

## RESEARCH ARTICLE

# How do plant communities differ between fire refugia and fire-generated early-seral vegetation?

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## Abstract

**Aims:** Wildfires in dry forest ecosystems in western North America are producing fire effects that are more severe than historical estimates, raising concerns about the resilience of these landscapes to contemporary disturbances. Despite increasing fire activity, relatively little is known about the structure and composition of fire refugia – unburned or low-severity burned patches where trees survived fire – or the degree to which their understory composition differs from fire-generated early-seral forests.

**Locations:** Four recent large fires in dry mixed-conifer forest in eastern Oregon, USA.

**Methods:** We sampled vegetation and environmental factors in 187 plots (100-m<sup>2</sup>) in fire refugia ( $n = 52$ ) and stand-replacement patches (SRPs) ( $n = 135$ ). We used non-metric multidimensional scaling, indicator species analysis, and randomization tests to compare understory plant communities and diversity in fire refugia and SRPs 12–17 years post-fire.

**Results:** Understory plant communities in fire refugia and SRPs showed strong compositional affinities, but exhibited shifts in reproductive trait prevalence and differences in landscape-scale species richness. There were no differences in plot-scale species richness or the occurrence of two prominent invasive annual grasses (*Bromus tectorum*, *Ventenata dubia*). The abundance of common obligate seeding species was similar between plot types, but resprouting and seed-banking species became substantially more abundant in SRPs. Significantly more plant species occurred only in fire refugia, and significantly fewer in SRPs, than expected by chance.

**Conclusions:** Similarities in understory plant communities between fire refugia and early-seral forest in SRPs provide evidence for the resilience of historically frequent-fire forest understory communities to contemporary fire effects. However, fire refugia may serve an ecologically important role as patches with relatively intact forest structure, seed sources that contribute to post-fire forest recovery, and as reservoirs of species and age structure that may be absent from the higher-severity burned matrix.

## KEYWORDS

invasive grasses, mixed-conifer forest, plant species diversity, post-fire succession, refugia, resilience, US Pacific Northwest, wildfire

## 1 | INTRODUCTION

Fire is a globally important disturbance process that interacts with topography, fuels, and weather to create mosaics of burn severity – the ecological impacts of fire. Burn severity patterns are changing in dry forest ecosystems of the western United States (Hessburg, Agee, & Franklin, 2005; Reilly et al., 2017), raising questions about the resistance and resilience of these landscapes to contemporary fire effects. Although high-severity fire effects were a component of pre-European fire regimes in dry mixed-conifer forests (Hessburg, Salter, & James, 2007; Heyerdahl, Loehman, & Falk, 2019), contemporary fires regularly produce stand-replacement patches (SRPs) that are larger than historical estimates (Fornwalt et al., 2016; Reilly et al., 2017; Stephens et al., 2013). Recent research following high-severity fire in dry mixed-conifer forests has focused primarily on post-fire forest regeneration in high-severity patches, driven in part by concerns about low survival of seed sources for obligate seeders and unfavorable climatic conditions (Chambers, Fornwalt, Malone, & Battaglia, 2016; Stevens-Rumann et al., 2018). Comparatively little attention has been paid to fire refugia – locations that burn less frequently or less severely than the surrounding landscape (Kolden, Lutz, Key, Kane, & van Wagtenonk, 2012; Krawchuk et al., 2016) – or to understory plant communities, which directly or indirectly sustain much of the floristic and faunistic diversity in some forest ecosystems (Halpern & Spies, 1995). To better understand the effects of contemporary burn mosaics on the biodiversity of dry forest ecosystems, it is necessary to characterize the structure and composition of fire refugia, and determine whether refugia support understory plant communities that differ substantially from early-seral vegetation regenerating in SRPs.

Recent fire refugia research coincides with broader efforts to identify relatively ecologically stable locations that may contribute to ecosystem resilience in the context of rapid global change. Refugia may serve as “safe havens” in the context of anthropogenic climate change and its biological effects (Keppel et al., 2011). In addition to climate change, the refugia concept is applicable to climate-associated disturbances, including wildfire (Meddens et al., 2018). Here, we identify fire refugia specifically as unburned or low-severity burned locations within fire perimeters where overstory trees survived large fire events. As the most fire-resistant components of the forest landscape during a fire event, refugia constitute the remaining, intact forest structure within fire perimeters, especially in landscapes where high-severity fire has converted extensive forest-capable areas to an early-seral state.

Early-seral forests that establish following stand-replacement fire can support high species diversity in some ecosystems (Campbell & Donato, 2014; Hutto et al., 2016; Swanson et al., 2011). However, in dry forests where high-severity fire was not a substantial component of pre-European fire regimes (Agee & Skinner, 2005; Allen et al., 2002; Heyerdahl et al., 2019), stand-replacing fire effects may drive enduring conversions toward non-forested states with potentially negative consequences for forest-dependent biota (Chambers et al., 2016; Coop, Parks, McClernan, & Holsinger, 2016).

The persistence of particular plant species during and after fire depends, in part, on species’ life-history traits. Certain adaptive traits provide fitness advantages in the context of a given fire regime (Rowe, 1983), and these traits influence post-fire successional trajectories in spatially heterogeneous burn mosaics (Haire & McGarigal, 2008; Turner, Romme, Gardner, & Hargrove, 1997). For example, species that resprout or produce seed banks are well adapted to survive and reestablish following high-severity fire (Airey Lauvaux, Skinner, & Taylor, 2016; Keeley, Pausas, Rundel, Bond, & Bradstock, 2011), and therefore do not depend on refugia to persist in burned areas. In contrast, species that are easily killed by fire, as well as those that depend on seed sources that survive fire, tend to rely on low-severity or unburned areas to persist within burn perimeters and recolonize high-severity areas (Adie, Kotze, & Lawes, 2017; Landesmann & Morales, 2018; Wood, Murphy, & Bowman, 2011).

