29±5 [a]	18±3 [ab]	13±5 [b]	**4.55**	**0.034**
pH (1:1 slurry:extract)	7.42±0.05	7.46±0.1	7.20±0.12	2.10	0.166
Electrical conductivity (μS cm^{-1})	392±71	617±93	456±131	1.31	0.305
Coarse fragments (% weight)	15±4 b	32±2 [a]	27±6 [ab]	**4.12**	**0.043**
Coarse fragments (% volume)	7±2	14±1	11±3	3.24	0.075
Bulk density (g cm^{-3})	0.88±0.04 [a]	0.66±0.03 [b]	0.64±0.07 [b]	**6.20**	**0.014**

[1]Textural classes are clay loam for severely burned and loam for moderately burned and unburned.

Figure Captions

Figure 1. Examples of severely, moderately, and unburned locations within the 2018 Klamathon Fire, Cascade-Siskiyou National Monument, Oregon. Photo by C. D. Schelz, July 2018. Repeat photos are in Supplemental Figure S1, available online only.

Figure 2. Mean cover of plants among burn-severity categories from one to three years after the 2018 Klamathon Fire, Cascade-Siskiyou National Monument, Oregon. Within each plant group, means without shared letters differ among severity × year categories at $P < 0.05$. Error bars are + 1 SEM. Cover data sub-divided for all nativity-longevity-growth form plant combinations is in Table S2.

Figure 3. Mean plant diversity variables among burn-severity categories from one to three years after the 2018 Klamathon Fire, Cascade-Siskiyou National Monument, Oregon. Within each plant group, means without shared letters differ among severity × year categories at $P < 0.05$, except for native species richness which only had a significant main effect of year. Error bars are + 1 SEM.

Figure 4. Variation in plant community composition among burn-severity categories from one to three years after the 2018 Klamathon Fire, Cascade-Siskiyou National Monument, Oregon. Non-metric multidimensional scaling ordinations display vectors correlated ($r^2 \geq 0.40$) with community compositional variation within years and convex hulls connecting plots within burn severities for all years combined. Ordination statistics and associated multi-response permutation procedures comparing community composition across burn severities are provided in Table S3. Indicator values (IV) are shown for species with IV ≥ 50 and $P < 0.05$ for a burn-severity category within years.

Figures

Figure 1

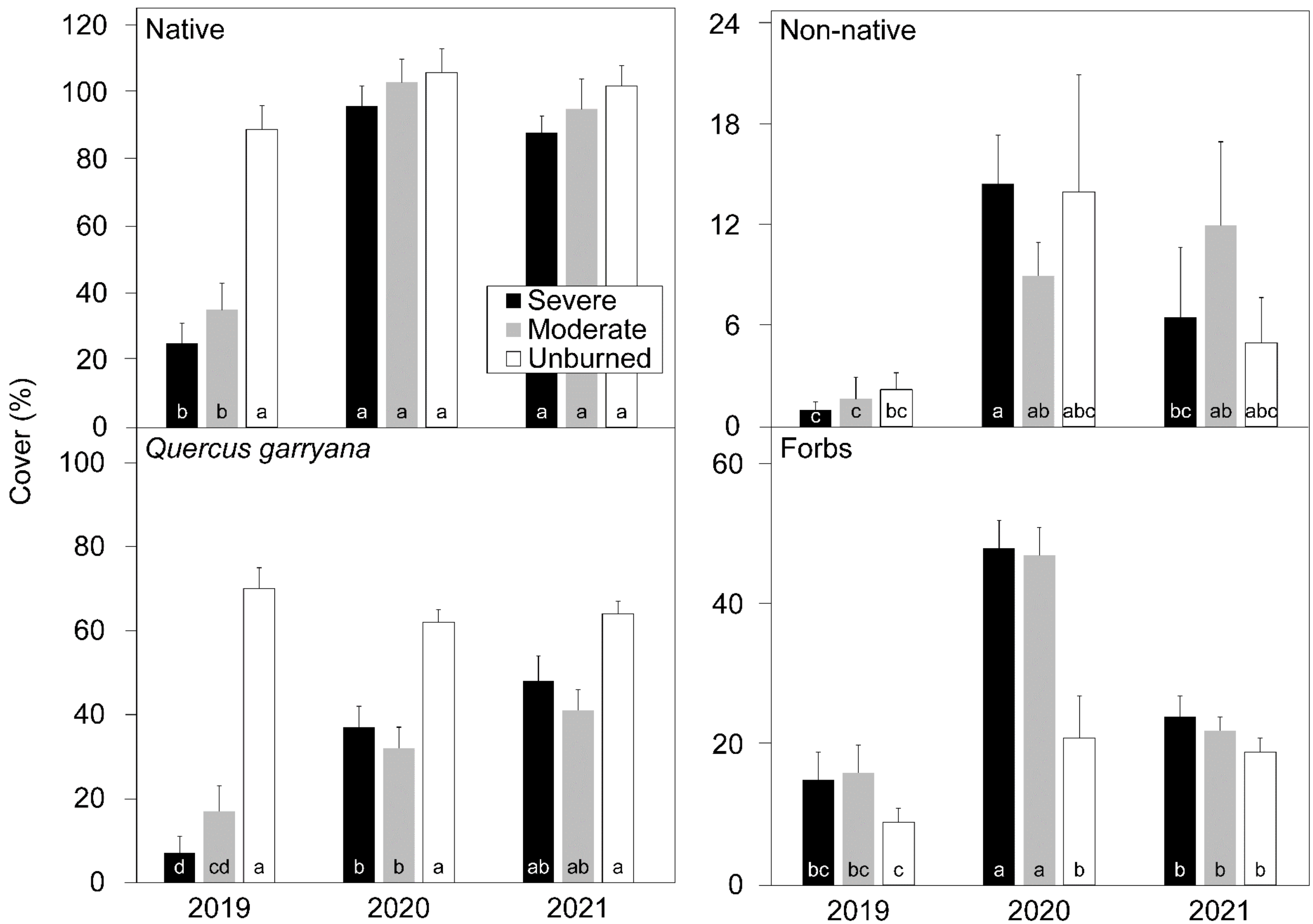
Native
Non-native
Quercus garryana
Forbs
Cover (%)
Severe
Moderate
Unburned
2019
2020
2021
0
20
40
60
80
100
120
6
12
18
24
b b a a a a a a a
c c bc a ab abc bc ab abc
d cd a b b a ab ab a
bc bc c a a b b b b

