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Mesic mixed-conifer forests are resilient to both historical high-severity fire and contemporary reburns in the US Northern Rocky Mountains

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ABSTRACT

High-severity fires and short-interval reburns strongly influence forest structure and composition and may overwhelm forest ecosystem resilience and catalyze persistent shifts to non-forest conditions. Recent increases in annual area burned and severity in the western United States (US) highlight the need to better understand the long-term effects of high-severity fire, including interactions with subsequent fires. In the early 20th century, the northern US Rocky Mountains experienced several fire seasons with widespread, high-severity fires, under fire weather comparable with extreme conditions today. The Selway-Bitterroot Wilderness in north-central Idaho has remained an active fire regime with limited suppression and management, making it an ideal location to investigate long-term effects of initial high-severity fires, as well as ecosystem resilience to contemporary reburning. Using field sampling informed by fire history data from 1870 to 2020, we investigated the influence of fire frequency (once, twice, and thrice burned from 1910 to 2017) on forest structure, conifer regeneration, and fuel loading in mesic mixed-conifer forests that burned at high severity in either 1910 or 1934. Tree regeneration was abundant across all three burn histories, and 99% of sample sites were <200 m from the nearest conifer seed source when sampled in 2021. Abundance of snags and coarse woody material was less affected by fire frequency and more impacted by time since last fire. High shrub biomass occurred only on steep southwest aspects with low overstory basal area and was not related to burn history. Live tree composition and density differed across forests with contrasting recent fire histories, but even thrice-burned sites supported abundant conifer tree regeneration, indicating that northern Rocky Mountain mesic mixed-conifer forests that experienced fire during the twentieth century currently remain resilient to wildfire. Wildfire as an ecological process in the Selway-Bitterroot Wilderness likely contributed to ecosystem resilience.

1. Introduction

Mesic mixed-conifer forests of the US Northern Rocky Mountains are highly flammable ecosystems (Hessburg et al., 2019). The convergence of seasonally dry conditions, high productivity and plentiful fuels, and abundant ignition sources leads to widespread fires. When fire-enabling climate and weather conditions align, conflagrations of immense scale (Morgan et al., 2008) and high severity (Larsen, 1925) can occur. Empirical field research that advances the scientific understanding of ecosystem resilience following wildfire in mesic mixed-conifer forests is needed because of ongoing climate change and the trend of increasing area burned at high severity across the western United States (Cansler and McKenzie, 2014; Abatzoglou and Williams, 2016a; Parks and Abatzoglou, 2020a). Studies of high-severity fires and reburn sequences are of particular importance because these events may overwhelm forest ecosystem resilience and compromise ecosystem function (Coop et al., 2020). Such research informs forest management decision making and supports climate change adaptation efforts before (Hessburg et al., 2021) and after wildfires (Larson et al., 2022).

High-severity fires (i.e., fires killing >70% of canopy trees; Morrison

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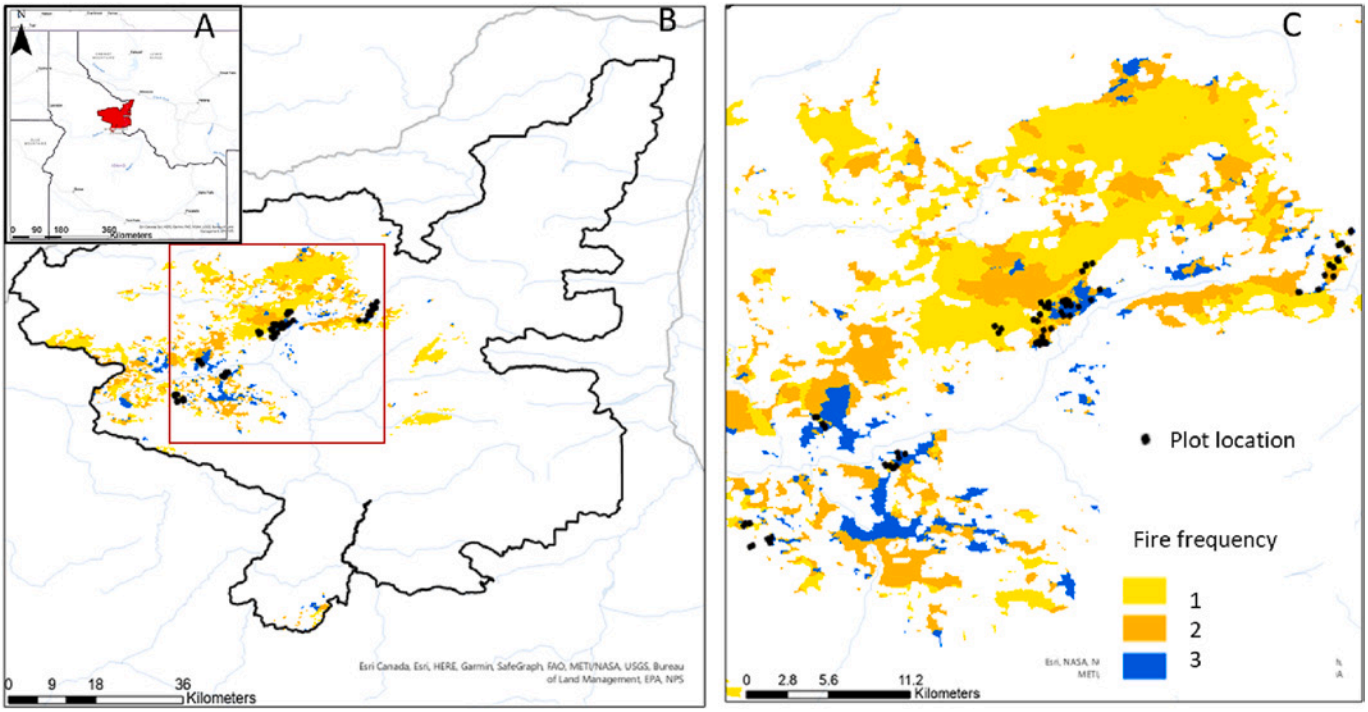

Fig. 1. The location of the study. (A) Location of the Selway-Bitterroot Wilderness (SBW; red polygon) within the western United States. (B) The study area location within the SBW and the fire perimeters of high-severity fires that burned in either 1910 or 1934 and were buffered inward 120 m to ensure sample sites were in historical fire perimeters. (C) Inset of all the plots (black dots) with burn history. Yellow = one burn; orange = two burns; blue = three burns. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

and Swanson, 1990) create lasting effects on vegetation across large landscapes by resetting succession and forest structural development (Larsen, 1925). Areas that experienced wide-spread high-severity fires, such as the US northern Rocky Mountains in the early 20th century, serve as a model system for investigations of the long-term legacies of high-severity fire. These climate-enabled and weather-driven wildfires (Brunelle et al., 2005; Morgan et al., 2008) burned under extreme conditions that are comparable to or exceed fire weather even today (Diaz and Swetnam, 2013). They thus provide an opportunity to investigate long-term effects of large, high-severity fires, as well as interactions with contemporary wildfires.

Short-interval reburns—successive fires with a fire-return interval less than about 30 years—have been implicated as compound stressors capable of causing persistent state shifts to non-forest communities (Coop et al., 2020), or transitions to novel forest conditions (Hoecker and Turner, 2022). Contemporary reburns are increasingly well studied in western forest conifer forests (e.g., Larson et al., 2013; Stevens-Rumann and Morgan, 2016; Berkey et al., 2021a; Steel et al., 2021). However, a common limitation of these observational studies of wildfire effects is that pre-fire conditions and prior fire histories are often unknown. Long-term studies of forest development following fires of known origin date and severity that include interactions with subsequent reburns are especially rare. Investigations of reburn effects and ecological resilience to wildfire would be strengthened by a study design that controlled for initial conditions, especially the severity of the initial fire in reburn sequences.

The remoteness and early wilderness designation of the SBW (administratively classified as a primitive area in 1936 and congressionally designated as wilderness in 1964) precluded timber harvest and reforestation activities, allowing post-fire succession to proceed naturally after large, severe early 20th century fires. Changes in wilderness fire management policy in 1972 restored fire as an ecological process to the SBW after a relatively brief and largely ineffective period of fire suppression, allowing for a contemporary active fire regime in the SBW for the last half century (Larson, 2016; Berkey et al., 2021b). This history provides a unique opportunity to investigate the long-term effects of initial high-severity fire and subsequent reburning in a modern active fire regime on forest ecosystem resilience, including forest structure, tree regeneration, and fuels—a critical research need in the context of ongoing and anticipated forest ecosystem changes (Abatzoglou and Williams, 2016; Littell et al., 2018; Parks and Abatzoglou, 2020; Davis et al., 2023).

Here, we investigate the resilience of northern Rocky Mountain mesic mixed-conifer forest ecosystems to wildfire in terms of tree regeneration, stand structure, species composition, and fuels. We compare sites that experienced high-severity fire in the early 20th century and ask how tree regeneration, forest structure and composition, and fuels differ across areas that have not burned, burned once, or burned twice after an initial high-severity fire in the early 20th century.

2. Methods

2.1. Study area

This research was conducted in the Selway-Bitterroot Wilderness (SBW) (Fig. 1). The SBW is a 545,372 ha congressionally designated wilderness area situated in western Montana and north central Idaho, USA. The elevational range of the SBW is 531 m to 3,096 m and it has a mean annual precipitation 1221 mm and a mean annual temperature of 3.5 °C, Daly et al., 2002). Low and middle elevation forests in the study area are composed of ponderosa pine (*Pinus ponderosa*) and Douglas-fir (*Pseudotsuga menziesii*) on warm and dry sites, with variable mixtures of western redcedar (*Thuja plicata*), grand fir (*Abies grandis*), western white pine (*Pinus monticola*), and Engelmann spruce (*Picea engelmannii*) on mesic sites (Finklin, 1983; Rollins et al., 2000; Berkey et al., 2021a).