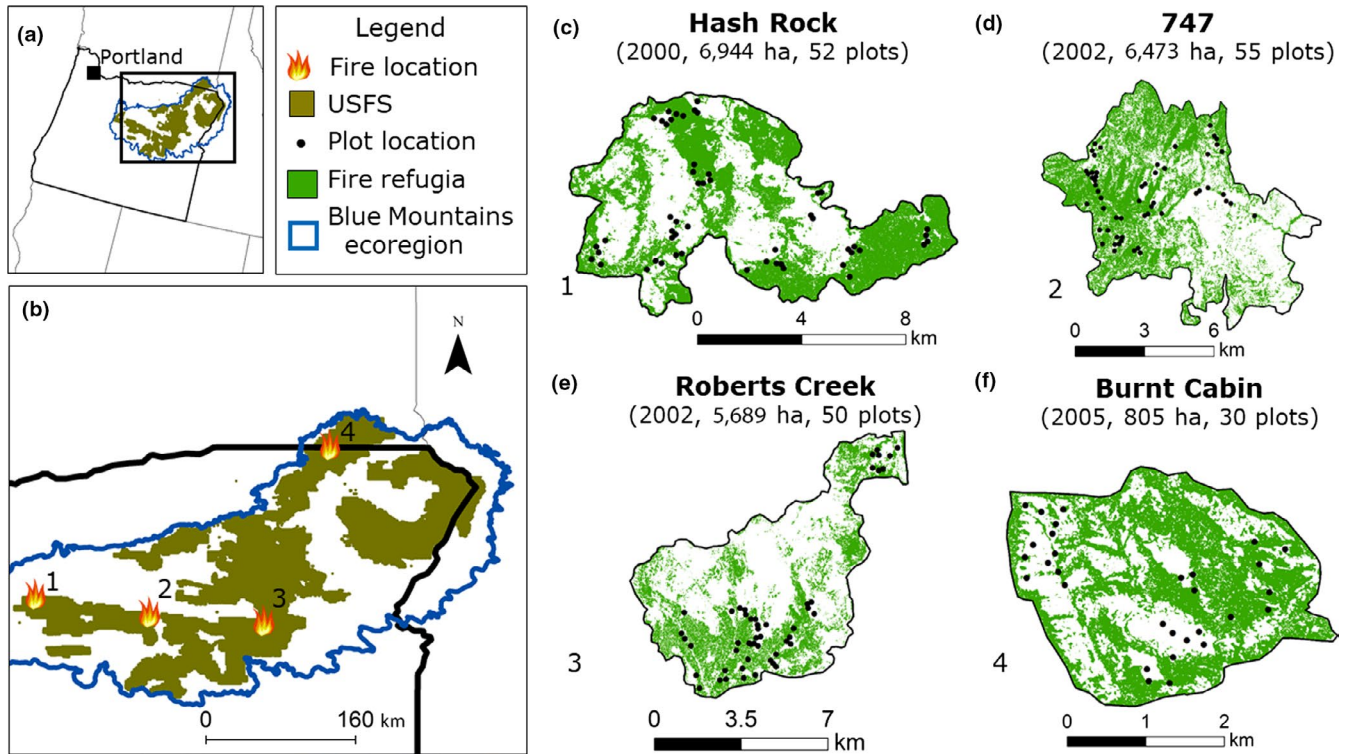
In dry forest ecosystems, a better understanding is needed of the contributions of both fire refugia and surrounding high-severity areas to biodiversity and diversity of successional stages. In this study, we characterize the structure and composition of plant communities in fire refugia and higher-severity burned areas within dry mixed-conifer landscapes of Oregon’s Blue Mountains. Specifically, we compare fire refugia and SRPs in terms of understory plant species diversity, understory community composition, and abundance of reproductive life-history traits.

## 2 | METHODS

### 2.1 | Study region

The Blue Mountains ecoregion extends from central Oregon east to the Snake River Plain near Idaho, and north to the Columbia River in southeastern Washington (Figure 1). Composed of a series of small sub-ranges bisected by deep, rugged river canyons, the Blue Mountains are topographically and biologically complex. The majority of precipitation falls in the winter as snow, and thunderstorms that ignite wildfires are common during warm, dry summers (Seidel & Beebe, 1983). The forested extent of the Blue Mountains spans broad environmental gradients: the 30-year (1981–2010) average across the study region for maximum August temperature range was 16–34°C, the average minimum January temperature range was –12 to 1°C, and the annual precipitation range was 200–1,800 mm (PRISM Climate Group, 2018).

Dry mixed-conifer forests in the Blue Mountains occupy the warmer, drier portions of the region’s climatic gradients, and are composed primarily of ponderosa pine (*Pinus ponderosa*), Douglas-fir (*Pseudotsuga menziesii*), grand fir (*Abies grandis*), and lesser amounts of western larch (*Larix occidentalis*) and lodgepole pine (*Pinus contorta*). Common herbaceous species include yarrow (*Achillea millefolium*), pinegrass (*Calamagrostis rubescens*), mountain brome (*Bromus carinatus*), woodland strawberry (*Fragaria vesca*), heartleaf arnica (*Arnica cordifolia*), and elk sedge (*Carex geyeri*). Common shrub species include snowbrush ceanothus (*Ceanothus velutinus*), snowberry



**FIGURE 1** The study area and study fires in central and northeastern Oregon. (a) The study was performed in the Blue Mountains ecoregion (b). All study fires burned between 2000 and 2005, primarily on land managed by the US Forest Service (USFS). (c–f) Fire refugia within our four study fires, mapped using 1-m resolution aerial imagery. Sample plots, shown using black dots, were located in either fire refugia where overstory trees survived fire, or in stand-replacement patches where all overstory trees were killed by fire [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

(*Symphoricarpos albus*), wood rose (*Rosa gymnocarpa*), and creeping Oregon grape (*Mahonia repens*).

Fires burned frequently in Blue Mountain dry mixed-conifer forests prior to fire exclusion, which began in the late 1800s soon after European settlement of the region. Pre-settlement fire return intervals in the southern Blue Mountains averaged 10–21 years (Johnston, Bailey, & Dunn, 2016), and slightly longer in the northern part of the range where the climate is cooler and wetter (Heyerdahl, Brubaker, & Agee, 2001). Contemporary fire return rotations for *Pinus ponderosa* and *Pseudotsuga menziesii*/*Abies grandis* forests in the Pacific Northwest are now estimated to be 265–380 years, an order of magnitude longer than prior to fire exclusion, and the amount and scale of high-severity fire effects likely are outside the historical range of variability (Hessburg et al., 2005; Reilly et al., 2017).

## 2.2 | Study design

We collected field data in the summer of 2017 in 187 plots located within the perimeters of four large, lightning-caused fires that occurred 12–17 years prior to sampling (Figure 1). To minimize the influence of management, we selected fires that burned primarily in designated roadless or wilderness areas, and we avoided areas with pre- or post-fire timber harvest, fuels treatments, or tree replanting.

We mapped fire refugia as patches of surviving overstory tree canopy using post-fire aerial imagery from the 1-m resolution National Agriculture Imagery Program (NAIP). NAIP imagery was acquired for 2012 and 2014, 7–14 years post-fire. Methods for mapping fire refugia are described in Downing et al. (2019) and Walker et al. (2019). Fire refugia density was calculated for each 1-m pixel inside the fire perimeter based on the sum of fire refugia cells within a 301 m × 301-m moving window divided by their distance to the focal cell. Sampling was stratified along this gradient of fire refugia density, which provided sample locations ranging from neighborhoods dominated by refugia to neighborhoods with sparser, smaller fire refugia patches where the dominant landscape feature was stand-replacement fire effects.

We generated a population of random sample points stratified along the fire refugia density gradient in both refugia and SRPs. We identified areas of stand-replacement fire using the differenced Normalized Burn Ratio (dNBR) derived from 30-m Landsat TM/ETM+ satellite imagery (US federal database available online: <http://mtbs.gov>; Eidenshink et al., 2007). From the dNBR products we constrained SRP sampling to areas that experienced moderate/high or high-severity (dNBR > 440, Key & Benson, 2006). This constraint excludes areas like grasslands, scree fields, and bare ground that were not forested prior to fire. The dNBR constraint was not imposed in the case of our smallest study fire (Figure 1, Burnt Cabin, 805 ha). However, in this case, sampling in SRPs remained restricted to areas

forested prior to fire based on field assessments. We excluded all areas <150 m from fire perimeters and roads to avoid the locations most heavily impacted by fire suppression activities. To facilitate access, all sample plots were within either 1 km of a trail or 3 km of a road.