Figure 2

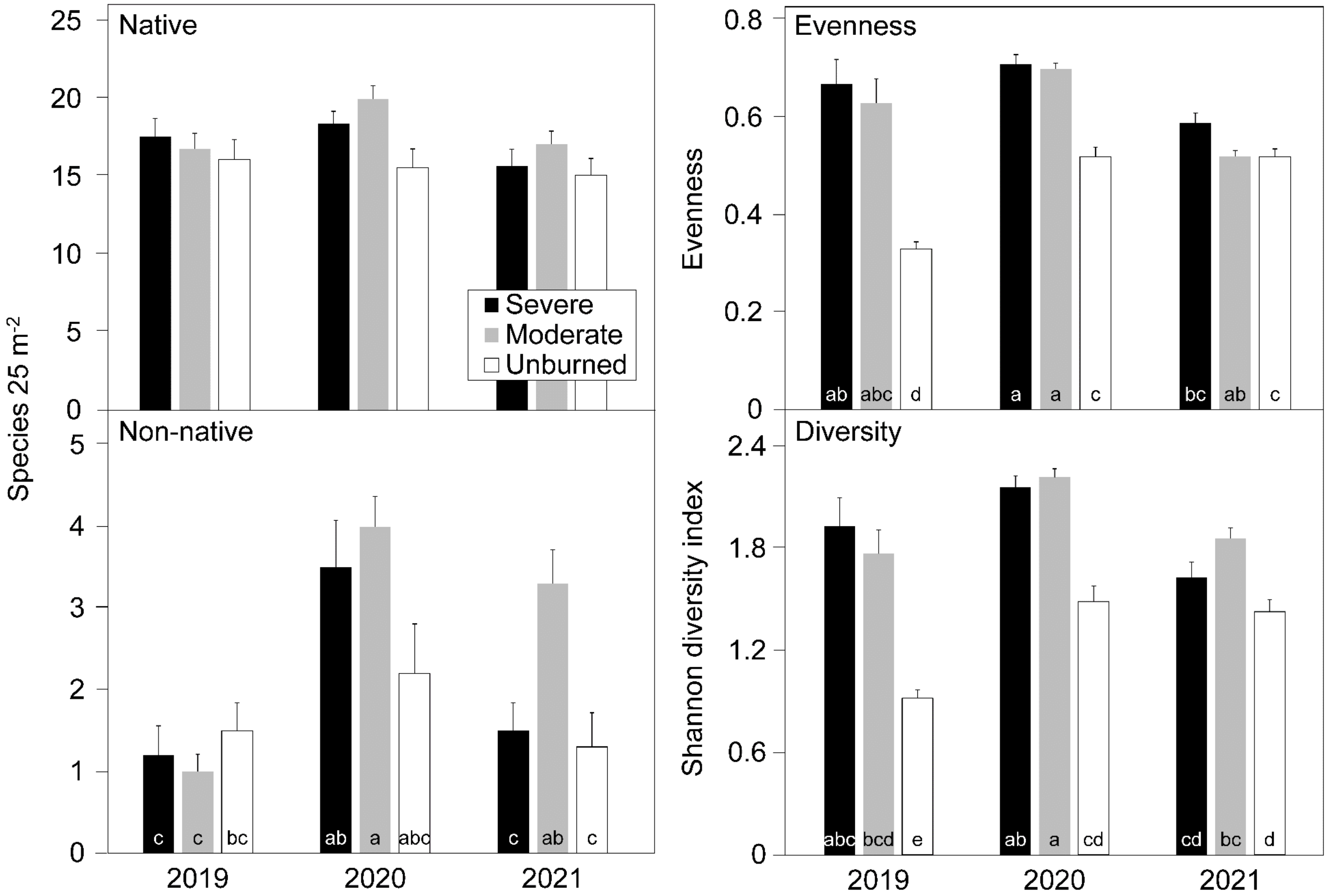
Native
Non-native
Species 25 m-2
Severe
Moderate
Unburned
Evenness
Diversity
Shannon diversity index
ab
abc
d
a
a
c
bc
ab
c
c
c
bc
ab
a
abc
c
ab
c
abc
bcd
e
ab
a
cd
cd
bc
d
2019
2020
2021

Figure 3

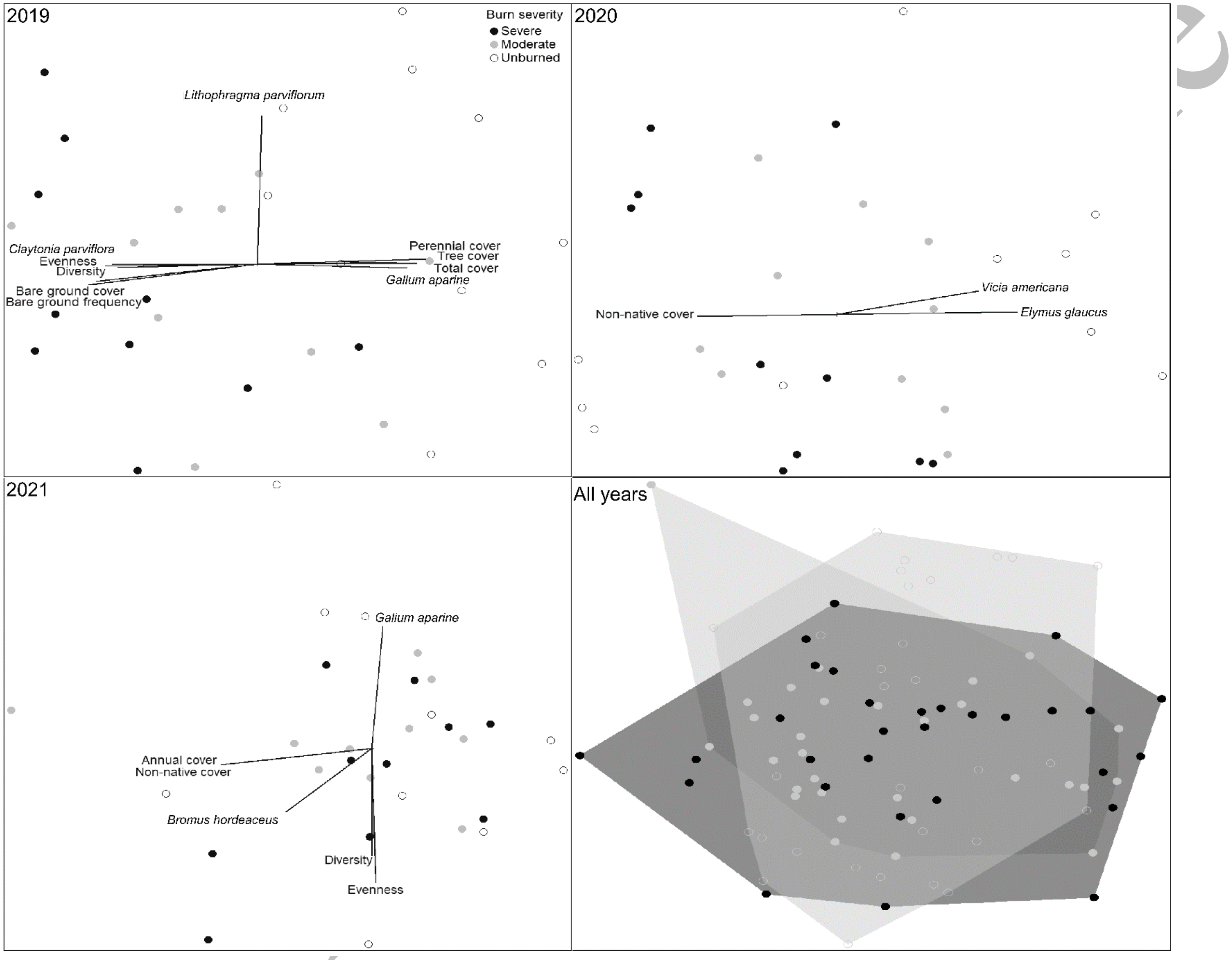
2019
Burn severity
Severe
Moderate
Unburned
Lithophragma parviflorum
Claytonia parviflora
Evenness
Diversity
Bare ground cover
Bare ground frequency
Perennial cover
Tree cover
Total cover
Galium aparine
2020
Vicia americana
Non-native cover
Elymus glaucus
2021
Galium aparine
Annual cover
Non-native cover
Bromus hordeaceus
Diversity
Evenness
All years

Figure 4

Supplemental Material

Abella, S. R., and C. D. Schelz. Resilient plant communities and increasing native forbs after wildfire in a southwestern Oregon oak shrubland. Northwest Science.

TABLE S1. Univariate plant community and substrate variables analyzed in oak shrublands within the Klamathon Fire, Cascade-Siskiyou National Monument, Oregon.