Table 1
Forest structure, plant life form, and fuels metrics derived from field measurements in this study.

Variable	Units
1-hour fuel load	kg/m^2
10-hour fuel load	kg/m^2
100-hour fuel load	kg/m^2
Average depth of litter per plot	cm
Average depth of duff per plot	cm
Coarse woody material (CWM)	m^3/ha
Total seedlings (<1.37 m tall)	stems/ha
Total saplings (>1.37 m tall and <10 cm DBH)	stems/ha
Shrub load	kg/m^2
Herb load	kg/m^2
Basal area of live trees	m^2/ha
Basal area of dead trees	m^2/ha
Quadratic mean diameter of live overstory trees (QMD)	cm

2.2. Fire history records and sample design

We created a fire atlas of burn perimeters and fire severity for the SBW for 1870–2020, combining 1) a historical dataset of fire perimeters and severity from 1870 to 2000 (Morgan et al., 2017); 2) a modern dataset of fire perimeters and satellite-derived severity metrics from 1972 to 2015 (Parks et al., 2015), which we extended to the years 2016–2020 using similar methods. The historical dataset contains fire perimeters and fire severity patches (high, moderate, low) delineated by hand and determined by photo-interpreted evaluation of tree mortality (Morgan et al., 2017). The modern dataset was generated from fire perimeters identified with satellite imagery (Parks et al., 2015). To determine what areas burned at high severity in the early 1900s for field sampling, we combined the historical and modern datasets into a single fire occurrence and severity atlas, after verifying that high-severity classification was consistent among the two datasets (Appendix A).

Sampling was constrained by severity of the first fire: all initial fires had to be high severity and to have occurred in regional fire years, as defined by Morgan et al. (2008). Regional fire years of the early 20th century in the SWB were 1910, 1919, and 1934. These are the years in which area burned exceeded the 90th percentile of annual fire extent from 1900 to 2003 (Morgan et al., 2008). Prior to the first high-severity fire, all sampling areas had not burned since at least 1870 (the earliest year in the fire atlas). These areas burned again up to a total of three times with the second and third fires occurring in the modern period, after 1979. The areas identified as close to one another within the same watershed that had the target fire history—that had been burned once, twice, and three times—are hereafter referred to as a block. The most recent fire burned in 2017, giving four years for conifer tree seedlings to establish and begin a post-fire successional trajectory (Clark-Wolf et al., 2022). The first, second, and third fires all had to be within the same watershed in any sampling block. Given these constraints, the sites selected for sampling had initial high-severity fire in 1910 and 1934. Sampling was also constrained by vegetation type. LANDFIRE Environmental Site Potential (ESP; LANDFIRE, 2016) was used to locate potential sampling areas in the Northern Rocky Mountain Dry-Mesic Montane Mixed Conifer Forest and Northern Rocky Mountain Mesic Montane Mixed Conifer Forest.

The fire weather of 1910 and 1934 was arid and extreme even by today's standards (Diaz and Swetnam, 2013). The mean temperature in 1910 and 1934 was 5.5 °C and 7.7 °C, respectively; while the average temperature from the last 15 years (2007–2022) was 5.6 °C (PRISM Climate Group, 2014). Similarly, the mean vapor pressure deficit (VPD) was 7.56 hPa and 8.83 hPa in 1910 and 1934, respectively; while the mean VPD for the last 15 years has been 7.11 hPa (PRISM Climate Group, 2014).

We calculated severity for the fires identified by the modern dataset (Parks et al., 2015) using the modelled composite burn index (CBI) (Key and Benson, 2006) from remote sensing imagery using methods and code from Parks et al. (2019). Then, we determined what CBI cut-off corresponded to a high-severity classification in the historical dataset using the temporal overlap of the datasets (1972–2020). Using a moving window summary, we smoothed the satellite-derived severity of the modern dataset to match the patch size and composition of the historical dataset (Appendix A). A patch being an area of the fire that burned at a severity classification. We created binary classifications of high-severity and non-high-severity fire for the smoothed raster. We then created an interior buffer of 120 m (4 pixels), delineating core high-severity patches to reduce the likelihood of potential projection or delineation error that may have occurred in the creation of the historical dataset (Appendix A).

We then randomly selected three sample points in each fire history patch for a total of nine plot locations per block. We sampled nine blocks with nine plots per block, for a total of 81 plots. We ensured that it was feasible to reach each plot and that they were on a slope of 40° or less for safety through a review of satellite imagery and slope layers.

2.3. Field measurements

We recorded plot locations using submeter GPS (Juniper Systems, Geode GNSS receiver), as well as slope, aspect, elevation, and the distance to nearest live conifer seed tree (measured with a laser rangefinder). We censused all mature trees (≥10 cm DBH) within a 17.84 m fixed radius of plot center, recording species, diameter at breast height (DBH), and mortality status for each tree. We censused saplings (trees >1.37 m tall and <10 cm DBH) within a 5.64 m fixed radius plot, recording species, DBH in bins of 2.5 cm, and mortality status. A 20 m transect oriented at a random azimuth was used to sample tree seedlings (<1.37 m tall), canopy cover, and fuels. Established seedlings were censused within a 2 m by 20 m rectangular plot (1 m on either side of the central transect). We recorded seedling species, mortality status, and height (within 40 cm height classes). First year seedlings were not recorded, as high seedling mortality is possible during the first growing season (Rank et al., 2022). Canopy cover was assessed using a point intercept method with a densitometer (GRS densitometer) at one-meter intervals along the transect from 2 to 22 m, starting two meters away from plot center, in a random direction, to avoid trampling plot center. At 6 m, 11 m, 16 m, and 21 m along the transect, litter and duff depth were measured to the nearest 0.1 cm by excavating to bare mineral soil. Fine woody surface fuels and live fuels (herbs and shrubs) were measured using the photoload method (Keane and Dickinson, 2007) with 1 m^2 microplots located at 6 m, 11 m, 16 m, and 21 m along the transect for a total of four microplots per plot. Coarse woody material (CWM) are 1000-hour fuels (diameter >7.62 cm) with no minimum length. CWM was measured within a 100 m^2 (10 m × 10 m) plot. Within the plot, we measured the small and large end diameters and length of the portions of all CWM laying with the plot boundaries as well as length and decay class (Lutes et al., 2006). If there were more than ten CWM pieces, we estimated diameters and length of remaining pieces. We also measured canopy fuel height, recording the average crown base height and lowest crown base height (Lutes et al., 2006).

2.4. Data reduction and analysis

All measured forest structure and fuels variables were summarized at the plot level (Table 1). We averaged the four litter and duff measurements taken within the plot to derive a single value. CWM was converted from small and large end diameters and length to volume using the Smalian method (Filho et al., 2000). All other woody fuels were directly measured in kg/m^2 (Keane and Dickinson, 2007). Live and dead tree basal area, CWM, seedlings, and saplings were expressed on a per hectare basis.

Topographic Wetness Index (TWI) and heat load are important environmental covariates that that can impact fire behavior and fire effects, as well as post-fire forest development (Heyerdahl et al., 2001; Meigs et al., 2020). TWI is a measurement of topographic convergence

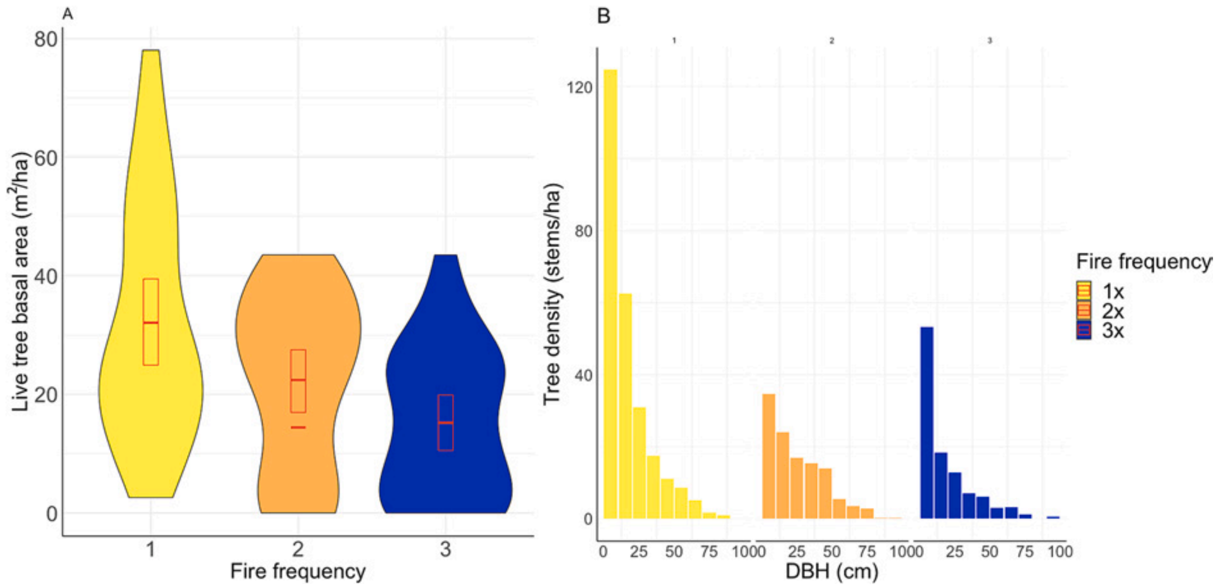

Fig. 2. Live tree structure variables. Saplings (1.37 m in height to 10 cm in DBH) are included in the DBH distribution. (A) Basal area of live trees by number of times burned. (B) Distribution of diameter at breast height (DBH) classes by trees per hectare in 10 cm bins.