Final plot selection was made in the field based on three criteria. We rejected plot locations with: (a) no evidence of forest prior to fire in SRP plots; (b) observational evidence of potentially confounding management histories; or (c) inaccessible or unsafe terrain. In the rare event that a plot was misidentified according to our NAIP-based maps (i.e., plot identified as a refugium but no residual trees present), we sampled the plot and categorized it appropriately (refugium or SRP) based on evidence in the field. Plot locations were separated by a minimum distance of 150 m to reduce possible spatial autocorrelation.

### 2.3 | Data collection

We sampled vegetation inside 100-m<sup>2</sup>, circular sample areas for 52 fire refugia plots and 135 SRP plots. We recorded the percent cover for all vascular plant species occupying >0.25 m<sup>2</sup>. Cover values were recorded as the midpoint of eight cover ranges: 0.5% (0.25%–1%), 2.5% (1%–5%), 7.5% (5%–10%), 17.5% (10%–25%), 29% (25%–33%), 41.5% (33%–50%), 62.5% (50%–75%), 87.5% (>75%). When individuals lacked developed flowers or fruit and could not be identified to the species level, we classified to the genus level if possible. Approximately 1% of total observations could not be identified to the species or genus level and were not included in analysis. Plant nomenclature follows USDA NRCS (2018). At each sample plot we recorded elevation, aspect, slope, and distance to nearest surviving pre-fire tree. To characterize overstory tree composition in refugia, we recorded the species and diameter at breast height for all live and dead trees rooted within refugia plots. We recorded any evidence of fire (e.g., bole scorch, charred coarse woody debris) to determine if refugia plots were unburned or experienced some degree of fire effects in the most recent fire.

We used spatial data archives of mean annual temperature and precipitation for each plot location to support analyses examining understory plant community composition along climatic gradients. We downscaled climate data from Climate WNA (Wang, Hamann, Spittlehouse, & Carroll, 2016) for the year of burn to 2015 and averaged across years to characterize the general post-fire climatology of each plot location. To characterize the plot-level microclimate, we calculated heat load using aspect, slope, and elevation data collected in the field (McCune & Keon, 2002).

### 2.4 | Analysis

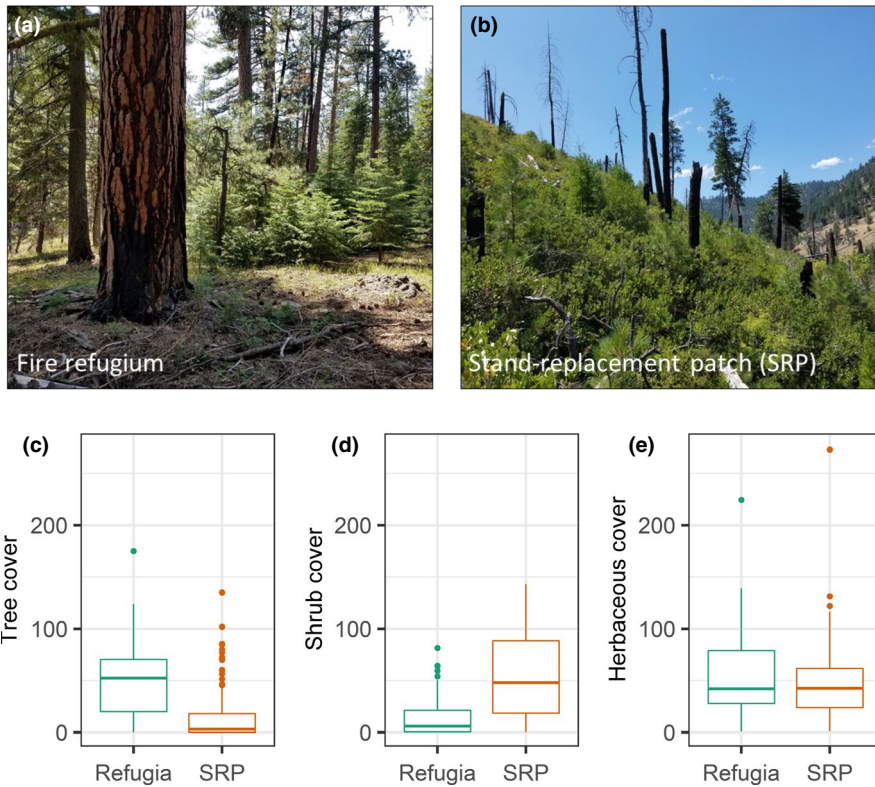
We used a combination of univariate and multivariate analyses to compare observations from fire refugia and SRPs. First, we compared estimates of tree, shrub, and herbaceous cover using two-sample *t* tests to evaluate differences in structural attributes between plot types. Second, we tested for differences in species diversity

between refugia and SRPs at both the plot and landscape scale. At the plot scale, we used two-sample *t* tests to assess differences in species richness and Shannon's diversity between plot types. At the landscape scale, we conducted a permutation test, following the methods of Coop, Massatti, and Schoettle (2010). First, we tallied the number of species that occurred in both plot types, as well as the number of species "exclusive" to either plot type (i.e., observed in only one plot type). We then tested whether these species tallies were significantly higher or lower than randomly generated permutations of the full dataset. Specifically, each plot was reassigned at random (without replacement) to groups of 52 and 135 plots (the number of sampled refugia and SRP plots, respectively), and species tallies were recalculated for each group. From 10,000 randomizations, we calculated the proportion of runs that resulted in a species tally that was more extreme (higher or lower) than observed in the field. Proportions  $\leq 0.025$  were significant at  $\alpha = 0.05$ . Analyses of plot structural attributes and diversity were conducted in R statistical software (R Core Team, 2018).

We used a suite of multivariate tools to examine plant communities and their variability between plot types. We began by removing cover data for all overstory trees (>5 m in height) to focus on understory plant communities. The 5-m threshold eliminated the data strongly associated with the classification criteria for fire refugia (patches of surviving overstory trees), while preserving information about regenerating tree seedlings in SRPs and understory trees in refugia. We relativized columns by species maximum to decrease the influence of hyper-dominant species and to focus on community composition rather than raw species abundance (McCune & Grace, 2002). We used Multi-Response Permutation Procedures (MRPP) to test for differences in understory plant community composition between refugia and SRPs (McCune & Grace, 2002). MRPP analyses were conducted in R with the *vegan* package (Oksanen et al., 2017).

We used non-metric multidimensional scaling (NMS) to examine community relationships and evaluate community variability along environmental gradients. We graphed NMS ordinations with sample units ordinated in species space, overlaying biplots of environmental gradients to identify key drivers of community composition. Variables included in the environmental matrix were fire event, elevation, heat load, distance to nearest surviving pre-fire tree, plot type (SRP vs fire refugia), fire severity (dNBR), mean annual temperature, mean annual precipitation, and the total percent cover for three vegetation strata (tree, shrub, herbaceous). All NMS analyses were conducted with PC-ORD using Bray–Curtis dissimilarity (McCune & Mefford, 2016).