			Cover (%)											Species richness (25 m^2)							Diversity	
Burn status	Year	Plot	Native	NonNative	Oak	Forbs	Grasses	Shrubs	Trees	Annuals	Bare	Litter	Wood	Native	NonNative	Forbs	Grasses	Shrubs	Trees	Annuals	Evenness	Shannon
Moderate	2019	Bmed1	70.3	0.6	60.7	8.1	0.8	1.7	60.7	8.1	25.4	56.5	0.7	20	1	15	2	5	1	13	0.889	2.569
Moderate	2020	Bmed1	114.9	0.1	46.7	32.9	15.5	19.9	46.7	27.5	9.0	67.3	4.3	24	2	18	4	3	1	12	0.885	2.694
Moderate	2021	Bmed1	111.9	0.7	58.0	22.6	13.1	19.0	58.0	18.4	9.7	79.3	8.0	18	2	12	3	3	1	10	0.897	2.542
Moderate	2019	Bmed2	50.9	13.1	24.0	24.7	13.1	2.9	24.0	35.4	6.0	48.0	1.7	15	1	12	2	2	1	11	0.897	2.43
Moderate	2020	Bmed2	129.0	5.8	42.3	41.3	37.2	14.0	42.3	33.1	3.3	55.7	2.7	20	3	15	4	3	1	12	0.906	2.841
Moderate	2021	Bmed2	111.1	6.7	52.3	29.1	26.7	9.7	52.3	32.4	7.7	72.7	2.3	16	3	11	3	3	1	11	0.864	2.498
Moderate	2019	Bmed3	8.9	0.1	0.1	5.9	5.7	0.2	0.1	3.7	26.7	65.0	1.7	18	1	15	2	2	1	10	0.886	2.609
Moderate	2020	Bmed3	121.5	8.3	35.0	55.5	27.1	12.3	35.0	45.4	5.5	77.0	3.3	19	3	16	3	2	1	11	0.897	2.772
Moderate	2021	Bmed3	139.6	1.1	52.3	26.0	48.3	14.0	52.3	23.3	6.0	83.7	3.0	15	2	12	2	1	1	10	0.863	2.393
Moderate	2019	Bmed4	37.6	1.7	20.0	16.6	2.5	0.1	20.0	15.4	4.1	79.0	9.2	22	2	19	3	1	1	15	0.921	2.928
Moderate	2020	Bmed4	83.7	15.1	21.5	55.0	15.2	7.0	21.5	66.7	6.7	23.0	1.0	17	4	15	4	1	1	13	0.881	2.593
Moderate	2021	Bmed4	47.1	46.0	27.7	7.8	48.7	9.0	27.7	52.1	8.3	87.0	4.3	13	3	8	5	1	1	8	0.872	2.167
Moderate	2019	Bmed5	5.4	0.1	0.1	5.3	3.0	0.1	0.1	3.9	50.7	34.0	8.3	14	1	12	2	1	1	9	0.855	2.255
Moderate	2020	Bmed5	64.9	12.9	0.3	43.3	33.7	0.1	0.3	29.5	5.5	18.3	6.3	16	4	14	3	1	1	11	0.867	2.506
Moderate	2021	Bmed5	76.3	17.6	8.7	20.9	62.7	1.7	8.7	32.3	9.3	80.3	3.7	18	4	15	3	2	1	13	0.845	2.572
Moderate	2019	Bmed6	12.8	0.7	0.1	9.8	1.6	3.5	0.1	7.6	74.0	19.4	3.7	16	2	15	2	1	1	11	0.871	2.519
Moderate	2020	Bmed6	82.2	21.6	34.1	33.7	28.2	8.1	34.1	39.5	9.7	47.3	3.1	21	4	20	4	1	1	14	0.93	2.992
Moderate	2021	Bmed6	78.5	29.8	46.0	21.8	35.5	5.0	46.0	42.6	10.0	80.7	2.3	18	5	17	3	1	1	13	0.888	2.703
Moderate	2019	Bmed7	68.3	0.1	32.7	31.0	0.2	5.0	32.7	28.5	22.3	25.7	3.2	17	1	15	2	2	1	10	0.901	2.603
Moderate	2020	Bmed7	132.7	3.4	49.0	59.5	14.3	13.3	49.0	40.0	0.7	51.7	3.7	19	5	16	4	3	1	14	0.932	2.837
Moderate	2021	Bmed7	88.7	2.7	37.7	21.5	11.9	20.3	37.7	16.3	8.7	64.7	3.7	20	2	14	2	4	1	10	0.921	2.76
Moderate	2019	Bmed8	50.3	0.0	6.9	41.6	1.5	0.4	6.9	38.1	67.0	10.3	0.0	13	0	10	2	1	1	8	0.879	2.255
Moderate	2020	Bmed8	100.6	3.3	18.0	68.6	14.7	2.7	18.0	64.4	0.0	27.3	2.0	23	5	20	4	2	1	18	0.88	2.798
Moderate	2021	Bmed8	83.8	7.1	35.0	29.3	25.7	0.9	35.0	34.3	24.7	48.3	1.0	16	6	14	5	1	1	14	0.883	2.689
Moderate	2019	Bmed9	18.9	0.1	5.7	8.8	0.3	4.4	5.7	5.7	68.3	11.7	0.1	20	1	16	4	2	1	12	0.911	2.58
Moderate	2020	Bmed9	93.6	7.4	37.7	32.0	8.3	23.0	37.7	27.2	45.0	26.7	1.3	23	6	19	5	3	1	12	0.9	2.968
Moderate	2021	Bmed9	84.1	4.5	37.2	20.6	8.5	22.3	37.2	20.3	30.7	49.7	4.0	22	3	17	4	2	1	10	0.881	2.799
Moderate	2019	Bmed10	27.8	0.0	17.1	8.1	3.7	2.5	17.1	7.8	39.7	21.7	0.0	13	0	8	1	4	1	6	0.825	2.05