Table 2
√Live basal area linear mixed model (LMM) ANOVA table of the important explanatory variables and their associated coefficients, F-values, standard errors, and p-values. Fire frequency had two degrees of freedom.

Variable	Coefficient	F-value	Standard error	p-value
Fire frequency (2x)	−1.26	3.24	0.82	0.14
Fire frequency (3x)	−2.12		0.82	0.02
TWI	−0.04	0.04	0.18	0.72
Heat load	−2.94	5.46	1.26	0.02

that predicts net incoming and outgoing drainage with larger values corresponding to relatively wetter sites (Beven and Kirkby, 1979). Heat load is an adjusted version of solar radiation that is calculated from latitude, aspect, and slope; it accounts for south-west facing slopes being warmer (higher heat load values) than north-east facing slopes (lower heat load values) (McCune and Keon, 2002). We calculated TWI using the RSAGA package (Brenning et al., 2018) in R (R Core Team, 2021) and used the Jefferies and Welty (2018) dataset for heatload.

Linear mixed models were also used to determine the importance of fire frequency on live tree basal area (BA) and dead tree (snag) basal area, CWM, herb load, and shrub load. To account for the nested nature of the data (i.e. plots within fire history patches within blocks), we used linear mixed models (Zuur et al., 2009) with the nlme package (Pinheiro et al., 2022). Explanatory fixed-effects variables were burn, block, TWI, and heat load, and random-effect variable was burn-within-block (Block:Burn). We used this approach to account for variability among groups of plots with the same fire frequency within a block (Zuur et al., 2009). We ranked potential models using Akaike information criterion (AIC) (Eilers and Marx, 1996) and used 95% confidence intervals to determine significance. All response variables were square root transformed prior to analysis.

Principle Component Analysis (PCA) was conducted using forest structure, fuels, and regeneration data (Table 1) to visualize and explore

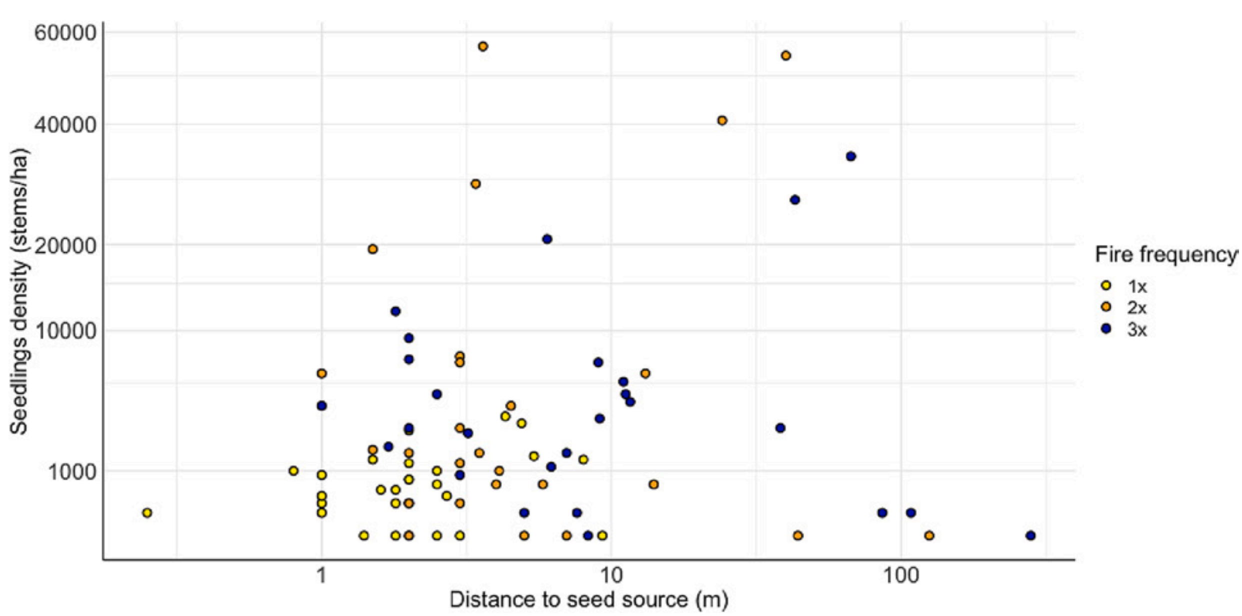

Fig. 3. Distribution of seedlings based on seed source proximity. X-axis is log base 10 transformed and y-axis is square root transformed.

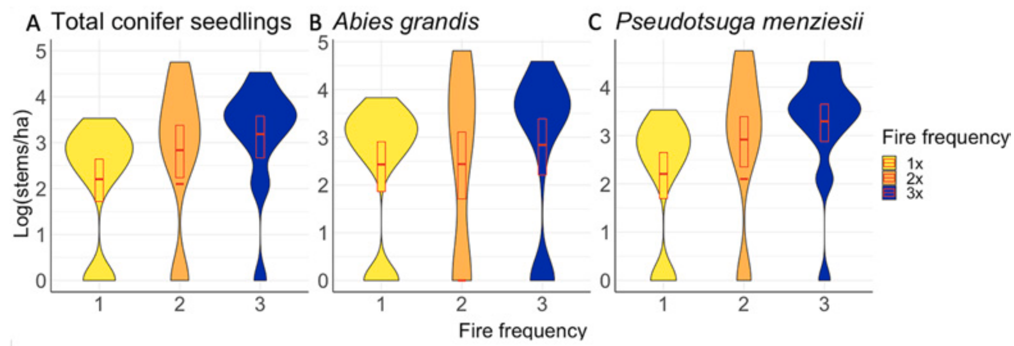

Fig. 4. Conifer tree regeneration by fire frequency. (A) Abundance of all seedlings of all species by burn frequency. (B) Abundance of *Abies grandis* seedlings by fire frequency. (C) Abundance of *Pseudotsuga menziesii* seedlings by fire frequency.

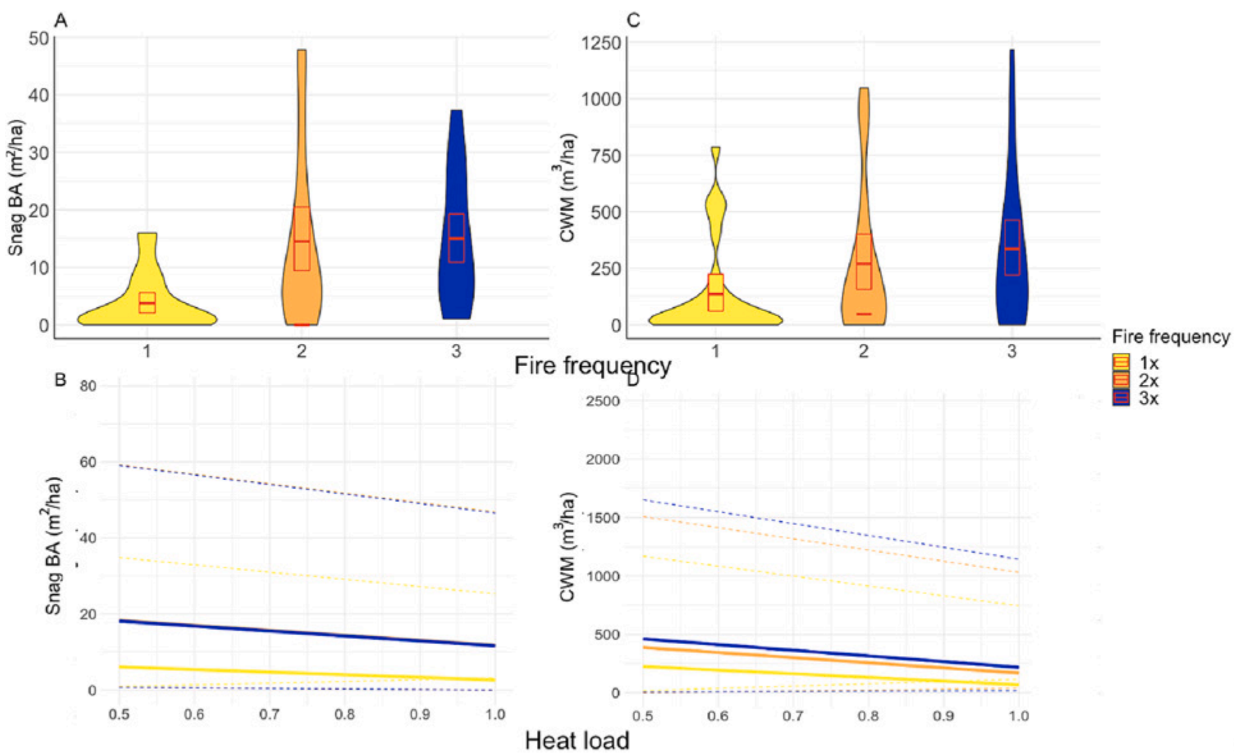

Fig. 5. Dead woody material variables. (A) Basal area of snags by fire frequency. (B) Predicted values of snag basal area across different burn histories and heat load with TWI held at the mean value. (C) Volume of coarse woody material (CWM) by fire frequency. (D) Predicted values of CWM across heat load and different burn histories with TWI held at the mean value.