To quantify the degree of species' affiliations to fire refugia and SRP plot types, we used indicator species analysis (ISA), which combines species' relative abundance with frequency of occurrence in different groups. The indicator value of a species is the product of two components, "exclusivity" and "fidelity" (Cáceres & Legendre, 2009). The indicator value (IV) of a species is maximum (100) when all individuals of a species occur in a single group and when the species occurs in all plots within that group (Dufrêne & Legendre, 1997). Monte Carlo randomizations were used to test the hypothesis that



**FIGURE 2** Photos demonstrate substantial structural differences between fire refugia (a) and stand-replacement patches (b) as a function of how we classified the post-fire landscape (surviving overstory trees present, or not). Boxplots represent a comparison of tree (c), shrub (d) and herbaceous (e) cover between fire refugia (Refugia) and stand-replacement patch (SRP) plots, prior to removing overstory tree data from the analysis. Cover values can sum to >100 where species overlap in space. Here, tree cover includes all sizes from seedlings and saplings to overstory dominants [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

IVs were higher than would be expected by chance. Indicator species analyses were performed in R with the *indicspecies* package (Cáceres & Legendre, 2009) with 999 randomizations in the Monte Carlo test.

We characterized species' reproductive life-history traits using information derived from the US Fire Effects Information System ([www.feis-crs.org/feis/](http://www.feis-crs.org/feis/)) and classified these data based on three traits: resprouter (yes/no), obligate seeder (yes/no), seed banker (yes/no). Species with multiple life-history traits (e.g., resprouter, seed banker) were classified as having both traits. We were unable to document life-history traits for all species, and we chose to restrict this analysis to species present in >5% of plots, a commonly used threshold in community analyses (McCune & Grace, 2002), which yielded 76 species (Appendix S2: Table S2). Because we were interested in examining the absolute abundance of life-history traits in our plots, we did not relativize species abundance data for this analysis. Community data for the 76 species were ordinated using NMS, and ordinations were overlaid with biplots and life-history trait abundance values for each plot, calculated by multiplying the community matrix by the trait matrix. We also compared the average abundance of traits in refugia and SRP plots using a two-sample *t* test.

Lastly, two invasive grass species — cheatgrass (*Bromus tectorum*) and ventenata (*Ventenata dubia*) — were common in parts of our study area and are of particular concern for managers in the Blue Mountains (Johnson, 1994; Wallace, Pavek, & Prather, 2015). We compared their abundance and frequency of occurrence in fire refugia and SRPs to determine whether invasibility differed between refugia and high-severity burned areas.

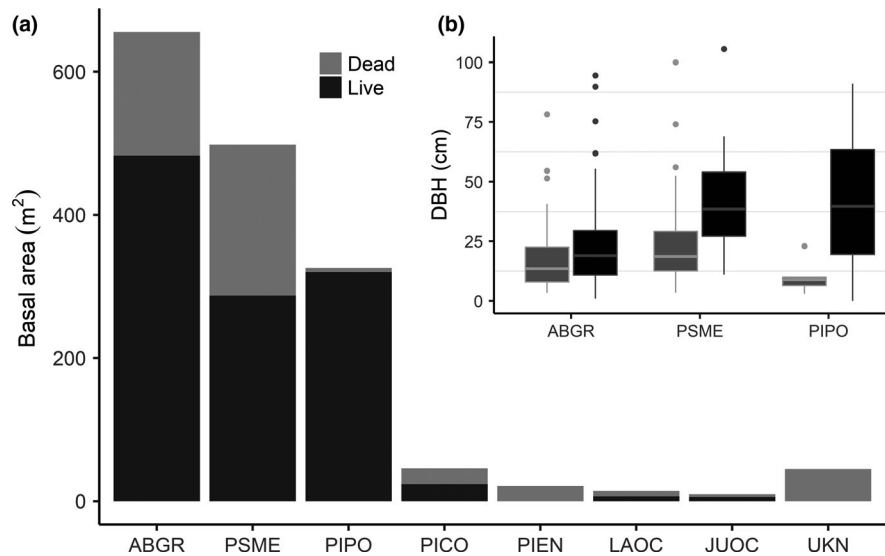
### 3 | RESULTS

#### 3.1 | Refugia abundance and overstory composition; comparisons between plot types by lifeform

Fire refugia are distinct from SRPs in composition and structure by virtue of this study's mapping criteria: refugia are where overstory trees persist, while SRPs are areas where all trees were killed by fire (Figure 2). The percentage of area classified as refugia by our NAIP-based analysis was 33%, 40%, 46%, and 60% for the Roberts Creek, Hash Rock, 747, and Burnt Cabin fires, respectively (Appendix S2: Table S1). The remainder of the landscape was primarily forest that experienced complete overstory mortality, although some areas were not forested prior to fire (grasslands, rock, etc.). Out of the 52 refugia plots sampled, we identified seven plots with no evidence of fire and 45 with evidence of low-severity surface fire. Fire severity as characterized by dNBR varied widely across our refugia and SRP sample plots (−5 to 966).

The most common overstory tree species within fire refugia were *Abies grandis*, *Pseudotsuga menziesii*, and *Pinus ponderosa* (Figure 3). A substantial proportion of smaller *Pseudotsuga menziesii* and *Abies grandis* trees were dead at the time of sampling, most likely due to surface fire.

Tree cover (including both overstory and understory trees) was substantially higher in refugia than SRPs ( $t = -6.55$ ,  $p < 0.001$ , Figure 2), despite high numbers of regenerating conifer seedlings in many SRP plots (median = 1,100 seedlings/ha; Downing et al., 2019). Shrub cover was substantially higher on average in SRPs plots than refugia ( $t = -8.40$ ,  $p < 0.001$ ), and herbaceous cover was similar between plot types ( $t = 1.144$ ,  $p = 0.3$ ).



**FIGURE 3** Overstorey tree composition in fire refugia and size distributions of common species. (a) Overstorey tree composition in fire refugia was dominated by *Abies grandis* (ABGR), *Pseudotsuga menziesii* (PSME), and *Pinus ponderosa* (PIPO). Substantial proportions of grand fir and *Pseudotsuga menziesii* basal area were dead at time of sampling. *Pinus contorta* (PICO), *Picea engelmannii* (PIEN), *Juniperus occidentalis* (JUOC), and *Larix occidentalis* (LAOC) constituted only a small proportion of the total overstorey basal area within fire refugia. We were not able to determine the species identity of some dead trees due to decay or bark loss, and these individuals were classified as “unknown” (UKN). (b) Surviving trees in fire refugia were larger in diameter (breast height, DBH) than trees dead at time of sampling, particularly for *Pseudotsuga menziesii* and *Pinus ponderosa*

### 3.2 | Species diversity

We identified a total of 286 plant species; 210 occurred in fire refugia plots, 240 occurred in SRP plots, and 164 species occurred in both plot types (see Appendices for species–area and dominance curves, and a complete species list). At the plot scale, average species richness was 19.5 (range = 1–46 species), and species richness did not differ significantly ( $t = 0.26$ ,  $p = 0.8$ ) between SRPs (19.6,  $SE = 0.7$ ) and refugia (19.3,  $SE = 1.1$ ). Average Shannon's diversity was 1.8 (range = 0–3.3), with no difference ( $t = 0.53$ ,  $p = 0.6$ ) between SRPs (1.8,  $SE = 0.05$ ) and refugia (1.7,  $SE = 0.09$ ).