Moderate	2020	Bmed10	102.8	9.5	34.7	47.4	16.3	13.9	34.7	16.5	2.7	25.0	2.0	18	4	12	3	6	1	5	0.913	2.588
Moderate	2021	Bmed10	128.0	5.3	54.7	25.0	25.7	27.3	55.3	21.5	1.0	92.4	5.0	15	3	9	1	5	2	6	0.853	2.364
Severe	2019	Bsev1	8.8	0.1	0.1	8.4	0.2	0.1	0.1	5.4	73.3	15.3	1.3	21	1	16	3	2	1	12	0.915	2.693
Severe	2020	Bsev1	86.5	10.8	23.7	53.8	9.5	10.3	23.7	44.1	20.7	27.3	3.5	22	4	20	4	1	1	13	0.919	2.957
Severe	2021	Bsev1	74.5	5.0	42.6	25.3	5.7	0.0	48.6	14.9	29.0	56.3	2.3	20	2	16	4	0	2	13	0.89	2.752
Severe	2019	Bsev2	4.7	0.7	0.3	4.8	0.0	0.3	0.3	4.8	77.1	10.7	4.1	15	1	14	0	1	1	14	0.928	2.38
Severe	2020	Bsev2	93.8	0.7	38.7	28.0	8.1	21.3	38.7	26.1	32.3	49.0	2.4	22	1	14	4	4	1	11	0.897	2.641
Severe	2021	Bsev2	92.5	0.0	58.7	15.5	8.3	10.0	58.7	14.6	21.0	63.3	0.3	13	0	8	2	2	1	7	0.888	2.279
Severe	2019	Bsev3	18.9	0.0	0.5	18.3	0.7	0.1	0.5	13.1	56.5	16.8	0.7	24	0	21	2	1	1	17	0.887	2.819
Severe	2020	Bsev3	99.3	9.5	33.2	46.1	20.3	9.1	33.2	24.5	23.0	31.3	0.3	19	5	18	3	2	1	14	0.937	2.976
Severe	2021	Bsev3	102.7	8.0	48.0	32.1	23.3	7.3	48.0	26.8	21.7	69.3	0.0	19	1	13	4	2	1	10	0.915	2.742
Severe	2019	Bsev4	6.5	0.0	0.2	5.3	0.0	0.9	0.2	2.1	88.7	0.0	2.8	14	0	12	0	1	1	9	0.84	2.153
Severe	2020	Bsev4	109.5	17.4	43.3	54.1	15.6	13.9	43.3	48.9	43.3	24.7	1.0	18	4	14	4	3	1	12	0.907	2.76
Severe	2021	Bsev4	94.7	1.0	64.7	15.9	3.0	12.2	64.7	14.3	22.3	67.3	1.0	15	1	11	2	2	1	11	0.915	2.478
Severe	2019	Bsev5	50.6	0.1	34.7	11.5	0.3	4.1	34.7	9.6	48.3	1.9	1.9	20	2	16	4	1	1	13	0.86	2.618
Severe	2020	Bsev5	103.9	14.5	55.7	35.0	17.7	10.0	55.7	27.9	22.3	35.3	2.3	20	6	17	7	1	1	12	0.899	2.777
Severe	2021	Bsev5	81.1	2.0	54.0	8.7	10.3	10.0	54.0	9.1	16.3	68.7	1.3	16	2	11	5	1	1	10	0.888	2.517
Severe	2019	Bsev6	31.2	0.1	22.3	6.8	0.1	2.1	22.3	5.4	62.0	1.3	1.7	13	1	10	1	2	1	9	0.862	2.211
Severe	2020	Bsev6	103.1	23.4	50.3	54.8	10.1	11.3	50.3	50.3	14.0	33.7	0.7	17	2	12	3	3	1	11	0.893	2.581
Severe	2021	Bsev6	87.7	2.7	55.0	15.7	7.3	12.3	55.0	18.3	14.7	72.7	6.3	12	1	8	2	2	1	9	0.875	2.245
Severe	2019	Bsev7	14.2	3.7	0.3	10.5	5.1	2.0	0.3	10.0	89.1	2.1	0.3	17	1	12	2	3	1	10	0.885	2.558
Severe	2020	Bsev7	119.3	9.3	38.7	50.9	22.7	16.3	38.7	33.9	21.3	33.7	0.0	14	2	11	2	2	1	10	0.934	2.589
Severe	2021	Bsev7	99.8	0.0	46.0	45.8	0.0	8.0	46.0	8.5	16.0	77.3	0.0	12	0	8	0	2	1	5	0.904	2.169
Severe	2019	Bsev8	40.8	0.0	2.9	37.7	1.7	0.2	2.9	36.1	51.0	8.8	0.1	15	0	13	1	1	1	11	0.825	2.05
Severe	2020	Bsev8	92.3	11.0	38.3	52.0	0.0	13.0	38.3	46.3	5.3	50.0	1.0	16	1	13	0	3	1	9	0.923	2.559
Severe	2021	Bsev8	103.5	0.5	58.0	27.3	0.0	18.7	58.0	25.6	22.6	68.7	1.0	12	2	9	0	3	1	7	0.892	2.288
Severe	2019	Bsev9	52.7	0.9	8.7	30.8	2.7	11.5	8.7	29.5	61.0	6.4	0.3	21	3	14	6	3	1	11	0.872	2.735
Severe	2020	Bsev9	107.3	13.9	45.3	66.7	8.1	1.0	45.3	60.7	6.7	48.7	1.3	19	5	16	6	1	1	15	0.848	2.583
Severe	2021	Bsev9	95.0	2.4	54.0	29.0	12.7	1.7	54.0	18.7	16.7	68.7	2.7	20	3	17	3	1	1	13	0.919	2.753
Severe	2019	Bsev10	25.9	4.1	0.3	13.9	4.1	11.7	0.3	14.3	92.7	0.7	0.2	16	3	13	4	1	1	11	0.902	2.608
Severe	2020	Bsev10	46.1	34.6	0.3	38.2	29.4	12.7	0.3	62.6	23.7	18.0	3.3	17	5	15	4	2	1	13	0.889	2.705
Severe	2021	Bsev10	51.0	43.3	0.3	27.7	54.0	12.3	0.3	64.7	26.3	63.0	0.7	18	3	13	5	1	1	11	0.906	2.669
Unburned	2019	UNB1	90.7	9.5	79.5	8.5	9.5	2.7	79.5	12.7	4.0	80.0	0.7	11	1	9	1	1	1	8	0.804	1.928
Unburned	2020	UNB1	100.3	49.0	78.7	18.6	48.0	4.0	78.7	55.7	0.0	73.0	1.7	10	2	9	1	1	1	7	0.855	2.125
Unburned	2021	UNB1	94.8	0.0	66.7	22.5	0.7	2.7	66.7	22.5	0.3	79.7	3.4	13	0	9	1	1	1	9	0.719	1.786
Unburned	2019	UNB2	123.0	0.0	84.7	5.5	0.0	32.8	84.7	2.1	0.0	99.3	1.3	11	0	8	0	2	1	5	0.809	1.864
Unburned	2020	UNB2	97.7	0.0	55.7	8.1	0.7	33.3	55.7	0.7	0.0	80.0	4.3	13	0	9	1	2	1	3	0.854	2.192

Unburned	2021	UNB2	72.9	0.0	43.7	11.6	0.5	17.1	43.7	11.6	0.0	89.3	10.3	13	0	9	1	2	1	9	0.848	2.107
Unburned	2019	UNB3	119.8	0.0	89.3	5.7	22.6	0.5	91.0	3.2	0.0	0.0	0.0	17	0	13	1	1	2	8	0.898	2.49
Unburned	2020	UNB3	137.5	0.0	74.7	7.1	45.0	7.9	77.6	4.2	0.3	86.7	6.3	18	0	13	1	2	2	7	0.873	2.523
Unburned	2021	UNB3	139.7	0.0	67.7	10.9	48.7	5.3	74.9	10.9	0.0	93.3	6.5	16	0	11	1	2	2	11	0.883	2.448
Unburned	2019	UNB4	77.0	0.6	60.0	10.5	5.3	0.1	61.7	4.2	0.0	89.3	7.1	21	2	17	3	1	2	12	0.88	2.719
Unburned	2020	UNB4	112.1	7.8	59.0	22.5	34.9	1.7	60.9	13.4	0.3	72.3	5.5	22	4	17	6	1	2	10	0.905	2.947
Unburned	2021	UNB4	114.4	3.7	65.0	22.4	28.3	2.3	65.0	21.4	0.3	74.3	0.3	18	2	14	4	1	1	14	0.92	2.755
Unburned	2019	UNB5	69.8	0.5	50.1	6.3	5.9	6.6	51.5	5.6	0.0	96.7	0.8	18	1	12	3	2	2	8	0.881	2.595
Unburned	2020	UNB5	105.3	0.0	51.0	10.9	24.0	17.0	53.4	8.5	0.0	87.3	8.3	16	0	10	3	1	2	6	0.872	2.237
Unburned	2021	UNB5	113.2	0.1	61.3	14.7	21.5	15.7	61.3	14.7	1.7	87.0	6.3	12	1	9	2	1	1	9	0.863	2.213
Unburned	2019	UNB6	75.9	0.1	62.0	4.3	0.3	9.4	62.0	4.1	1.3	92.0	2.9	14	1	10	3	1	1	10	0.876	2.372
Unburned	2020	UNB6	107.2	0.3	58.7	26.2	6.3	16.3	58.7	25.4	1.0	82.7	6.2	11	2	8	3	1	1	8	0.862	2.21
Unburned	2021	UNB6	95.2	0.0	68.0	13.2	4.0	10.0	68.0	13.0	6.0	83.7	9.0	14	0	11	1	1	1	10	0.888	2.344
Unburned	2019	UNB7	64.6	0.8	50.0	5.9	3.7	0.1	56.0	5.9	2.0	96.0	0.1	19	2	15	5	1	2	14	0.942	2.869
Unburned	2020	UNB7	82.5	2.5	47.3	20.9	10.1	1.0	53.0	18.2	4.7	86.0	5.7	18	2	14	3	1	2	11	0.894	2.632
Unburned	2021	UNB7	87.5	1.7	47.7	16.0	8.5	17.0	47.7	17.2	11.0	80.7	6.9	19	2	13	5	2	1	13	0.885	2.653
Unburned	2019	UNB8	96.2	5.4	85.2	10.5	2.2	3.7	85.3	10.5	0.3	90.7	5.0	20	3	15	4	2	2	14	0.896	2.728
Unburned	2020	UNB8	85.7	28.5	68.0	9.9	30.6	5.7	68.0	31.8	0.0	71.0	9.3	17	5	12	7	2	1	12	0.886	2.697
Unburned	2021	UNB8	105.7	15.5	76.9	23.8	15.5	5.0	76.9	31.2	1.0	73.3	11.2	18	4	15	4	2	1	17	0.905	2.754
Unburned	2019	UNB9	63.3	4.9	53.0	9.5	4.5	1.1	53.0	13.9	1.3	79.9	10.8	11	3	10	2	1	1	11	0.855	2.255
Unburned	2020	UNB9	88.3	51.5	74.7	9.8	51.3	4.0	74.7	59.7	0.3	86.0	5.0	13	5	12	4	1	1	13	0.861	2.439
Unburned	2021	UNB9	96.4	24.7	74.0	19.4	24.7	3.0	74.0	44.1	0.0	95.7	3.7	9	2	7	2	1	1	9	0.906	2.173
Unburned	2019	UNB10	105.5	0.5	81.3	24.0	0.9	0.1	81.3	23.5	0.3	66.7	6.0	19	2	16	3	1	2	15	0.876	2.625
Unburned	2020	UNB10	143.7	2.7	56.3	71.6	15.1	0.0	59.7	69.4	0.3	86.3	2.7	18	2	12	6	0	2	12	0.892	2.626
Unburned	2021	UNB10	104.7	4.3	65.3	30.5	11.5	0.7	66.3	35.2	0.0	97.0	3.7	19	2	13	5	1	2	16	0.904	2.752