Table 3
√Dead Basal area linear mixed model (LMM) ANOVA table of the important explanatory variables and their associated coefficients, F-values, standard errors, and p-values. Fire frequency had two degrees of freedom.

Variable	Coefficients	F-value	Standard error	p-value
Fire frequency (2×)	1.81	8.3	0.53	0.004
Fire frequency (3×)	1.76		0.53	0.004
TWI	0.41	7.26	0.15	0.01
Heat load	−1.88	3.23	1.05	0.78

Table 4
√CWM area linear mixed model (LMM) ANOVA table of the important explanatory variables and their associated coefficients, F-values, standard errors, and p-values. Fire frequency had two degrees of freedom.

Variable	Coefficients	F-value	Standard error	p-value
Fire frequency(2x)	4.61	3.01	3.02	0.14
Fire frequency (3x)	6.46		3.03	0.05
TWI	1.74	3.65	0.94	0.07
Heat load (−)	−16.50	6.70	6.37	0.01

the relationship between fire frequency and forest structure, composition, and fuel load in multivariate space. The data matrix for PCA had 81 rows, one for each plot, and 13 columns. All data used in the PCA were centered and scaled prior to analysis.

3. Results

3.1. Fire history

The areas that burned once had an average time since fire of 103 years, as these areas only burned in either 1910 or 1934. Once-burned

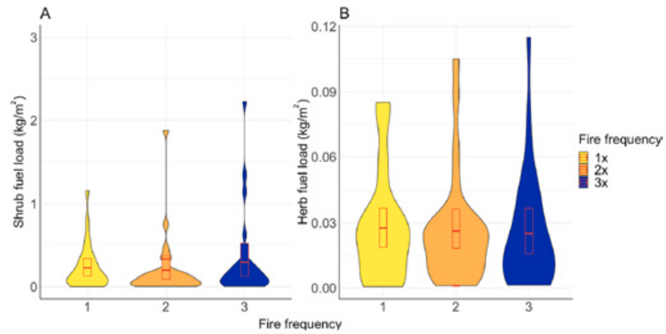

Fig. 6. Live fuels across fire frequency. (A) Shrub load by fire frequency. (B) Herb load by fire frequency.

Table 5
√Shrubs linear mixed model (LMM) ANOVA table of the important explanatory variables and their associated coefficients, F-values, standard errors, and p-values. Fire frequency had two degrees of freedom.

Variable	Coefficients	F-value	Standard error	p-value
Fire frequency (2×)	−0.17	0.81	0.09	0.08
Fire frequency (3×)	−0.15		0.10	0.14
TWI	0.01	0.0001	0.04	0.87
Heat load	0.20	3.02	0.24	0.42
Live tree basal area	−0.01	9.25	0.002	0.004

Table 6
√Herbs linear mixed model (LMM) ANOVA table of the important explanatory variables and their associated coefficients, F-values, standard errors, and p-values. Fire frequency had two degrees of freedom.

Variable	Coefficients	F-value	Standard error	p-value
Fire frequency (2×)	−0.01	1.18	0.02	0.65
Fire frequency (3×)	−0.03		0.02	0.18
TWI	0.01	1.04	0.01	0.29
Heat load	−0.003	0.29	0.06	0.96
Live tree basal area	−0.001	4.09	0.0006	0.05

areas make up 24% (129,682 ha) of the SBW. The areas that burned twice had an average time since fire of 11 years with the maximum time being 22 years and the minimum time being 4 years. Twice-burned areas make up 7% (38,014 ha) of the SBW. The areas that burned thrice had an average time since fire of 5 years with a minimum of 4 years and a maximum of 6 years. The average time between the first and second fire is 78 and years while the average time between the second and third fire was 14 years. The three times burned areas make up 1% (3999 ha) of the SBW.

3.2. *Live trees and tree seedlings*

There were six species of mature live trees detected in our field sample: *Abies grandis*, *Picea engelmannii*, *Pinus contorta* (lodgepole pine), *Pinus ponderosa*, *Pseudotsuga menziesii*, and *Thuja plicata*. Forty-six percent of overstory trees were *Abies grandis* (stem basis). The second most abundant species was *Pseudotsuga menziesii,* making up 33% of total composition. *Thuja plicata*, *Pinus ponderosa, Picea engelmannii,* and *Pinus contorta* were 10%, 8%, 2%, <1% of stems, respectively. *Abies grandis* was more abundant in the once-burned sites compared to the twice- and thrice-burned sites. Almost all *Picea engelmannii* was present in once-burned sites. *Pinus contorta* was quite rare, though a few were found in the thrice-burned areas. *Pinus ponderosa* was more abundant in the twice- or thrice-burned areas, particularly the latter. *Pseudotsuga menziesii* was most abundant in the twice-burned sites. *Thuja plicata* occurred most frequently in the once-burned sites.

Live tree basal area decreased with increasing fire frequency (Fig. 2; Table 2). The once-burned sites had a mean basal area of 32.1 m^2/ha (3.89 m^2/ha standard error) while twice- and thrice-burned had a mean basal area of 21.1 m^2/ha (2.74 m^2/ha standard error) and 14.2 m^2/ha (2.52 m^2/ha standard error), respectively. In the sites that burned two or three times, the mean dbh of trees was larger, compared to the sites that had not burned (Fig. 2). The average diameter of the trees for once-, twice-, and thrice-burned areas was 27 cm (0.48 standard error), 33 cm (0.65 standard error), 30 cm (0.86 standard error), respectively. Mean sapling density was highest in the once-burned sites (125 stems/ha), followed by thrice-burned (53 stems/ha), and twice-burned (35 stems/ha).

Tree regeneration was abundant across all three burn histories.

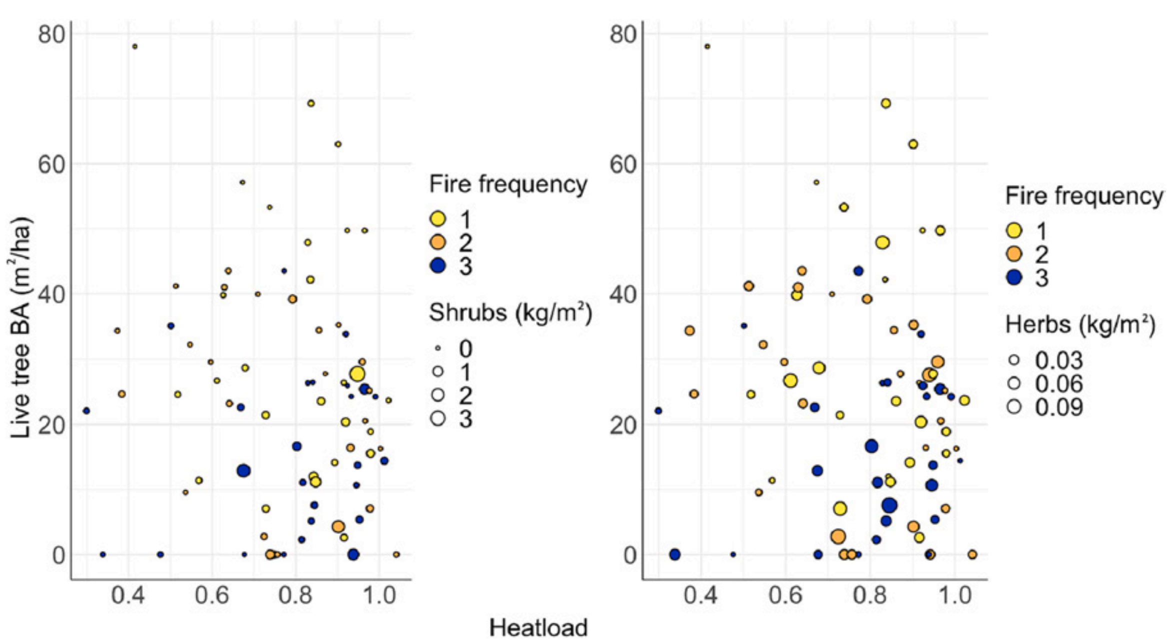

Fig. 7. (A) Variation of shrub biomass across live tree basal area (BA) and heat load. (B) Variation of herb biomass across live tree BA and heat load. Symbol color corresponds to fire frequency, symbol size refers to fuel loading (shrub/herb).

