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Leafing Out: Leaf Area Index as an Indicator for Mountain Forest Recovery Following Mixed-Severity Wildfire in Southwest Colorado

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Abstract: Wildfire is a critical driver of ecological processes in western U.S. forests, but recent shifts in climate, land use, and fire suppression have altered forest structure and disturbance regimes. Understanding post-fire recovery is essential for land management, particularly across complex montane landscapes like the southern Rocky Mountains. We assessed forest recovery in montane conifer forests, ranging from ponderosa pine to spruce-fir, following a large mixed-severity fire using field-based forest stand data and remotely sensed Leaf Area Index (LAI) measurements. Our objectives were to determine whether LAI is a meaningful proxy for post-fire vegetative recovery and how recovery patterns vary by forest type, burn severity, and abiotic factors. Stand characteristics predicted crown burn severity inconsistently and did not predict soil burn severity. LAI correlated strongly with live overstory tree density and shrub cover (R^2 = 0.70). Recovery trajectories varied by forest type, with lower-severity burns generally recovering four years post-fire, while high-severity burns showed delayed recovery. Regeneration patterns were strongly influenced by climate, with higher seedling densities occurring at wetter sites. Our findings highlight the utility of LAI as a proxy for vegetative recovery and underscore the importance of forest type, fire severity, and climatic factors when assessing post-fire resilience.

Keywords: wildfire recovery; remote sensing; forest resilience; disturbance ecology; stand conditions; regeneration; climate

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1. Introduction

Wildfires in the western United States are integral to the ecology of forested ecosystems [1]. Since the American colonists' settlement of the western United States, significant changes to forest structure have occurred, including logging large and old trees, sheep and cattle grazing, and fire suppression-based policies [2]. These changes, in congruence with warmer temperatures and decreased precipitation across the West in recent decades, have resulted in wildfires generally increasing in size and severity, sometimes with extensive, contiguous, high-severity burn patches [3,4]. These fires often cause significant impacts, including mass waste events that impact downstream water quality, loss of wildlife habitat, vegetation type conversion, and socioeconomic impacts on adjacent communities [5,6]. Consequently, land managers and government agencies must quantify post-fire forest recovery.

Disturbance histories of a given ecosystem can help determine the degree of recovery or resilience to an ecosystem's disturbance [1,7]. The recovery of ecosystems can be

demonstrated by ecosystem resilience, where essential functions are recovered [8,9]. Forests provide essential functions of clean water, wildlife habitat, carbon sequestration, recreation, and wood production. However, these functions may not return for decades or longer [10–12]. Each recovery metric may operate on different time scales; for example, wildfire smoke may dissipate once fires are no longer burning, but health effects can linger until affected individuals heal from adverse health effects. Other recovery metrics include when runoff into rivers returns to pre-fire levels and water turbidity is comparable to pre-fire conditions [12]. Vegetative recovery becomes a useful metric because plant cover and erosion are closely related, and it also helps capture some demonstrable ecosystem resilience. Once vegetative recovery occurs, land managers can shift their focus from post-fire flooding and slope stabilization impacts to adaptive ecosystem management.

A particular challenge with quantifying recovery in fires in mountainous systems of the southern Rocky Mountains includes the phenomenon that complex topography has a strong influence on vegetation and disturbance regimes [13]. In southern Colorado, this means that vegetation can rapidly change from ponderosa pine forests at lower elevations to mesic spruce-fir forests at higher elevations over short linear distances [7,14]. This corresponds to changes in disturbance regimes associated with different forest types [14–16]. Ponderosa pine has a frequent, low-severity-disturbance regime where disturbances occur once every 5–30 years, and occasional high-severity fire happens, whereas spruce-fir forests have an infrequent, high-severity-disturbance regime [17,18]. Between these extremes are intermediate disturbance regimes of xeric- and mesic-mixed conifer forests that vary in frequency and severity from 30–100+ years [15,18,19]. Each forest type will have its own recovery timeframe, often consisting of different recovery stages depending on the forest function metric being assessed. Combined with the complex topographic features of the Southern Rockies, this means that both forest type and disturbance regime rapidly change to create a mosaic of expected disturbance regimes that vary with forest type.

Due to the complexity of the anticipated disturbance regime and the actual disturbance regime, quantifying or measuring recovery over large fire areas can prove challenging [20]. Despite this, the negative social-economic effects of wildfires cause many individuals to want to know about post-fire recovery because recovery indicates that detrimental post-fire effects have subsided and ecosystems are generally functioning in ways similar to pre-fire conditions, regardless of the community composition of ecosystems [12]. In some circumstances, fire can enhance ecosystem function by restoring the disturbance regime to the forest; however, this depends on the fire intensity, severity, and the disturbance regime of the forest type in which the fire is burning. For example, low-severity fire in ponderosa may be restorative and enhancing. Similarly, mixed-severity fire in mixed conifer or a mosaic of high-severity fire in spruce-fir may be restorative [21,22]. A useful metric for ecosystem functioning is forest stand structure information, including live tree density or total shrub cover; however, these indicators are often limited to plot scale information and can be challenging to scale for large fires. Thus, remotely sensed data become particularly useful, specifically the Leaf Area Index (LAI), which is a powerful indicator that estimates the area of leaf cover for a given pixel. The leaf area index then becomes a useful proxy for vegetative cover [23]. LAI has been widely used to estimate information about vegetation cover, evapotranspiration, or productivity, and thus can serve as a valuable metric of recovery as it relates to vegetative growth [24–27]. LAI is particularly useful because it represents the total leaf area per unit area of ground as opposed to the fractional ground cover by vegetation represented by canopy cover. LAI is also closely related to the Normalized Differential Vegetation Index (NDVI); however, after certain LAI values, an increase in LAI does not result in an increase in NDVI. Therefore, LAI provides higher resolution than NDVI when fractional vegetation cover is high [28]. Tree

regeneration also serves as a reasonable proxy for what future forests may look like and thus can be a strong indicator of forest recovery [29,30].