TABLE S2. Cover data sub-divided for all nativity-longevity-growth form plant combinations in oak shrublands within the Klamathon Fire, Cascade-Siskiyou National Monument, Oregon.

			Native annuals		Native perennials				Non-native annuals		Non-native perennials	
Burn status	Year	Plot	Forbs	Grasses	Forbs	Grasses	Shrubs	Trees	Forbs	Grasses	Forbs	Grasses
Moderate	2019	Bmed1	7.5	0.0	0.4	0.0	1.7	60.7	0.0	0.6	0.0	0.0
Moderate	2020	Bmed1	27.3	0.0	5.5	15.5	19.9	46.7	0.1	0.1	0.0	0.0
Moderate	2021	Bmed1	18.3	0.0	4.3	12.3	19.0	58.0	0.0	0.1	0.0	0.7
Moderate	2019	Bmed2	22.3	0.1	1.7	0.0	2.9	24.0	0.0	13.1	0.0	0.0
Moderate	2020	Bmed2	27.3	0.0	12.6	32.7	14.0	42.3	1.3	4.5	0.0	0.0
Moderate	2021	Bmed2	25.7	0.0	1.7	21.7	9.7	52.3	1.7	5.0	0.0	0.0
Moderate	2019	Bmed3	3.6	0.0	2.2	2.8	0.2	0.1	0.1	0.0	0.0	0.0
Moderate	2020	Bmed3	40.4	0.0	6.8	27.0	12.3	35.0	8.3	0.1	0.0	0.0
Moderate	2021	Bmed3	22.3	0.0	2.7	48.3	14.0	52.3	1.1	0.0	0.0	0.0
Moderate	2019	Bmed4	13.6	0.1	2.2	1.5	0.1	20.0	0.8	0.9	0.0	0.0
Moderate	2020	Bmed4	51.6	0.0	1.9	1.7	7.0	21.5	1.5	13.5	0.0	0.0
Moderate	2021	Bmed4	6.1	0.0	1.0	3.3	9.0	27.7	0.7	45.3	0.0	0.0
Moderate	2019	Bmed5	3.8	0.0	1.5	0.0	0.1	0.1	0.0	0.1	0.0	0.0
Moderate	2020	Bmed5	16.7	0.0	18.8	29.0	0.1	0.3	7.9	4.7	0.0	0.0
Moderate	2021	Bmed5	14.7	0.0	5.2	46.0	1.7	8.7	0.9	16.7	0.0	0.0
Moderate	2019	Bmed6	6.9	0.0	2.3	0.0	3.5	0.1	0.5	0.1	0.0	0.0
Moderate	2020	Bmed6	17.9	0.0	6.4	15.7	8.1	34.1	9.1	12.5	0.0	0.0
Moderate	2021	Bmed6	12.9	0.0	2.3	12.3	5.0	46.0	6.5	23.2	0.1	0.0
Moderate	2019	Bmed7	28.4	0.0	2.1	0.1	5.0	32.7	0.1	0.0	0.0	0.0
Moderate	2020	Bmed7	36.6	0.0	20.5	13.3	13.3	49.0	2.5	0.9	0.0	0.0
Moderate	2021	Bmed7	15.7	0.0	3.8	11.2	20.3	37.7	0.0	0.7	2.0	0.0
Moderate	2019	Bmed8	38.1	0.0	3.5	1.4	0.4	6.9	0.0	0.0	0.0	0.0
Moderate	2020	Bmed8	62.7	0.0	3.5	13.7	2.7	18.0	2.3	1.0	0.0	0.0
Moderate	2021	Bmed8	27.3	0.0	0.7	20.0	0.9	35.0	1.3	5.7	0.1	0.0
Moderate	2019	Bmed9	5.6	0.0	3.0	0.2	4.4	5.7	0.1	0.0	0.0	0.0
Moderate	2020	Bmed9	20.1	0.0	8.8	4.0	23.0	37.7	2.8	4.3	0.3	0.0
Moderate	2021	Bmed9	16.1	0.0	4.2	4.3	22.3	37.2	0.0	4.2	0.3	0.0
Moderate	2019	Bmed10	7.8	0.0	0.3	0.0	2.5	17.1	0.0	0.0	0.0	0.0
Moderate	2020	Bmed10	11.7	0.0	26.3	16.3	13.9	34.7	4.8	0.0	4.7	0.0
Moderate	2021	Bmed10	18.8	0.0	0.9	25.7	27.3	55.3	2.7	0.0	2.7	0.0
Severe	2019	Bsev1	5.3	0.0	3.1	0.1	0.1	0.1	0.0	0.1	0.0	0.0
Severe	2020	Bsev1	33.3	0.0	17.8	1.4	10.3	23.7	2.7	8.1	0.0	0.0
Severe	2021	Bsev1	9.9	0.0	15.3	0.7	0.0	48.6	0.0	5.0	0.0	0.0
Severe	2019	Bsev2	4.1	0.0	0.0	0.0	0.3	0.3	0.7	0.0	0.0	0.0
Severe	2020	Bsev2	25.5	0.0	1.9	6.5	21.3	38.7	0.7	0.0	0.0	0.0
Severe	2021	Bsev2	14.6	0.0	0.9	8.3	10.0	58.7	0.0	0.0	0.0	0.0
Severe	2019	Bsev3	13.1	0.0	5.1	0.1	0.1	0.5	0.0	0.0	0.0	0.0
Severe	2020	Bsev3	14.9	0.0	25.7	16.3	9.1	33.2	5.5	4.0	0.0	0.0
Severe	2021	Bsev3	18.8	0.0	13.3	15.3	7.3	48.0	0.0	8.0	0.0	0.0
Severe	2019	Bsev4	2.1	0.0	3.2	0.0	0.9	0.2	0.0	0.0	0.0	0.0
Severe	2020	Bsev4	31.5	0.0	14.3	6.4	13.9	43.3	8.2	9.2	0.0	0.0
Severe	2021	Bsev4	13.3	0.0	2.6	2.0	12.2	64.7	0.0	1.0	0.0	0.0
Severe	2019	Bsev5	9.5	0.0	2.1	0.2	4.1	34.7	0.0	0.1	0.0	0.0
Severe	2020	Bsev5	13.4	0.0	16.9	7.9	10.0	55.7	4.7	9.8	0.0	0.0
Severe	2021	Bsev5	7.1	0.0	1.6	8.3	10.0	54.0	0.0	2.0	0.0	0.0