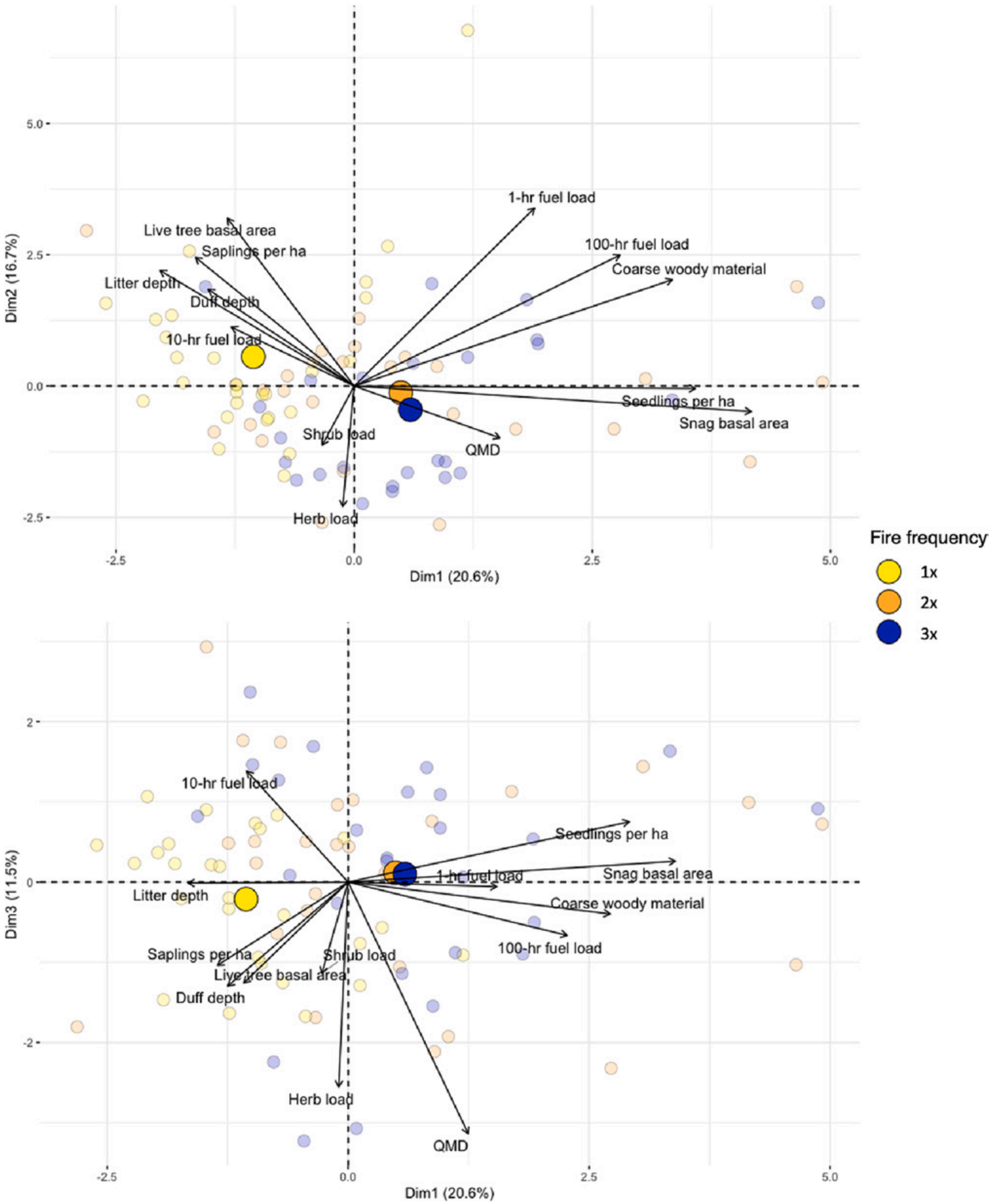

Fig. 8. Principal Component Analysis of forest structure and fuels variables for each fire frequency. The first three principal components explain 48.8% of the total variability in the dataset. The large bold symbols are the mean of each burn history, and the smaller more muted symbols are the individual sample plots.

Regeneration was not limited by seed source availability as 99% of plots (all but one) were within 200 m of a seed source when sampled in 2021. Distance to seed source following the initial early 20th century fires is unknown, but measured distance to seed source in 2021 is a reasonable index of recent propagule pressure that would have contributed to establishment of seedlings measured in 2021 in all three burn histories. The average distance to seed source for once-burned, twice-burned, and thrice-burned sites was 2.6 m, 11.9 m, and 28.1 m, respectively. Increasing distance to seed source did not impact seedling recruitment (Fig. 3).

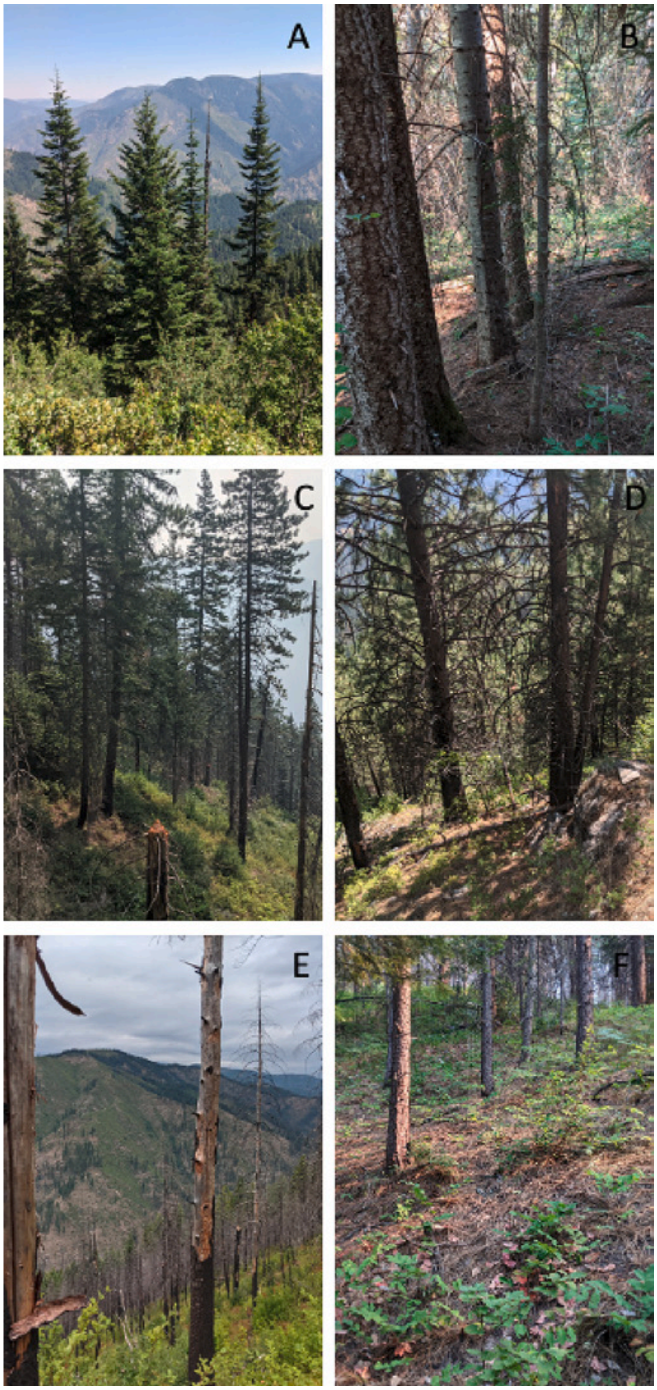

Fig. 9. Photos (taken in 2021) illustrating representative conditions from select sample plots. (A & B) once-burned, (C&D) twice-burned, (E&F) thrice-burned. Northern Rocky Mountain Mesic Montane Mixed Conifer Forest (LANDFIRE 2016), Selway-Bitterroot Wilderness, Idaho, USA.

There were more seedlings in the twice- and thrice-burned sites compared to the once-burned sites (Fig. 4a), with mean seedling density for once-, twice-, and thrice-burned of 796 (S.E. 6.3 stems/ha), 8,732 (S.E. 32.9 stems/ha), and 6,087 stems/ha (S.E. 21.4 stems/ha), respectively. Seedlings species found within the study area included *Abies grandis, Pseudotsuga menziesii, Picea engelmannii, Pinus ponderosa, Thuja plicata*, though most were *Abies grandis* and *Pseudotsuga menziesii*. *Abies grandis* was the most abundant species of tree regeneration but was proportionally higher in the once-burned sites, while *Pseudotsuga menziesii* was proportionally higher in the twice- and thrice-burned sites. *Abies grandis* had a mean of 1,519 stems/ha (8.6 stems/ha standard error) in the once-burned area and had mean 9,830 stems/ha (33.9 stems/ha standard error) and mean 6,990 stems/ha (24.2 stems/ha standard error) in twice- and thrice-burned area, respectively (Fig. 4b). *Pseudotsuga menziesii* had even fewer seedlings in the once-burned with a mean of 46 stems/ha (0.3 stems/ha standard error) with a larger contrast to the twice- and thrice-burned with a mean of 6777 stems/ha (S.E. 43.0 stems/ha) and a mean of 4519 stems/ha (S.E. 19.7 stems/ha), respectively (Fig. 4c).

There were 13 plots in which conifer seedlings were not present. 10 of those 13 plots contained live overstory trees, and once-burned (in 1910 or 1934) sites were the most common burn history without conifer seedlings in 2021 ($n = 6$). Ninety-six percent of field plots were in communities that were either persisting as or regenerating to coniferous forest (i.e., either live overstory trees or tree saplings present in the plot). All three plots with no live overstory trees and no seedlings experienced fire in 2017; of these, two plots were in twice-burned patches and the remaining plot was in a thrice-burned area. In no case did conifer regeneration failure occur in all three sample plots within any block-burn history combination.

3.3. Standing dead trees and down woody material

Standing dead tree basal area increased with increasing fire frequency (Fig. 5; Table 3). Once-burned sites had a mean dead basal area of 3.8 m^2/ha while twice- and thrice-burned had a mean basal area of 14.0 m^2/ha and 15.0 m^2/ha, respectively. Dead basal area was inversely related to heat load (Table 3).

Volume of CWM increased with increasing fire frequency (Fig. 5, Table 4). The mean fuel load for CWM for once-, twice-, and thrice-burned sites was 184 m^3/ha, 303 m^3/ha, and 306 m^3/ha, respectively. As seen in Fig. 5D, the predicted lines for twice- and thrice-burned are very similar but there is a large departure from the once-burned predicted values.