Landscape-scale patterns of plant richness in SRPs and fire refugia differed from random expectations (Figure 4). Far more species were exclusive to refugia (46) than expected by random chance (24), while fewer species were exclusive to SRPs (76) than expected (99). Similarly, more total species occurred in refugia (210), and fewer total species occurred in SRPs (240) than the random expectation (187 and 261, respectively).

### 3.3 | Community composition

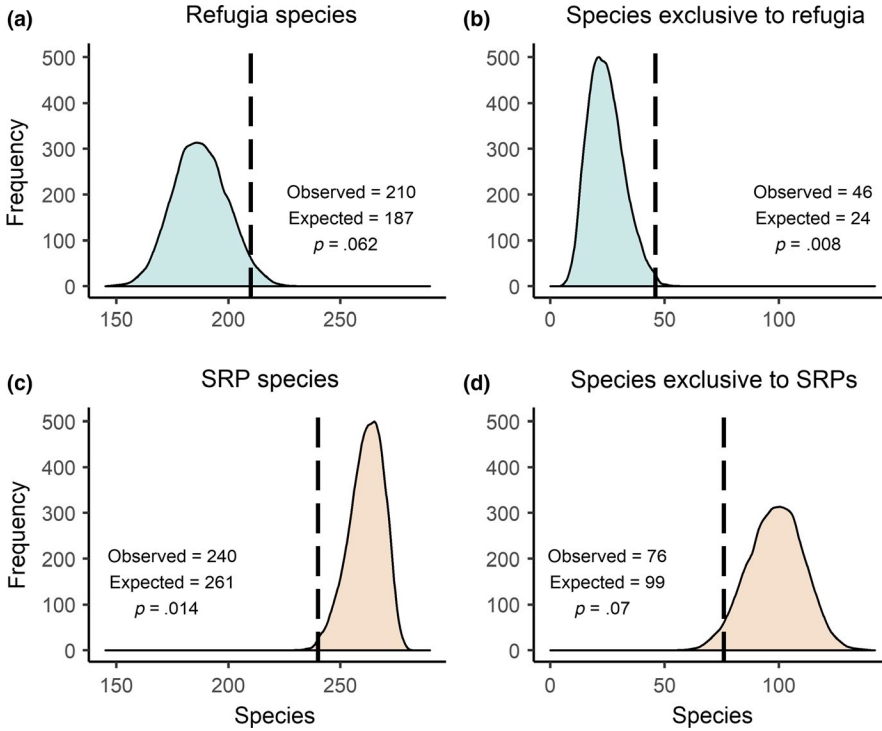
Multivariate analyses of understory plant communities did not identify strong compositional differences between understory plant communities in fire refugia and SRPs. MRPP results indicated a difference in composition between refugia and SRPs ( $p < 0.001$ ), but the effect size was very small ( $A = 0.025$ ), demonstrating substantial heterogeneity within groups and overlap between groups. The NMS ordination of fire refugia and SRPs resulted in a three-dimensional solution with a final stress of 0.21 (Figure 5). The

environmental gradients most strongly associated with axis 1 were elevation ( $R^2 = 0.2$ ) and mean annual temperature ( $R^2 = 0.23$ ). Axis 2 was associated with mean annual precipitation ( $R^2 = 0.32$ ), and axis 3 was associated with shrub cover ( $R^2 = 0.24$ ). No other measured factors were strongly associated with the ordination axes ( $R^2 < 0.2$ ), including distance to nearest surviving pre-fire tree and fire severity (dNBR). NMS results were consistent with the low effect size ( $A$ ) detected with MRPP analysis, with fire refugia and SRP plots overlapping substantially in species space (Figure 5).

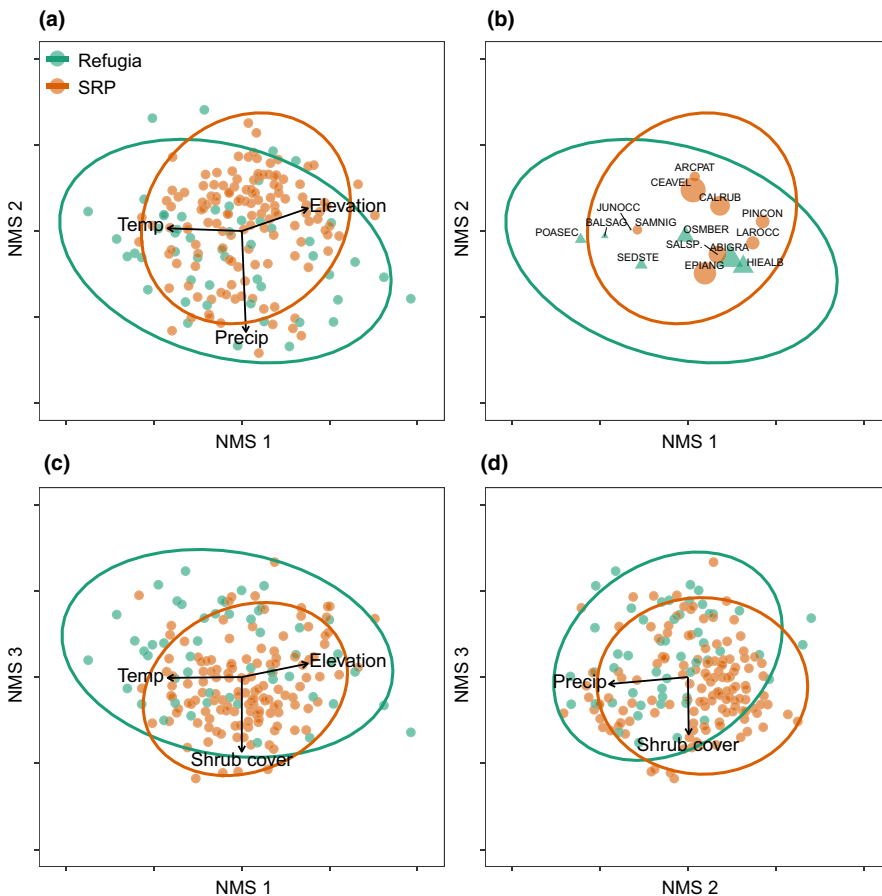
The most abundant species in the understory of fire refugia, in decreasing order of abundance, were *Carex geyeri*, *Abies grandis* seedlings, *Ceanothus velutinus*, *Calamagrostis rubescens*, and *Arnica cordifolia*. The most abundant species in SRPs were *Ceanothus velutinus*, *Calamagrostis rubescens*, *Carex geyeri*, *Ceanothus sanguineus*, and *Pinus contorta* seedlings. Although the composition of understory plants was similar in fire refugia and SRPs, ISA identified several statistically significant indicator species. Eight species were associated with SRPs, and seven were associated with fire refugia (Figure 6b, Table 1). Indicator values were lower on average ( $t = 2.2$ ,  $p = 0.05$ ) for refugial species (mean = 18.9,  $SE = 8.8$ ) than those associated with SRPs (mean = 34,  $SE = 17.5$ ).