Severe	2019	Bsev6	5.3	0.0	1.5	0.0	2.1	22.3	0.0	0.1	0.0	0.0
Severe	2020	Bsev6	26.9	0.0	13.5	1.0	11.3	50.3	14.3	9.1	0.0	0.0
Severe	2021	Bsev6	15.7	0.0	0.0	4.7	12.3	55.0	0.0	2.7	0.0	0.0
Severe	2019	Bsev7	6.3	0.0	4.1	1.5	2.0	0.3	0.0	3.7	0.0	0.0
Severe	2020	Bsev7	24.6	0.0	17.3	22.3	16.3	38.7	9.0	0.3	0.0	0.0
Severe	2021	Bsev7	8.5	0.0	37.3	0.0	8.0	46.0	0.0	0.0	0.0	0.0
Severe	2019	Bsev8	36.1	0.0	0.9	0.0	0.2	2.9	0.0	0.0	0.0	0.0
Severe	2020	Bsev8	35.3	0.0	5.7	0.0	13.0	38.3	11.0	0.0	0.0	0.0
Severe	2021	Bsev8	25.5	0.0	1.3	0.0	18.7	58.0	0.1	0.0	0.3	0.0
Severe	2019	Bsev9	28.6	0.0	1.8	2.1	11.5	8.7	0.4	0.5	0.0	0.0
Severe	2020	Bsev9	50.9	0.1	2.8	7.2	1.0	45.3	13.0	0.9	0.0	0.0
Severe	2021	Bsev9	16.9	0.0	11.4	11.0	1.7	54.0	0.0	1.7	0.7	0.0
Severe	2019	Bsev10	10.2	0.0	3.3	0.4	11.7	0.3	0.3	3.7	0.0	0.0
Severe	2020	Bsev10	28.3	0.0	4.3	0.3	12.7	0.3	5.5	29.1	0.0	0.0
Severe	2021	Bsev10	21.3	0.0	6.3	10.7	12.3	0.3	0.0	43.3	0.0	0.0
Unburned	2019	UNB1	3.2	0.0	5.3	0.0	2.7	79.5	0.0	9.5	0.0	0.0
Unburned	2020	UNB1	6.7	0.0	10.9	0.0	4.0	78.7	1.0	48.0	0.0	0.0
Unburned	2021	UNB1	22.5	0.0	0.0	0.7	2.7	66.7	0.0	0.0	0.0	0.0
Unburned	2019	UNB2	2.1	0.0	3.5	0.0	32.8	84.7	0.0	0.0	0.0	0.0
Unburned	2020	UNB2	0.7	0.0	7.4	0.7	33.3	55.7	0.0	0.0	0.0	0.0
Unburned	2021	UNB2	11.6	0.0	0.0	0.5	17.1	43.7	0.0	0.0	0.0	0.0
Unburned	2019	UNB3	3.2	0.0	2.3	22.6	0.5	91.0	0.0	0.0	0.0	0.0
Unburned	2020	UNB3	4.2	0.0	2.9	45.0	7.9	77.6	0.0	0.0	0.0	0.0
Unburned	2021	UNB3	10.9	0.0	0.0	48.7	5.3	74.9	0.0	0.0	0.0	0.0
Unburned	2019	UNB4	3.6	0.0	6.9	4.8	0.1	61.7	0.1	0.5	0.0	0.0
Unburned	2020	UNB4	5.6	0.0	16.8	27.1	1.7	60.9	0.1	7.7	0.0	0.0
Unburned	2021	UNB4	17.7	0.0	4.7	24.7	2.3	65.0	0.0	3.7	0.0	0.0
Unburned	2019	UNB5	5.1	0.0	1.2	5.4	6.6	51.5	0.0	0.5	0.0	0.0
Unburned	2020	UNB5	8.5	0.0	2.5	24.0	17.0	53.4	0.0	0.0	0.0	0.0
Unburned	2021	UNB5	14.7	0.0	0.0	21.5	15.7	61.3	0.1	0.0	0.0	0.0
Unburned	2019	UNB6	4.0	0.0	0.3	0.2	9.4	62.0	0.0	0.1	0.0	0.0
Unburned	2020	UNB6	25.1	0.0	1.1	6.0	16.3	58.7	0.0	0.3	0.0	0.0
Unburned	2021	UNB6	13.0	0.0	0.2	4.0	10.0	68.0	0.0	0.0	0.0	0.0
Unburned	2019	UNB7	5.1	0.0	0.7	2.7	0.1	56.0	0.0	0.8	0.0	0.0
Unburned	2020	UNB7	15.7	0.0	5.1	7.7	1.0	53.0	0.1	2.4	0.0	0.0

Unburned	2021	UNB7	15.5	0.0	0.5	6.8	17.0	47.7	0.0	1.7	0.0	0.0
Unburned	2019	UNB8	5.1	0.0	1.7	0.5	3.7	85.3	3.7	1.7	0.0	0.0
Unburned	2020	UNB8	6.7	0.0	0.9	4.5	5.7	68.0	2.3	22.8	0.0	3.3
Unburned	2021	UNB8	18.5	0.0	5.3	0.0	5.0	76.9	0.0	12.7	0.0	2.7
Unburned	2019	UNB9	9.1	0.0	0.1	0.0	1.1	53.0	0.3	4.5	0.0	0.0
Unburned	2020	UNB9	8.2	0.0	1.4	0.0	4.0	74.7	0.2	51.3	0.0	0.0
Unburned	2021	UNB9	19.4	0.0	0.0	0.0	3.0	74.0	0.0	24.7	0.0	0.0
Unburned	2019	UNB10	22.9	0.1	1.1	0.0	0.1	81.3	0.1	0.5	0.0	0.0
Unburned	2020	UNB10	66.7	0.0	4.9	12.4	0.0	59.7	0.0	2.7	0.0	0.0
Unburned	2021	UNB10	30.5	0.3	0.0	6.9	0.7	66.3	0.0	4.3	0.0	0.0

TABLE S3. Statistics for ordinations and multi-response permutation procedures (MRPP) examining variation in plant community composition across burn severities within years (2019–2021 spanning 1–3 years post-fire) and for all years combined after the 2018 Klamathon Fire, Cascade-Siskiyou National Monument, Oregon. Statistics correspond with the ordinations shown in Figure 4 of the paper. For MRPP, different sets of letters show Bonferroni-corrected pairwise comparisons of community composition across burn severities within columns (years). In the all years column, the MRPP is a blocked MRPP incorporating repeated measures on plots across years. The *A*-statistic is the chance-corrected within-group agreement. *A* is maximized when all items are identical within groups, 0 when heterogeneity within groups equals expectation by chance, and is negative when there is less agreement within groups than expected by chance.

	2019	2020	2021	All years
Ordination statistics				
	Stress			
Axis 1	53	51	42	49
Axis 2	24	24	23	28
Axis 3	16	15	15	22
	Cumulative r^2			
Axis 1	0.39	0.36	0.41	0.29
Axis 2	0.60	0.61	0.71	0.54
Axis 3	0.72	0.80	0.84	0.70
Permutation procedures				
	Statistics			
T-statistic	-5.61	-4.14	-1.69	-10.88
A-statistic	0.055	0.042	0.014	0.025
P	< 0.001	< 0.001	0.056	< 0.001
	Multiple comparisons			
Severe	b	j	m	z
Moderate	b	j	m	y
Unburned	a	k	m	x

TABLE S4. Comparing heterogeneity in plant community variables among burn severities after the 2018 Klamathon Fire, CascadeSiskiyou National Monument, Oregon. Within years for each variable, letters compare coefficients of variation among burn severities using Bonferroni-corrected Fligner-Killeen tests ($P < 0.017$ in bold).