Other fuels variables measured include 1-, 10-, and 100-hour fuels as well as litter and duff. One-hour fuels were very similar across all three burn histories but skewed higher slightly for the once-burned (median 0.06 kg/m^2) compared to twice- (median 0.05 kg/m^2) and thrice-burned (median 0.05 kg/m^2) sites. Ten-hour fuels had the highest mean (0.11 kg/m^2) but the lowest median (0.04 kg/m^2) in the once-burned compared to the twice-burned (mean 0.08 kg/m^2, median 0.05 kg/m^2) and thrice-burned (mean 0.09 kg/m^2, median 0.06 kg/m^2). Hundred-hour fuel loadings were highest in the twice-burned (mean 0.18 kg/m^2) followed by the thrice-burned (0.14 kg/m^2) and once-burned (0.12 kg/m^2). Both litter and duff depths were inversely related to fire frequency with litter having deepest average depth in once-burned (1.9 cm) followed by twice-burned (1.0 cm) and thrice-burned having the shallowest average (0.9 cm). Duff had a similar pattern having the deepest average depth in once-burned (1.4 cm) followed by twice burned (0.9 cm) and thrice-burned having the shallowest average (0.5 cm).

3.4. Live fuels: shrubs and herbs

Shrub load was not related to fire frequency (Table 4; Fig. 6) or TWI and marginally related to heat load. Mean shrub load for once-, twice-, and thrice-burned sites was 0.46 kg/m^2, 0.24 kg/m^2, and 0.39 kg/m^2 (Fig. 6A), respectively. Herb load was not related to fire frequency and had a mean of 0.04 kg/m^2 for all burn histories (Table 5; Fig. 6B). Heat load and TWI were also not related to herb load (see Table 6).

Shrub dominated sites were characterized by high heat load and low overstory tree basal area, independent of fire history (Fig. 7). High shrub loads only occurred at sites where both heat load was >0.65 and live tree basal area was <30 m^2/ha. Herb load had a similar but less drastic pattern. Herbs were more abundant on sites with high heat load (>0.6) and low live overstory tree basal area (<40 m^2/ha).

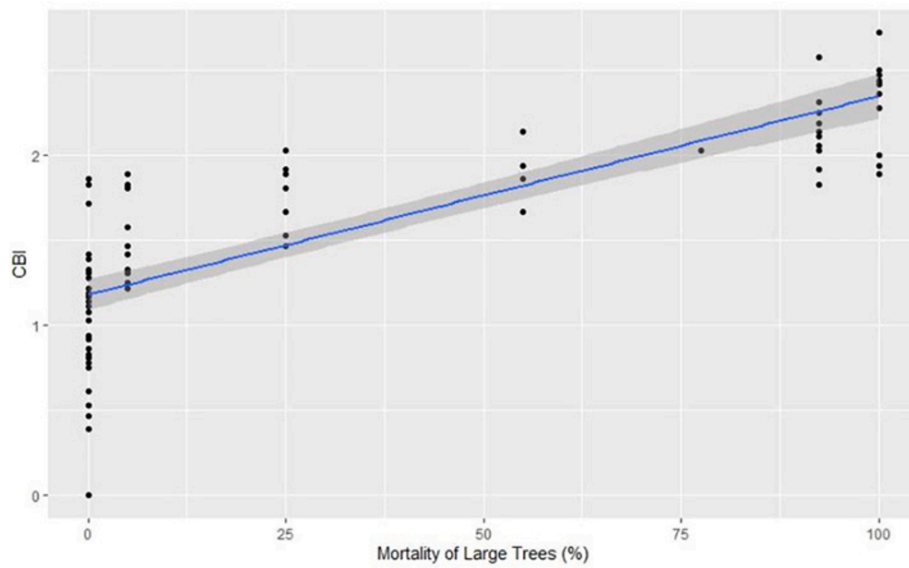

Fig. A1. Linear regression of composite burn index (CBI) on percent large tree mortality.

Table A1
The CBI equivalent of percent mortality for the different severity cutoffs.

Severity	% Mortality of Large Trees	CBI
High	<70%	≤2.00
Moderate	20%–70%	1.54–1.99
Low	>30%	≥1.53

3.5. *Forest structure, composition, and fuels in PCA space*

Differences of forest structure, composition, and fuels as described by the variables in Table 1 among fire frequencies were evident in the PCA analysis (Fig. 8). The first three axes of the PCA explained 20.6%, 16.7%, 11.5% of variation in the data, respectively. Number of times burned in the twentieth century showed the greatest separation across PCA1, with once-burned occupying the left end of the gradient, and twice- and thrice- burned on the right. This first PC is therefore interpreted as representing a gradient of structural conditions ranging from lower fire resistance/longer time since fire (left) to higher fire resistance/shorter time since fire (right). The second axis represents life form dominance, where low or negative values correspond to shrub and herb dominated areas and high or positive values represent more tree dominated areas. The third axis is correlated with a tree size gradient. There is little separation of burn history across axes two and three. This is consistent with the analysis of shrub and herb fuel loading in relation to fire history (Fig. 6), where these variables were not related to fire history.

4. Discussion

Mesic mixed-conifer forest ecosystems of the US northern Rocky Mountains we sampled remain resilient to wildfires, including short-interval reburns that occurred between 1979 and 2017. These sites are largely either persisting as, or regenerating to, forest ecosystems. Twice- and thrice-burned sites supported mean live overstory basal areas of 21.1 m^2/ha and 14.2 m^2/ha, respectively (Fig. 2). Conifer regeneration was abundant in almost all our field plots, and broadly reflected the landscape species composition of mature, seed producing trees. Subtle compositional differences of regenerating conifer trees were apparent along the fire frequency gradient we sampled, but they were relatively minor and consistent with expectations from successional theory and species traits. Our results confirm the general findings of Davis et al. (2023), who showed that the wetter and cooler portions of the northern Rockies ecoregion are expected to remain climatically suitable for post-fire conifer regeneration through mid-century. This is important because our field plots occupy the largest geographic gap in the Davis et al. (2023) dataset—the vast forested region of northcentral Idaho and northwest Montana dominated by mesic mixed-conifer forests. Thus, while the compound stressors of climate change and repeated severe fires are already compromising ecosystem resilience and causing transitions to non-forest on stressful dry sites (Coop et al., 2020; Steel et al., 2021), these sites in the northern Rockies mesic mixed-conifer forests appear to remain resilient to wildfire (Hessburg et al., 2019).

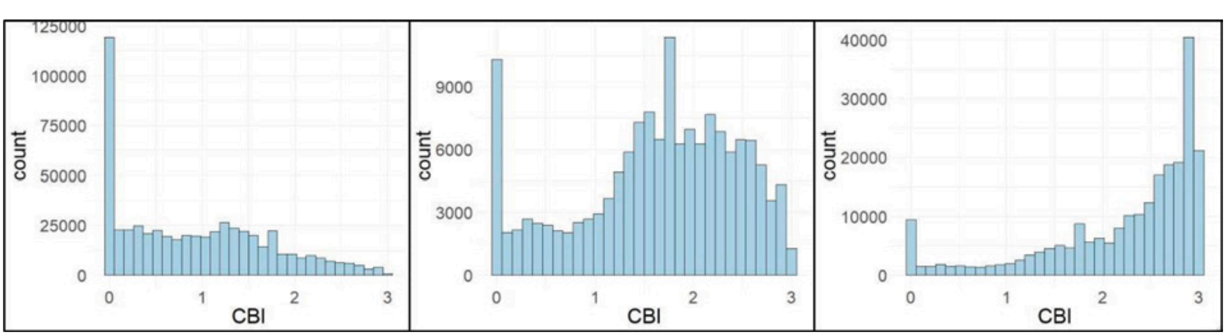

Fig. A2. CBI of historical dataset (A) fire perimeters classified as low severity (B) fire perimeters classified as moderate severity (C) fire perimeters classified as high-severity.

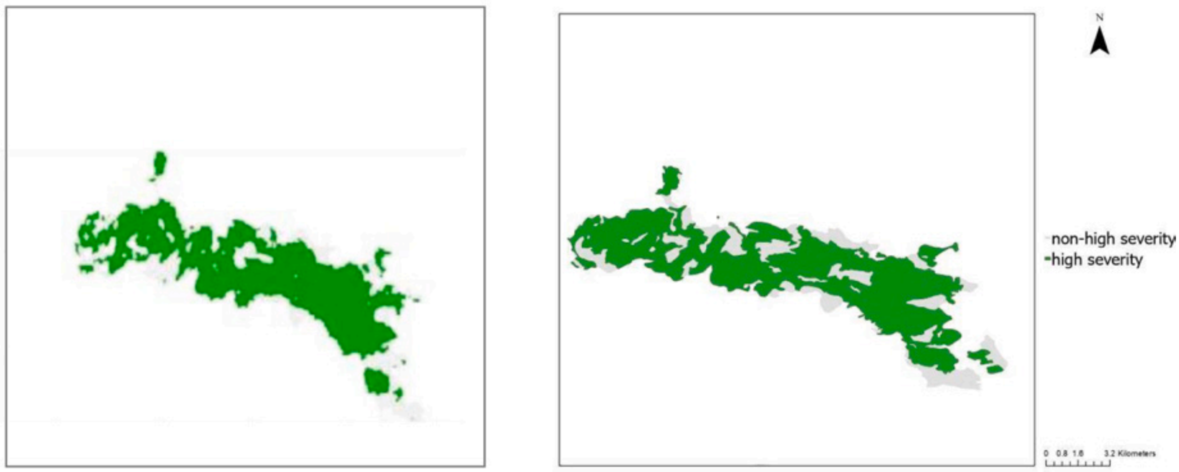

Fig. A3. (A) CBI classified fire perimeter with a 7 × 7 moving window summary. Historical is pixels with ≥2 CBI and grey <2 CBI. (B) photo-interpreted classification of severity with green being high-severity and grey non-high severity. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Table A2
Confusion matrix output for 7 × 7 moving window summary.