### 3.4 | Reproductive life-history traits

The abundance of species capable of producing seed banks and re-sprouting was higher in SRPs than in fire refugia ( $t = -8.3$ ,  $p < 0.001$ ;  $t = -5.8$ ,  $p < 0.001$ ), but there was no evidence of a difference in the abundance of obligate seeding species between plot types ( $t = -1.6$ ,  $p = 0.12$ ). Results from a three-dimensional NMS solution



**FIGURE 4** Observed and expected number of species in fire refugia (Refugia, blue) and stand-replacement patch (SRP, orange) plots. The dashed vertical line represents the number of species observed; the distribution represents species counts generated by 10,000 randomizations of the dataset. We tested for differences in total number of species found in each plot type (a, c) and the number of species exclusive to each plot type (b, d) [Colour figure can be viewed at wileyonlinelibrary.com]



**FIGURE 5** Non-metric multidimensional scaling ordinations of fire refugia and stand-replacement patch plots, and indicator species. (a, c, d) Understory plant communities in fire refugia (Refugia, green) and stand-replacement patches (SRP, orange) occupy similar portions of species space. Arrowed lines indicate the strength and direction of correlations with environmental variables. Ellipses represent 95% confidence intervals for plots types. (b) Indicator species associated with SRPs (circles) had higher indicator values on average than species associated with fire refugia (triangles). Symbol sizes in panel b are scaled to represent the indicator value for each species. Table 1 provides species names and functional traits for all species represented in panel (b) [Colour figure can be viewed at wileyonlinelibrary.com]

(final stress = 0.18) were consistent with comparisons of mean abundance: seed bankers and resprouters were more abundant in SRPs than in refugia, whereas seed obligate species did not differ

(Figure 6). The abundance of species capable of producing long-lived seed banks was positively associated with shrub cover ( $R^2 = 0.54$ , axis 3) and negatively associated with elevation ( $R^2 = 0.23$ , axis 1).

**TABLE 1** Indicator species associated with stand-replacement patch and fire refugia plots

Species	ID	Group	Exclusivity	Fidelity	IV	p-value	Obligate seeder	Resprouter	Seed banker
<i>Ceanothus velutinus</i>	CEAVEL	SRP	0.88	0.73	64	0.001	○	●	●
<i>Epilobium angustifolium</i>	EPIANG	SRP	0.85	0.61	52	0.006	○	●	○
<i>Calamagrostis rubescens</i>	CALRUB	SRP	0.75	0.56	42	0.005	○	●	○
<i>Salix</i> spp.	SALSP.	SRP	0.78	0.44	35	0.009	○	●	○
<i>Pinus contorta</i>	PINCON	SRP	0.89	0.27	24	0.025	●	○	●
<i>Larix occidentalis</i>	LAROCC	SRP	0.86	0.27	23	0.027	●	○	○
<i>Arctostaphylos patula</i>	ARCPAT	SRP	0.99	0.17	17	0.03	○	●	●
<i>Sambucus nigra</i>	SAMNIG	SRP	0.93	0.17	16	0.038	○	●	●
<i>Abies grandis</i>	ABIGRA	Refugia	0.69	0.49	43	0.039	●	○	○
<i>Hieracium albertinum</i>	HIEALB	Refugia	0.81	0.35	29	0.004	●	○	●
<i>Osmorhiza berteroi</i>	OSMBER	Refugia	0.76	0.31	24	0.050	●	○	●
<i>Sedum stenopetalum</i>	SEDSTE	Refugia	0.67	0.24	16	0.036	●	○	○
<i>Poa secunda</i>	POASEC	Refugia	0.86	0.14	15	0.006	○	●	○
<i>Balsamorhiza sagittata</i>	BALSAG	Refugia	0.80	0.14	12	0.011	○	●	○
<i>Juniperus occidentalis</i>	JUNOCC	Refugia	0.92	0.12	11	0.010	●	○	○

Note: The ISA identified eight species associated with stand-replacement patch (SRP) plots and seven species associated with fire refugia (Refugia) plots. Exclusivity is the probability that a plot belongs in the assigned category, given that the species occurs in that plot. Fidelity is the probability of encountering the species in a plot based on its assigned category. Reproductive life-history traits for each species were assigned as present (●) or not (○). Species possess traits (e.g., obligate seeders, resprouters) that generally support their ISA classification.

Resprouting species abundance was negatively associated with tree cover ( $R^2 = 0.20$ , axis 2) and mean annual precipitation ( $R^2 = 0.28$ , axis 2). Seed obligate species abundance was positively associated with mean annual precipitation and tree cover.

### 3.5 | Invasive annual grasses

The frequency and abundance of the two non-native grasses we assessed did not differ between refugia and SRPs. We found no evidence of a difference between the percentage of fire refugia (21%,  $SE = 6\%$ ) and SRP plots (27%,  $SE = 4\%$ ) occupied by *Bromus tectorum* ( $\chi^2_{df=1} = 0.349$ ,  $p = 0.55$ ), nor did we find evidence of a difference in *Bromus tectorum* cover (mean = 4%, range = 0.5–29%) between plot types ( $t = -1.04$ ,  $p = 0.30$ ). Similarly, we found no evidence of a difference in the percentage of refugia (12%,  $SE = 5\%$ ) and SRP plots (10%,  $SE = 3\%$ ) that contained *Ventenata dubia* ( $p = 0.014$ ,  $p = 0.91$ ), or *Ventenata dubia* cover (mean = 8%, range = 0.5–29%) between plot types ( $t = -0.87$ ,  $p = 0.38$ ).

## 4 | DISCUSSION

Understory plant community composition 12–17 years post-fire was broadly similar between fire refugia and SRPs in Blue Mountain dry mixed-conifer forests that historically experienced frequent fire. These results provide evidence for the resilience of understory plant communities to high-severity fire effects in our study area, despite the obvious change in forest structure from stand-replacing fire. However, many species occurred only in refugia, and some of these