	Cover				Species richness		Diversity	
	Native	Non-native	Forbs	*Quercus*	Native	Non-native	Evenness	Shannon
2019	Coefficient of variation [lower, upper 95% confidence interval]							
Severe	**70 [44,99]** ^{a}	161 [72,230]	75 [58,114]	**171 [69,249]** ^{a}	21 [16,28]	94 [47,135]	25 [18,37]	28 [21,40]
Moderate	**69 [41,96]** ^{a}	246 [206,402]	78 [58,115]	**114 [55,166]** ^{a}	19 [15,26]	66 [19,104]	25 [10,41]	25 [11,44]
Unburned	**25 [20,35]** ^{b}	145 [60,209]	63 [48,101]	**23 [19,31]** ^{b}	25 [19,36]	72 [29,108]	14 [9,21]	16 [11,23]
2020								
Severe	21 [8,35]	**63 [37,101]** ^{k}	**24 [16,35]** ^{jk}	42 [8,71]	14 [10,20]	53 [31,79]	9 [7,12]	**10 [8,16]** ^{jk}
Moderate	22 [15,31]	**73 [44,107]** ^{jk}	**27 [20,37]** ^{k}	46 [14,77]	14 [11,19]	29 [19,42]	5 [3,8]	**7 [5,9]** ^{k}
Unburned	19 [15,29]	**147 [40,208]** ^{j}	**93 [73,152]** ^{j}	17 [14,24]	24 [17,34]	88 [25,130]	14 [11,19]	**19 [16,26]** ^{j}
2021								
Severe	18 [9,30]	**203 [159,339]** ^{xy}	44 [29,64]	37 [4,67]	21 [18,29]	72 [29,108]	12 [8,19]	18 [15,26]
Moderate	29 [19,42]	**122 [77,180]** ^{y}	27 [9,45]	37 [16,57]	15 [11,23]	41 [31,61]	6 [5,9]	10 [7,15]
Unburned	18 [12,28]	**168 [88,244]** ^{x}	34 [26,47]	17 [10,27]	23 [16,32]	102 [32,152]	10 [8,15]	15 [12,22]

TABLE S5. Comparing multivariate dispersion in plant community composition among burn severities after the 2018 Klamathon Fire, Cascade-Siskiyou National Monument, Oregon. Values are within-group Sørensen similarity (%). Multivariate dispersions differed only between moderately burned and unburned plots in 2020 using Bonferroni-corrected *P* values within years ($P < 0.017$).

	2019	2020	2021
Severe	39	42	44
Moderate	43	47	46
Unburned	39	33	37

Abella SR, Schelz CD. 2024. Resilient plant communities and increasing native forbs after wildfire in a southwestern Oregon oak shrubland. Northwest Science 97(3): *in press*.


07/25/2018 10:54 AM
Azimuth and Bearing (TNP)
185° S5W

Note: This article has been peer reviewed and accepted for publication in *Northwest Science*. Copy-editing may lead to differences between this version and the final published version.


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07/25/2018 10:52 AM
N 4651761, E 535133
Alt. 1360 m
Azimuth and Bearing (TNP)
5° N5E

Figure S1. Repeat photo pairs in oak shrubland within the Klamathon Fire, Cascade-Siskiyou National Monument, Oregon. In the photo pairs, the left-side or top photos were taken in August 2018, just after the Klamathon Fire. The right-side or bottom photos were taken in autumn 2022. Photos by C.D. Schelz.

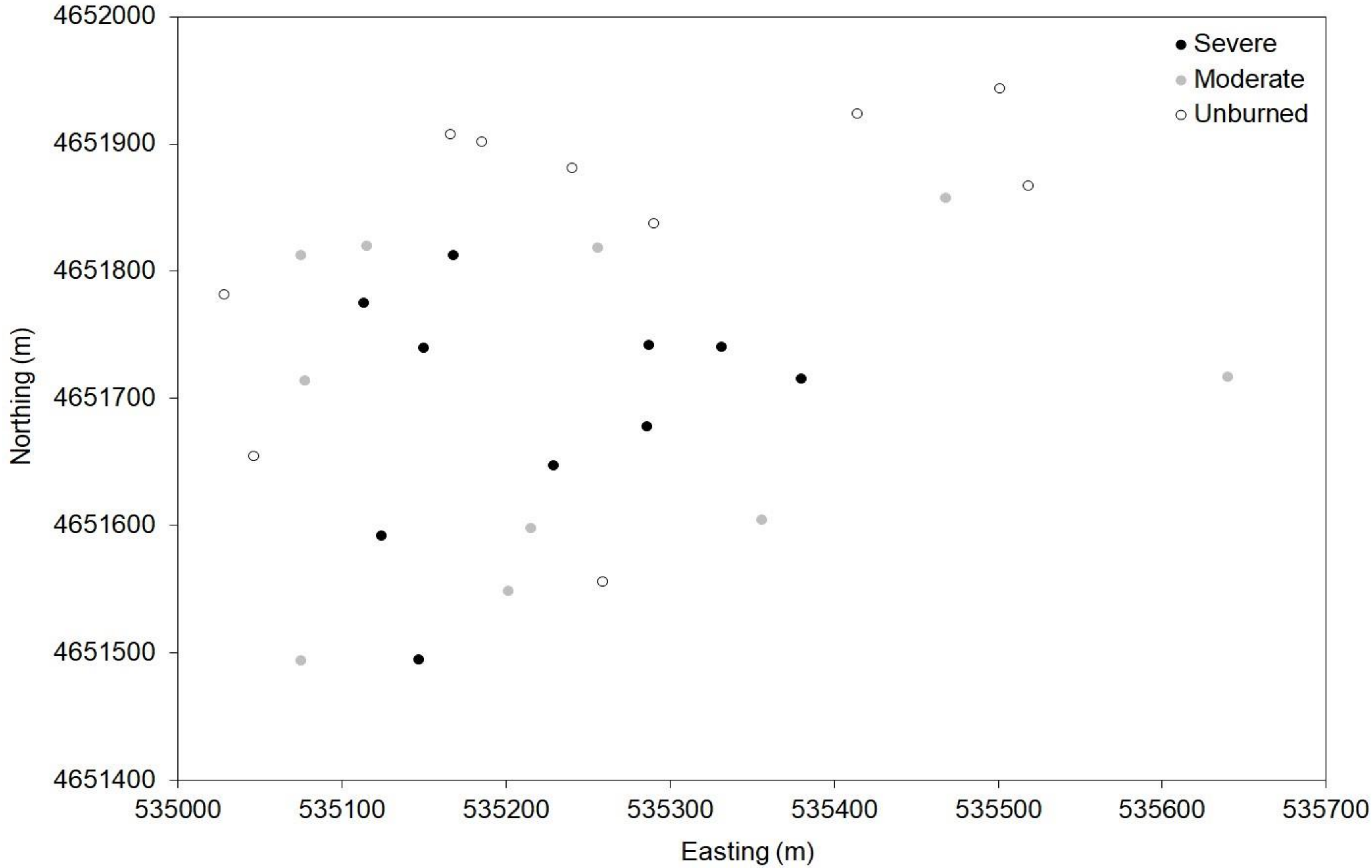
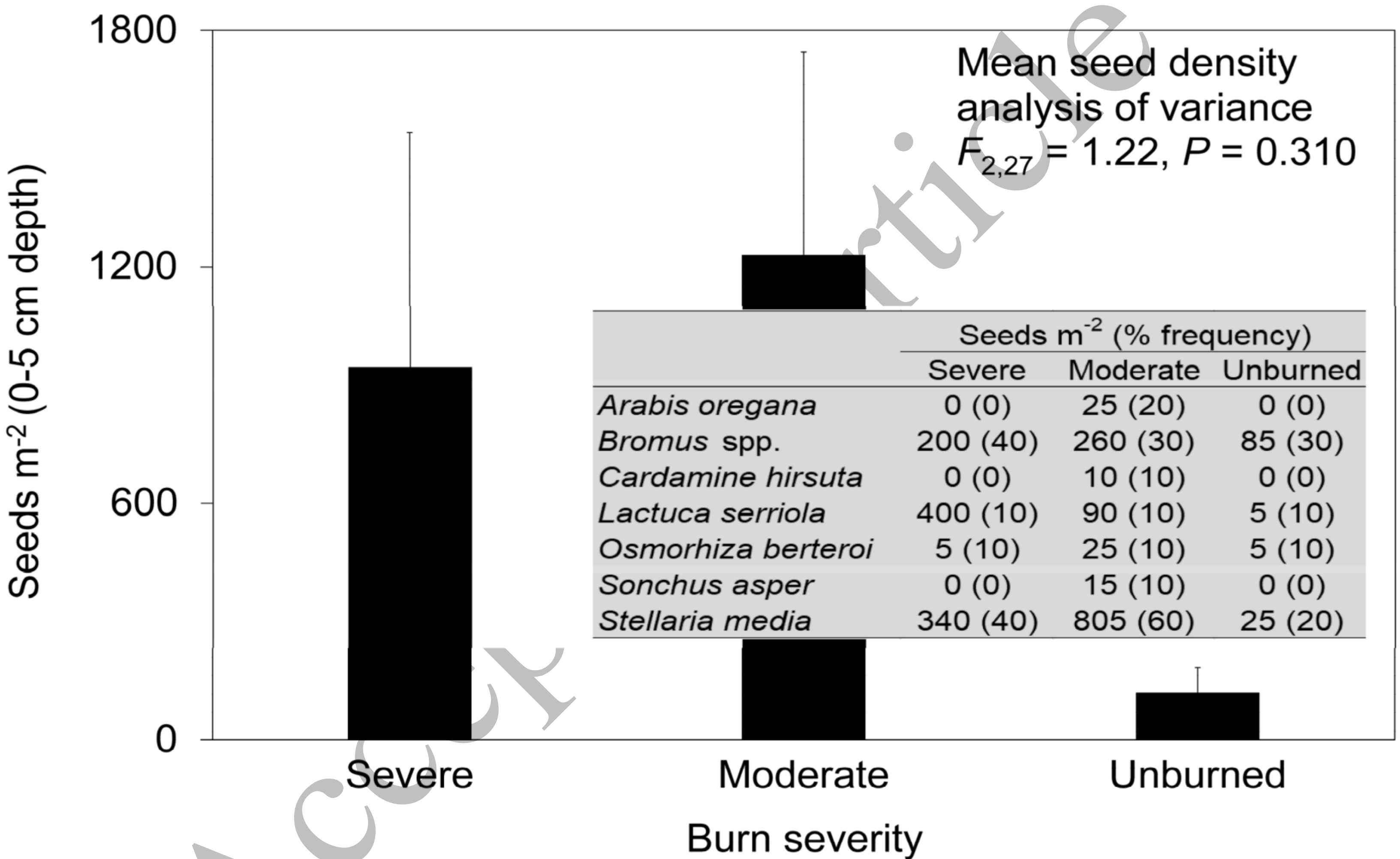