	Photo-Interpretation Method		
CBI Severity Method		Non-high severity	High-severity
	Non-high Severity	1,116,490	63,203
	High-Severity	33,421	164,677

4.1. Forest structure and composition reflects fire frequency

Fire frequency affects composition and abundance of both mature trees and seedlings. Fire tends to kill smaller trees because they have less developed fire-resistance traits than mature trees (i.e., thinner bark and lower crowns) of the same species (Agee, 1993; Keane et al., 2002). Regeneration was especially more abundant in forests that had burned two or three times, despite the dominant species *Pseudotsuga menziesii and Abies grandis* not being the most fire-resistant (Stevens et al., 2020). Fire frequency increased live tree QMD and decreased density, indicating a thin-from-below effect of fires on forest structure. This finding is illustrated in the contrast between the once-burned photo example (Fig. 9B) and the thrice-burned photo example (Fig. 9F), where the once-burned example has small trees and saplings, and the thrice-burned example has only widely spaced large trees.

Though some recent studies have found widespread evidence of regeneration failure in dry conifer forests (Stevens-Rumann et al., 2018; Davis et al., 2019), this was not the case in our study. Regeneration was not limited in terms of seedling abundance or seed source. Recently burned (i.e., twice- and thrice-burned) sites had more seedlings than sites that burned only once. Given the relatively mesic environment of SBW, trees are regenerating across all fire histories, similar to findings from other moist mixed-conifer forests (Povak et al., 2020; Clark-Wolf et al., 2022). In contrast to several previous studies, seed source was

Fig. A4. Progression of interior buffering. (A) The initial high-severity patches without buffering for a single example fire perimeter. (B) Buffering by one pixel. (C) Buffering by two pixels. (D) Buffering by three pixels. (E) Buffering by four pixels.

Table A3
Confusion matrix of 7 × 7pixel moving window summary with 120 m interior buffer.

	Photo-Interpretation Method		
CBI Severity Method		Non-high severity	High-severity
	Non-high Severity	0	0
	High-Severity	10,594	96,077

not a limiting factor for any burn history, likely because all plots were within 200 m of seed-bearing trees (McDonald, 1980). It is possible that future extreme fire events may create very large high-severity patches that exceed threshold dispersal distances, resulting result in conifer tree regeneration failure, though we did not find evidence of this in our dataset.

Pseudotsuga menziesii was especially more abundant in areas that burned two and three times, indicating early seral successional role for this species in this forest type, where open canopy and less litter and duff favored regeneration (Clark-Wolf et al., 2022). *Abies grandis* was more abundant (in relative terms) in the once-burned sites. This species was able to regenerate in more closed canopy areas with higher litter and duff levels, acting as a later seral species. True shade-intolerant species regeneration (*Pinus ponderosa, Pinus contorta,* and *Larix occidentalis*) was rare. This is consistent with the rarity of these species in the overstory—there is limited seed source for these species across the study area. Even with an active fire regime, with a lack of local seed source, these shade-intolerant species were unlikely to regenerate at our sites.

4.2. Fire history impacts fuels for decades

Both standing dead trees and CWM were lowest in the once-burned sites and increased with increasing fire frequency. Standing dead trees and CWM ultimately originate from the same source—live trees—but have different pathways and residence times to reach their status. Live trees become snags, then snags' tops break or rot topples them and they become CWM (Harmon et al., 1986; Franklin et al., 1987; Stevens-Rumann et al., 2020). Fires also accelerate transition of standing snags to CWM when fires burn through snag bases, causing snags to fall (Cansler et al., 2019). Conversion of snags to CWM is also impacted by site condition due to decay rates (Lydersen et al., 2019; Stevens-Rumann et al., 2020), which may be why heat load and TWI were important explanatory variables for standing dead wood and CWM. Once-burned sites have the lowest snag BA because the original inputs from the high-severity fires in the early twentieth century had mostly decomposed by the time of our sampling, but little dead wood from the current overstory has recruited due to the lack of additional fires to cause tree mortality (Agee and Huff, 2011). The differences between the twice- and thrice- burned sites for these fuels is likely caused by additional fires both consuming dead wood and increasing the pool of dead wood through fire-caused mortality (Donato et al., 2016). CWM has a longer residence time than snags and has two potential fates: fire immediate consumption in reburns (Fig. 9E & F), or slow decomposition in the absence of fire (Fig. 9B) (Ward et al., 2017).

The smaller woody fuels were highly variable in space and time, typical of these variables (Keane, 2015), and few differences were observed across burn histories in 1-hour, 10-hour, and 100-hour fuels. The lack of differences is likely driven, in part, by the sampling occurring in tree-dominated areas where fine fuels are both ephemeral and mobile. They may originate from either live or dead wood and thus the supply is potentially high compared to the losses. In our study, ground fuels have an inverse relationship with fire frequency, which may be related to time since fire. Litter and duff take time to accumulate and have high consumption rates in most fires regardless of severity (Cansler et al., 2019; Larson et al., 2020; Stevens-Rumann et al., 2020).

4.3. Live fuels: shrubs and herbs

Neither shrubs nor herbs were significantly related to fire frequency. In stands with higher basal areas there were fewer shrubs, suggesting a potential competitive effect of overstory trees on the growth and biomass accumulation of shrubs in the understory (Tepley et al., 2018a; Jaffe et al., 2021). Plots with high shrub and herb biomass tended to occur on high heat load sites, irrespective of fire history (Fig. 7), suggesting the abundance of these plant life forms is more sensitive to site environmental conditions than to burn history.

Though other studies have identified type changes from forest to shrub-dominated conditions, we found no evidence of this in the majority of sample plots. Hotter and drier sites, with higher heat load, are more likely to have converted from forest to shrublands following the

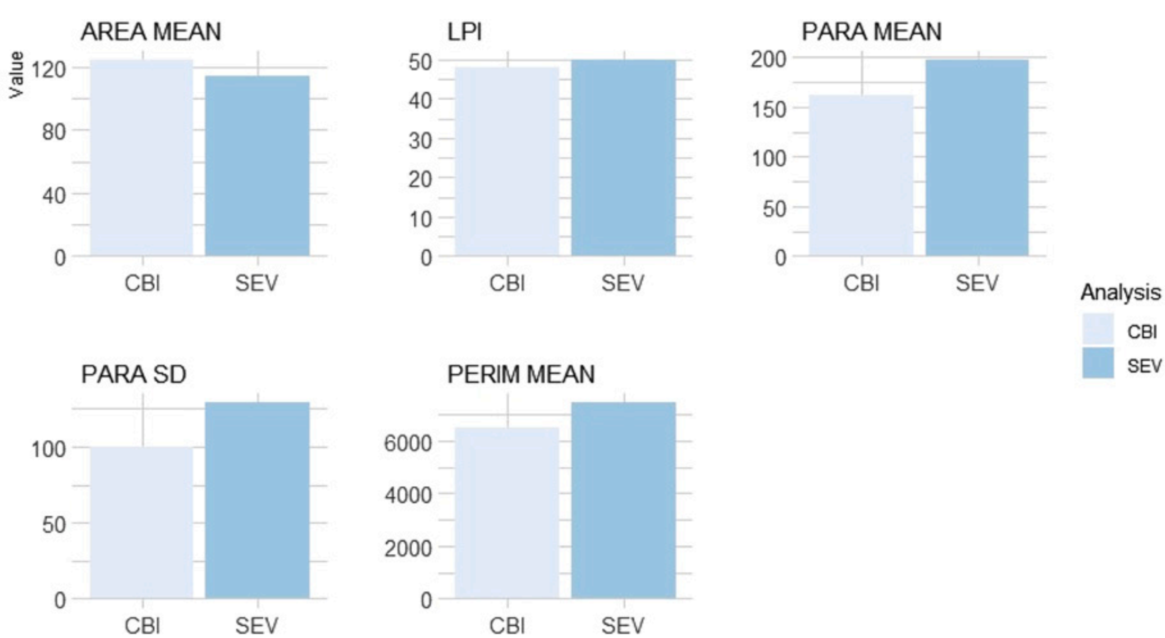

Fig. A5. Patch metrics for CBI and photo-interpretation method for core high-severity patches. Variables investigated were mean perimeter area ratio (PARA MEAN), perimeter area ratio standard deviation (PARA SD), mean patch area (AREA MEAN-ha), mean patch perimeter (PERIM MEAN-m), largest patch index (LPI-%).

initial high-severity fire in the early 20th century (Coop et al., 2020). However, this pathway was rare in our dataset, and most sites regenerated to tree-dominated forest communities. When forests types do change to shrub types, shrubs can remain in this alternative stable state and sometimes sustain more frequent burning (Coppoletta et al., 2016; Ferguson and Byrne, 2016; Tepley et al., 2018). In these situations, trees are either unable to re-establish or establish sparsely interspersed with mature shrubs. This suggests that shrubs become more competitive in these post-burn environments (Donato et al., 2016; Stevens-Rumann and Morgan, 2016; Harvey et al., 2016).