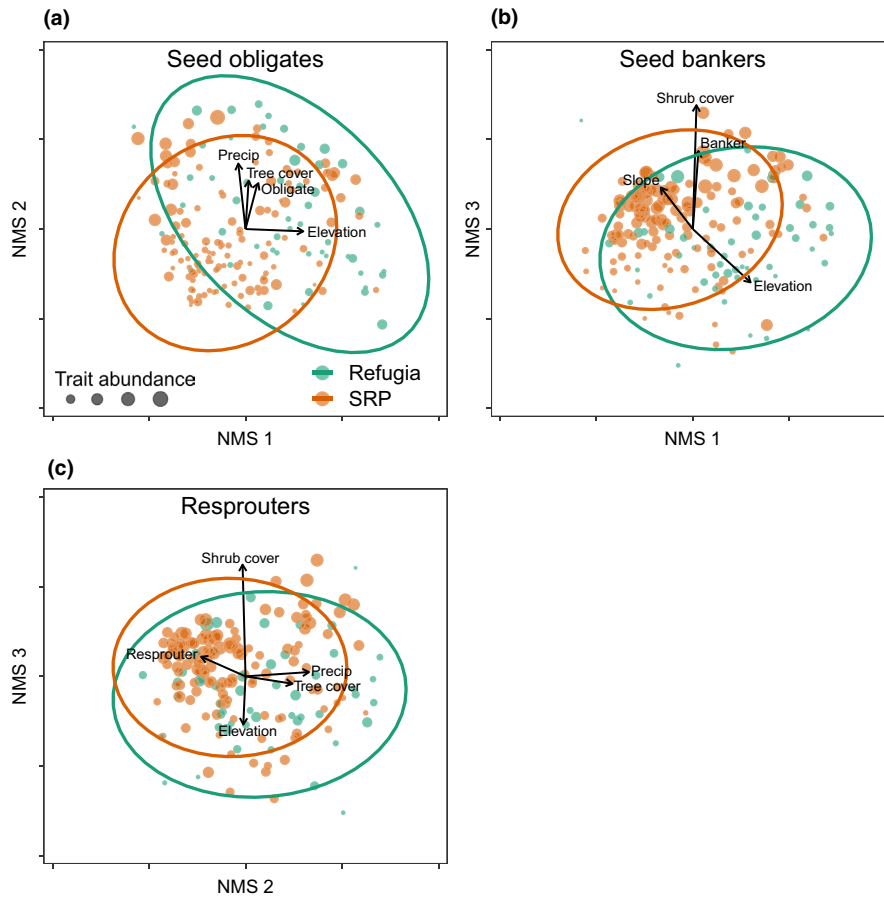
are of particular ecological or cultural value. Species richness and diversity were similar between plot types at the plot scale, but richness was higher than expected in refugia at the landscape scale, suggesting that fire refugia may contribute disproportionately to post-fire species diversity within fire perimeters. Resprouting and seed-banking species were more abundant in SRPs, but many species without these reproductive life-history traits (e.g., obligate seeders) have also re-colonized SRPs, suggesting that remnant vegetation that survived fire in refugia is an important seed source contributing to species assemblages in the early-seral forest matrix (Downing et al., 2019; Landesmann & Morales, 2018).

### 4.1 | Species diversity

Our finding of no difference in plot-scale species diversity between fire refugia and the higher-severity burned matrix is consistent with other studies of dry forest ecosystems in the Pacific Northwest (Donato, Fontaine, Robinson, Kauffman, & Law, 2009; Kerns, Thies, & Niwa, 2006). Our results demonstrate that fire refugia and SRPs in our study area are neither comparatively species-rich nor species-poor at the plot scale, and compositional similarities between plot types provide little evidence that high-severity fire reduces biodiversity. Instead, mosaics of fire effects, from unburned to stand-replacement, appear to support high levels of overall plant diversity within burn perimeters in our study area.

Although species assemblages were similar in fire refugia and SRPs, we did identify important differences at the landscape scale, with refugia harboring significantly more species not found elsewhere. Our NMS ordinations further illustrate how SRP plots





**FIGURE 6** Non-metric multidimensional scaling ordinations of common plant species (present in >5% of plots) with points representing plots scaled by the abundance of fire-adaptive life-history traits, calculated by multiplying the community matrix by the trait matrix. Arrowed lines indicate the strength and direction of correlations with environmental variables. Ellipses represent 95% confidence intervals for plot types. (a) The abundance of obligate seeding species was positively associated with precipitation and tree cover, but there were not strong differences in the abundance of this trait between plot types. (b) The abundance of seed-banking species was higher in SRPs and was positively associated with shrub cover. (c) Resprouting species were more abundant in SRPs, and this trait was negatively associated with precipitation and tree cover [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

occupy a contracted, more homogeneous portion of species space compared to the higher diversity among fire refugia plots. Species that occurred only in refugia were distributed across environmental gradients (elevation, mean annual temperature, precipitation, Appendix S1: Figure S2). These fire refugia-exclusive species either were present before the fire and survived it, or dispersed into favorable conditions provided by intact forest canopy. Only 20% of fire refugia-exclusive species occurred in more than one plot, but some of these species may be of particular importance to land managers or users, like those utilized by indigenous peoples as traditional foods (*Fritillaria pudica*, *Polygonum bistortoides*) and medicines (*Lomatium ambiguum*, *Lomatium dissectum*; Benedict, 2009; McCutcheon et al., 1992; Mullin, Peacock, Loewen, & Turner, 1997).

#### 4.2 | Community composition and indicator species

Community composition in our study area varied most strongly along environmental gradients of temperature and precipitation, rather than with fire severity (dNBR) or between plot types (refugia, SRPs). A suite of species were exclusive to either SRP or refugia plots, but all of them were rare (present in <5% of plots). The majority of species occurred in both refugia and SRPs. Overall, fire refugia and SRP plots occupied similar portions of species space. Notably, results were consistent between ordinations of unrelativized community data focused on life-history trait abundance and ordinations of relativized community data focused on community composition.

Had there been substantial differences in plot types driven by the abundance of a small number of hyper-dominant species, we would expect such differences to be clearly evident in ordinations using unrelativized abundance data.

Relatively rapid compositional recovery of understory plant communities in severely disturbed forest ecosystems has been reported in other parts of the northwestern US. For example, in *Pseudotsuga menziesii* forests in western Oregon, undisturbed and severely disturbed sites (logged and subsequently burned) differed five years following disturbance but had largely returned to their pre-fire composition 21 years post-treatment (Halpern, 1988). The resilience of understory plant communities in our study area is somewhat unexpected due to substantial departure from historical disturbance dynamics (Heyerdahl et al., 2019; Johnston et al., 2016), but our results are consistent with a similar study in the Klamath Siskiyou region where pre-European fire return intervals of 12–19 years are comparable to those documented in the Blue Mountains (Taylor & Skinner, 1998). Donato et al. (2009) reported that the composition of high-severity burned plots was similar to unburned controls two growing seasons after fire. Our results provide additional evidence that a long history of recurrent fire, including some proportion of stand-replacement fire, resulted in a native flora well adapted to a variety of fire effects.

Despite overall similarities, we identified a small number of indicator species with strong affinity to fire refugia or SRPs. Fire refugia indicator species are primarily fire-sensitive, obligate seeders like

white hawkweed (*Hieracium albiflorum*), or species associated with locations like rock outcrops and gravelly benches that may offer protection from fire like wormleaf stonecrop (*Sedum stenopetalum*) and *Juniperus occidentalis*. In contrast, SRP indicator species possess life-history traits well suited to high-severity burned environments, including the ability to resprout (e.g., *Calamagrostis rubescens*), long-lived seed banks (e.g., *Ceanothus velutinus*), and highly effective dispersal mechanisms (e.g., *Epilobium angustifolium*). Species associated with SRPs had higher indicator values on average, suggesting that the degree of specialization of these early-seral species is higher than species associated with less disturbed conditions in refugia.