Figure S2. Spatial distribution of plots in oak shrubland within part of the Klamathon Fire, Cascade-Siskiyou National Monument, Oregon.



	Seeds m^{-2} (% frequency)		
	Severe	Moderate	Unburned
Arabis oregana	0 (0)	25 (20)	0 (0)
Bromus spp.	200 (40)	260 (30)	85 (30)
Cardamine hirsuta	0 (0)	10 (10)	0 (0)
Lactuca serriola	400 (10)	90 (10)	5 (10)
Osmorhiza berteroi	5 (10)	25 (10)	5 (10)
Sonchus asper	0 (0)	15 (10)	0 (0)
Stellaria media	340 (40)	805 (60)	25 (20)

Figure S3. Soil seed banks among burn severities in 2021, three years after the 2018 Klamathon Fire, Cascade-Siskiyou National Monument, Oregon. Error bars are + 1 SEM.

Appendix S1. Soil seed bank assessment methods, results, and interpretation for samples collected three years post-fire within the Klamathon Fire, Cascade-Siskiyou National Monument, Oregon.

Methods

In March 2021, three years post-fire, we sampled soil seed banks by collecting 15 subsamples (totaling 1000 cm^3) of the 0–5 cm mineral soil from equally spaced locations along the perimeter of each plot just outside plots. After combining subsamples into one sample $plot^{-1}$, we spread the 1000 cm^3 of soil from each plot in a layer 2 cm thick on top of 3 cm of sterilized sand placed in a plastic flat. We randomly arranged flats on a bench under natural lighting in a research greenhouse (University of Nevada, Las Vegas). Temperature in the greenhouse ranged from 20–25 °C with 50–60% relative humidity. We watered samples once or twice daily to soil field capacity. We added the potential germination stimulants Gibberellic acid (500 ppm in May, September, and November 2021 and January 2022 and 1000 ppm in August 2021) and 20% liquid smoke (diluted using de-ionized water) in January 2022 (Wright's Brand Hickory Liquid Smoke, B&G Foods, Inc., Parsippany-Troy Hills, NJ). During an 11-month emergence period from April 2021–February 2022, we monitored seedling emergence at least biweekly, identifying, counting, and removing seedlings when mature.

To analyze the seed bank data, we compared mean seed density (seeds m^{-2}, Box-Coxtransformed) among burn-severity categories using one-way analysis of variance. For the most abundant seed bank species, the non-native, perennial forb common chickweed (*Stellaria media*), sufficiently frequent to analyze statistically, we assessed if there was an association between occurrence in the seed bank and vegetation using a Fisher's exact test.

Results

There were seven taxa (six species and *Bromus*) detected in 0–5 cm mineral soil seed banks sampled in 2021, the third post-fire year (Figure S3). All seven taxa were also detected in vegetation of at least one plot. The most frequently occurring seed bank species, the non-native perennial forb common chickweed, further had a significant association between occurrence in the seed bank of a plot and in the vegetation of that plot (Fisher's exact test $P = 0.024$). If common chickweed occurred in a plot's seed bank, it also occurred in that plot's vegetation 75% of the time (9 of 12 plots). Likewise, if common chickweed was in vegetation, it was in the seed bank 64% of the time (9 of 14 plots). Although not significantly statistically due to high variability in quantities among plots within a burnseverity category, mean seed bank density varied by an order of magnitude from 120 seeds m^{-2} in unburned plots to 1230 seeds m^{-2} in moderately burned plots.

Interpretation

Key findings from the assay of readily germinable soil seed banks three years post-fire included that qualitatively more seeds were detected in burned than unburned plots, seed banks were not speciesrich, seed bank taxa occurred in vegetation of at least one plot, and seed banks mostly contained seeds of non-native species along with some natives. A factor potentially associated with the relatively small soil seed banks (compared with many other ecosystem types including those recently disturbed) could be that fire consumed the O horizon (litter and surficial, decomposing organic matter), which can contain much of the seed in western forests (Pratt et al.

1984, McGee and Feller 1993, Buonopane et al. 2013). This, coupled with potential emergence of seedlings from the mineral soil after fire, could have depleted the seed bank and made the qualitatively larger post-fire seed banks on burned plots (compared with unburned plots) largely a function of post-fire inputs of seeds (Vose and White 1987). This could also at least partly account for the high seed bank:vegetation presence of species we found, where all seed bank taxa were detected in vegetation of at least one plot. Our finding of high correspondence in species composition between the seed bank and vegetation is unusual relative to a general principle of low correspondence in ecosystems globally (Hopfensperger 2007). However, relatively high correspondence is consistent with three of our prior studies in western dry conifer forests and montane chaparral (Abella et al. 2007, Abella and Springer 2012, Abella 2022). If a pulse of seed inputs to the seed bank did occur by fire-stimulated plants on our present study's burned plots and represents a main mechanism for seed bank replenishment, then this could also at least partly account for why seed bank density was exceptionally low on unburned plots.

Several of the seed bank species we detected were previously reported as common constituents of seed banks in global ecosystems. The most abundant seed bank species we detected, common chickweed, had seeds that lived 30 years in soil in a seed burial experiment in Europe (Sobey 1981). In the seed bank of a Washington State ponderosa pine (*Pinus ponderosa*) forest, common chickweed was the second most abundant among 57 species (Pratt et al. 1984). Moreover, common chickweed seed density was not reduced by heating mineral soil to 100 °C (Pratt et al. 1984). Prickly lettuce (*Lactuca serriola*), an annual forb not native to North America, was reported to form short-term seed banks persisting around three years and that were replenished by copious seed production (Chadha and Florentine 2021). Similar to our study, prickly lettuce was also abundant in seed banks of mixed conifer forest in Idaho (Kramer and Johnson 1987) and Washington (Buonopane et al. 2013). Another non-native annual forb we detected, spiny sowthistle (*Sonchus asper*), increased in post-fire seed banks in pine forests in Spain (Valbuena et al. 2001).

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