4.4. Conclusions and management implications

In this field study we showed that fires and fire history strongly influenced forest structure, composition, and fuels in the mesic mixed-conifer ecosystems of the Selway-Bitterroot Wilderness. A strength of our study design was the known history of high-severity fire early in the 20th century, which was common across our study sites. This design makes our inferences about the effects of recent fire history stronger than is often possible in retrospective, observational studies of fire effects. Here, contemporary fire history is not confounded by unknown earlier fire history and initial forest conditions. Crucially, we found that northern Rockies mesic mixed-conifer forests that have had limited suppression and experienced fire during the twentieth century are highly resilient to fire, including short-interval reburns—96% of plots either persisted as or are regenerating to coniferous forests. Thus, our new empirical data validate the prediction of Davis et al. (2023) that conifer regeneration in the mesic forests of the northern Rockies is likely to remain resilient to fires and climate change for at least the next few decades.

The fires of 1910 and 1934 burned under extremely hot and dry conditions, even by today's standards (Daly et al., 2002). These historical wildfires are thus comparable to contemporary wildfires in terms of fire season climatology and provide a valuable and relevant source of information. Investigations of tree regeneration, forest structure, and fuels after these high-severity fires can help us anticipate potential future fire effects and post-fire forest dynamics in Northern Rockies mesic mixed-conifer forests (Clark-Wolf et al., 2022).

The long history of managing wildfire as an ecological process in the Selway-Bitterroot Wilderness likely contributed to ecosystem resilience (Berkey et al., 2021b). By allowing naturally ignited fires to burn in a wide range of weather conditions, variable fire behavior and moderate severity effects are more likely to occur. This fire management approach contributes to a complex landscape mosaic with high structural variability, including mature trees that persist through fire events and provide abundant seed sources, contributing to forest resilience. Our on-the-ground measurements show that management to foster an active fire regime with managed wildfires has maintained structurally complex, resilient mixed-conifer ecosystems.

CRediT authorship contribution statement

Melissa R. Jaffe: Conceptualization, Methodology, Formal analysis, Investigation, Data curation, Visualization, Project administration, Writing – original draft, Writing – review & editing. **Mark R. Kreider:** Investigation, Data curation, Writing – review & editing. **David L.R. Affleck:** Formal analysis, Methodology, Writing – review & editing. **Philip E. Higuera:** Conceptualization, Supervision, Writing – review & editing. **Carl A. Seielstad:** Conceptualization, Supervision. **Sean A. Parks:** Conceptualization, Investigation, Resources, Supervision, Writing – review & editing. **Andrew J. Larson:** Conceptualization, Methodology, Investigation, Supervision, Project administration, Funding acquisition, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Acknowledgments

We recognize that the study area includes the unceded ancestral lands of the Nez Perce (Nimiipuu), Salish (Séliš), Kootenai, Shoshone-Bannock, and Lemhi-Shoshone peoples. We thank the USDA Forest Service Selway-Bitterroot Wilderness managers for making this study possible through their support and resources. We also thank Pat Greene for creating the historical fire severity dataset. We greatly appreciate Carmen Murrill, William DeGrandpre, and Mich Clarkson for assisting with field data collection.

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Appendix A

Cross walking datasets

The fire atlas (historical dataset), developed by Patricia Greene, retired USFS forest ecologist, was generated from historical drawn fire perimeters for 1870–1880 fires and aerial imagery for fires from 1880 to 2000 (Morgan et al. 2008). Fire year and general location of the fire were determined by USFS Region 1 fire history records, then actual fire perimeters were assessed by ocular analysis of aerial photography. The first aerial imagery was taken from 1927 to 1928 and was used to delineate fire perimeters from 1870 to 1926. Fires prior to 1880 were determined by hand drawn fire perimeters on map. From 1927 to 1954, imagery was temporally and spatially coarse, with an area flown approximately once a decade, with lots of imagery taken in 1948 and 1954. There is a gap in imagery from 1954 to 1980. After 1980, there was annual imagery from 1980–2000, except for 1996. The smallest fire perimeters were 0.53 ha.

Fire severity was determined by Patricia Greene as percent mortality of trees using method of Morrison and Swanson (1990), where >30% mortality was considered low severity, 30–70% was considered moderate severity, and >70% mortality is considered high severity. Mortality was determined in aerial photography based on number of snags and percent of forest openings. Due to the coarse temporal and spatial resolution of the dataset, the highest confidence is in the high-severity fire. The smallest severity patch was 0.29 ha.

The other dataset is the Parks et al. (2015) SBW fire atlas from 1972 to 2015, which has a minimum fire size of 3.5 ha. It is delineated by dNBR, then segmented by hand. This dataset was updated, calculating dNBR for all fires from 2016 to 2019 in Google Earth Engine, and estimated dNBR for 2020 using Landsat scenes from September 2019, and September 2020. We then compared the perimeters of the Idaho historical fires database (Weber and Yadav, 2020) with the dNBR for 2016–2020 and added any additional fire perimeters not originally in the historical fires database.

Due to the differences in resolution and methods to create the two datasets, certain steps were necessary to make the two datasets comparable and span the full range of years. The first step in this process was determining the severity of the Parks et al. (2015) dataset. We did this using the composite burn index (CBI), a field-based fire severity metric that incorporates the mortality of trees and other ground based factors (Key and Benson, 2006). We calculated CBI from remotely sensed imagery and benchmarking data using the code and methods from Parks et al. (2019). To determine the cutoff of CBI severity for the Parks et al. (2015) we created a linear regression model of mortality of large trees (a specific category in CBI classification) by CBI using the benchmarking data of Parks et al. (2019a) (Fig. A1). We then used the Morrison and Swanson (1990) cut offs for severity: >30% mortality was considered low severity, 30–70% was considered moderate severity, and >70% mortality is considered high severity to determine corresponding CBI is for each severity class (Table A1).

We calculated CBI for years 1988–2000 of the historical dataset and subset by the predetermined severities (Fig. A2). We calculated CBI for both datasets in these years and there were 641 perimeters in the historical dataset. For all three severity categories, we created histograms of the distribution of CBI (Fig. A2). Seventy percent of pixels in fire perimeters classified as high severity in the historical dataset had a CBI of ≤2.00. For moderate severity patches, 23% of pixels classified as such had a CBI with 1.54–1.99. Low severity patches had a 77% agreement between CBI and the classification of the historical dataset. This analysis gave us confidence that the historical dataset and the severity derived from CBI dataset are in high agreement of what constitutes as high severity.

To make the CBI severity classifications within the fire perimeters comparable to the classifications done by photo interpretations in the historical dataset, we took all 1988 fires, a year with both CBI classifications and photo interpretation. We ran the 1988 historical fire perimeters through GEE CBI analysis (Parks et al., 2019). To make the composition of the CBI classified perimeter smoother and more similar to photointerpretation classification, we ran an averaging moving window summary on CBI within the fire perimeter. Then, we classified pixels with CBI ≥2 as high-severity and <2 as non-high severity. We tried multiple moving windows and used a confusion matrix to determine which had the highest accuracy. The best window size was 7 × 7 pixels (210 m × 210 m) (Fig. A3) with a confusion matrix accuracy of 74.4% (Table A2).

To ensure field sample plots were located within high-severity areas and reduce any effect of potential projection or delineation errors and reduce potential edge effects such as the edge of self-limiting fire, we created a four-pixel interior buffer (120 m) (Fig. A4). This step delineated core high-severity patches.

To ensure core high-severity patches of the CBI delineated patches were similar to photo-interpreted high-severity patches on the pixel level we created a confusion matrix comparing core high-severity patches. This analysis showed a 90.1% accuracy (Table A3). Since high-severity patches were of interest, the interior buffering process made all non-core high-severity areas and non-high severity patches valueless (NA) and only input the core-high severity patches into the confusion matrix. This analysis shows the high level of agreement between the core high-severity patches that are derived from the two methods, which gave us confidence to proceed with field sampling and analysis.

We removed all patches that were <1 ha in size, then assessed the degree to which patch shapes and sizes were similar between the two methods. We used the landscapemetrics package (Hesselbarth et al., 2019) in R 3.6.1 (R Core Team, 2021) that is derived from FRAGSTATS (McGarigal and Marks, 1995). This analysis uses a moving window summary for each metric computation and applies an 8-cell neighborhood rule for all raster files. We chose five metrics to describe the patches: mean perimeter area ratio (PARA MEAN), perimeter area ratio standard deviation (PARA SD), mean patch area (AREA MEAN -ha), mean patch perimeter (PERIM MEAN-m), largest patch index (LPI-%). The difference between the CBI method and the photo-interpretation method can be seen in Fig. A5. For all fires in 1988, the photointerpretation method created 49 core high-severity patches and 44 core high-severity patches from the CBI method out of 13 original fire perimeters. Fig. A5 shows that both datasets are quite similar across all metrics. The most similar metrics are LPI and AREA MEAN meaning that the sizes of the patches are the very similar, meaning, both methods will delineate severity patches from the same fire perimeters of similar size, and the largest of the patches are extremely close in size. The two methods had differing size of perimeters, the perimeter to area ratio mean. Despite being of similar size, the shape of the high-severity patches is slightly different. The perimeters are slightly larger and thus the perimeter to area ratio is slightly larger for the historical dataset. Furthermore, the largest difference is the standard deviation in perimeter-area ratios, which is much higher for the historical dataset than for the dataset derived from CBI. Though these differences are small, the difference in LPI is 1.7% and the difference in PARA SD is 29.

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