### 4.3 | Reproductive life-history traits

Historically, frequent fire maintained a shifting, relatively fine-grained mosaic of forest and openings (Hessburg & Agee, 2003; Hessburg et al., 2005), within which plant species with different reproductive life-history traits persisted. The grain size of contemporary landscape mosaics is likely coarser as a result of fire exclusion and eventual large high-severity patch sizes (Hessburg et al., 2016), but our results demonstrate that understory plant communities remain capable of recolonizing SRPs via a variety of reproductive strategies. Stand-replacement fire effects favored resprouting and seed-banking species, but the abundance of these species does not appear to have prevented recolonization by obligate seeding species. The compositional similarity between plot types was due in part to similarities in obligate seeding species abundance. Prior research has demonstrated the importance of fire refugia as seed sources for the repopulation of obligate seeding tree species in high-severity burned areas (Downing et al., 2019; Landesmann & Morales, 2018), and our results suggest that refugia also support similar post-fire repopulations of other obligate seeding taxa. The average distance to the nearest refugial patch in contemporary high-severity burned dry forests is often relatively short (<40-m; Walker et al., 2019), and compositional similarities between fire refugia and SRPs may be partly a function of spatially complex burn severity mosaics that result in well-distributed refugial seed sources, which, together with seed sources outside of fire perimeters, contribute to post-fire revegetation.

### 4.4 | Invasive annual grasses

Although there was no evidence of a difference between fire refugia and SRP plots in the occurrence of the two most prominent invasive grasses in the study region, increased *Bromus tectorum* densities have been associated with higher-severity prescribed fire effects and canopy gaps in the Blue Mountains (Kerns et al., 2006). Very little is known about the biology and response to disturbance of *Ventenata dubia*, a relative newcomer to the Pacific Northwest (Wallace et al., 2015). *Ventenata dubia* has been primarily described in grassland and sagebrush ecosystems (Jones, Norton, & Prather, 2018; Wallace et al., 2015), but our study demonstrates that the species has expanded into dry forests in the

Blue Mountains, even into the roadless and wilderness areas we primarily sampled. In the absence of pre-fire data, we were unable to distinguish between exotic grass populations that were present prior to fire and those that established after fire, or if exotic grass cover increased following fire. However, similarities in invasive grass abundance indicate that fire refugia are not immune to *Ventenata dubia* or *Bromus tectorum* establishment following surface fire, and high-severity fire effects do not appear to substantially increase the invasibility of dry mixed-conifer forests in our study fires.

### 4.5 | Low-severity and unburned fire refugia

Low-severity fire in refugia substantially reduced small *Pseudotsuga menziesii* and *Abies grandis* basal area, potentially increasing the resistance of refugia to future high-severity fire. Surface fire effects in refugia are similar to those that managers seek to replicate with prescribed fire and mechanical thinning treatments, which are designed in part to reduce the risk of high-severity fire resulting from widespread infilling by shade-tolerant tree species (Agee & Skinner, 2005; Merschel, Spies, & Heyerdahl, 2014). In contrast, unburned refugia may be more vulnerable to future high-severity fire effects if increased fuel loads overwhelm any underlying topographic or microclimatic protection from fire in these locations (Kolden, Bleeker, Smith, Poulos, & Camp, 2017). It is possible that areas of infrequently burned forest that accumulate more fuel than the surrounding landscape were responsible in part for the occasional high-severity effects observed in the fire history record (Heyerdahl et al., 2019).

Although our ability to discern unburned areas was limited because of the amount of time that has elapsed since fire, we encountered locations within fire perimeters that exhibited no evidence of recent fire effects, some as large as several hectares. Nevertheless, our sample suggests that unburned refugia constitute a relatively small proportion of the area within large fire perimeters in the Blue Mountains, consistent with post-fire observations from other dry forest systems (Campbell, Donato, Azuma, & Law, 2007). The small sample size precluded testing compositional differences between low-severity and unburned refugia. Future analyses with a larger sample may reveal important ecological attributes of unburned plots, as others have demonstrated that the difference between truly unburned patches and patches that experienced low-severity fire may be important for species like epigeic beetles (Gandhi, Spence, Langor, & Morgantini, 2001), fire-sensitive bryophytes (Barbé, Fenton, & Bergeron, 2017), and some rodents (Swan, Galindez-Silva, Christie, York, & Di Stefano, 2016).

### 4.6 | Study limitations

A key assumption of our study is that the locations sampled in fire refugia were similar to locations sampled in SRPs prior to fire. We believe this assumption is reasonable based on our experience in

the field and our finding that plot types were compositionally similar 12–17 years post-fire, but we acknowledge that we were unable to control for important attributes such as soil properties, pre-fire understory composition, or soil seed banks, which may have influenced our results. Additionally, stronger compositional differences between plot types before the fire, or in the years immediately post-fire, may have declined in the 12–17 years since fire. The strong influence of site characteristics (elevation, temperature, and precipitation), rather than fire effects (dNBR, plot type), may be a function of sampling across the broad environmental gradients of the region, and stronger compositional differences between refugia and SRPs may exist within narrower ranges of these environmental gradients.

Stronger community differences also could be possible at a subset of fire refugia associated with topographic features that predictably moderate fire effects. For example, studies conducted in Patagonia, Australia, and South Africa reported that fire-sensitive tree and shrub species were associated with fire refugia in sparsely vegetated areas or near rock outcrops that decrease fire intensity and frequency (Adie et al., 2017; Clarke, 2002; Landesmann, Gowda, Garibaldi, & Kitzberger, 2015; Wood et al., 2011). Long-lived, fire-sensitive species like Alaska yellow cedar (*Callitropsis nootkatensis*) and mountain mahogany (*Cercocarpus ledifolius*) do occur in some parts of the Blue Mountains, and there is some indication that these species are associated with topoedaphic features that may support persistent fire refugia with less frequent or severe fire effects (Dealy, 1975; Frenkel, 1974). Lastly, our results may have been influenced by the fact that the total area we sampled (~2 ha) was necessarily a fraction of the entire area affected by our study fires (20,000 ha), and we acknowledge that species identified as “exclusive” to one plot type or the other were only exclusive in the context of our sample data.

## 5 | CONCLUSIONS

Our results provide novel insights into the composition of fire refugia in dry mixed-conifer forests of Oregon's Blue Mountains and highlight the resilience of these landscapes to contemporary fire effects. Fire refugia are ecologically important as patches of relatively intact forest structure, as reservoirs of species that may be absent from the higher-severity burned matrix, and as seed sources that contribute to post-fire forest recovery in SRPs (Coop et al., 2019; Downing et al., 2019; Landesmann & Morales, 2018). Although we did identify a suite of species that were recorded only in fire refugia, compositional similarities between refugia and early-seral forest regenerating in SRPs indicate that high-severity fire effects in the Blue Mountains have not resulted in substantial losses of flora and plant communities. However, such high-severity fires can threaten a range of other ecological and social values, providing the impetus for fuels reduction treatments that can mitigate fire severity and promote the survival of pre-fire forest (Agee & Skinner, 2005). The baseline understanding of fire refugia composition and structure provided by this study will support future investigations into the functions,

vulnerability, and management implications of these important landscape elements.

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## AUTHOR CONTRIBUTIONS

WD, MK, JC, CM, EW, and GC conceived of the research idea; WD and CT collected data; WD performed statistical analyses; WD with contributions from all authors wrote the paper, and all authors discussed the results and commented on the article.

## DATA AVAILABILITY STATEMENT

Data are stored online at the Open Science Framework (osf.io).

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

**Appendix S1.** Boxplots of species richness and diversity in fire refugia and stand-replacement patches, NMS ordination of species exclusive to fire refugia, species dominance curves, species–area curves, and study fire summary data

**Appendix S2.** Complete list of taxa and reproductive life-history traits assigned to common species

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