Because LAI represents a proxy of vegetation cover, it becomes a useful proxy for post-fire vegetation recovery [31]. A challenge with LAI as a proxy for post-fire recovery has been that different forest types often show divergent LAI responses, and this could be the result of forests with different disturbance regimes responding differently to different disturbance severities [32]. Additionally, there are no studies that have paired LAI with field-based plots to better understand which variables (i.e., tree density or shrub cover) are driving changes in LAI after wildfire. For example, one might predict that low-severity fire in Ponderosa pine increases LAI because the overstory canopy is minimally impacted but prolific understory growth occurs after the fire; in contrast, high-severity fire will likely reduce LAI because of the mortality of overstory trees, but in systems adapted to high-severity-disturbance recovery of the understory may occur more quickly [33,34]. An interesting caveat could be that fire injury in trees in low and moderate-severity burned areas could make trees more susceptible to other disturbance agents, like bark beetle, resulting in a continued decline in LAI over time, and thus delaying recovery as fire-weakened trees die [35].

To better understand forest recovery following a large mixed-severity fire, we utilized a combination of field plots to quantify forest characteristics at the stand level. We remotely sensed LAI data to document ecosystem responses at the burn perimeter area. Our study area is in the Southern Rocky Mountain region that has a strong elevation gradient consisting of forests ranging from dry montane forests with a frequent to infrequent historical fire regime to mesic subalpine forests with infrequent fire disturbances [7,23]. We first explore if a relationship exists between plot-based stand structure data and remotely sensed LAI data. We then explore trajectories of ecosystem recovery by quantifying changes in LAI across the burn perimeter area and then again use stand data to reflect on vegetation composition to discuss the resilience of these systems regarding the degree of recovery and trajectory of stand conditions. An additional objective is to relate forest stand conditions to abiotic variables to assess the trajectory of recovery post-disturbance. The primary objective of this study is to determine whether or not LAI as a proxy for forest recovery is correlated with meaningful site-specific forest structural traits, like overstory or understory plant cover. Within this objective, we have several specific hypotheses about forest recovery following wildfires. As a secondary objective, we compared the relationship between soil burn severity and crown burn severity on the leaf area index.

H1: *Forest stand characteristics will predict crown burn severity, but not necessarily soil burn severity.*

H2: *LAI will correlate to live overstory tree density and shrub cover.*

H3: *Low and moderate crown severity fire will have minimal impact on leaf area index in ponderosa pine, mixed conifer, and spruce-fir systems, and these ecosystems will demonstrate recovery 1-year post-fire.*

H4: *High crown severity fire will significantly reduce LAI with multiyear persistence in this pattern, and this reduction of LAI will be greatest in ponderosa pine ecosystems and xeric-mixed conifer.*

H5: *Shrub cover will be highest in sites that experienced high crown burn severity but are adapted to high-severity fire.*

H6: *There will be more regeneration in cooler/wetter sites for each respective forest type.*

H7: *Soil burn severity will have a minimal relationship with LAI, whereas crown burn severity will have a strong relationship with LAI.*

Further, soil burn severity, often defined as organic matter consumed and other fire effects on soils, is often the primary burn severity metric assessed post-fire because of its prominent role in influencing erosion susceptibility, landslide potential, and water quality [36–38]. Despite this importance, it is often the case that crown burn severity, the fire effects on overstory tree composition, are much more important in determining ecosystem trajectories because of the direct biotic effects on seed source availability and associated plant community composition [39–42]. This creates a dynamic overlay in fire effects on ecosystems because not all places that burned at high soil severity will also burn at high crown severity [43].

2. Materials and Methods

2.1. Study Area

The study site is located approximately 21 km north of Durango, Colorado, in the southern portion of the San Juan National Forest adjacent to Hermosa Creek within the Hermosa Special Management Area and Hermosa Wilderness (Figure 1) [44]. The study area ranges in elevation from 2277 m to 2470 m on steep slopes that range from 30 to 45 degrees. Average daily temperatures range from a maximum of 26.7 °C in July to a minimum of −12.2 °C in January. Average annual precipitation is 58.4 cm, with the most significant amounts occurring in July and August due to summer thunderstorm activity. Precipitation from November to March is dominated by snowfall [45]. The dominant vegetation type of the 416 Fire burn area is forest, based on National Land Cover Classification Data (Figure 1) [46]. The study area is in a geography where soils are derived from the Hermosa Group Limestone parent material and are generally cobbly to stony loams that are superactive eutric haplocaryalfs. Specifically, ponderosa pine, mixed conifer and spruce-fir forests occupy 90% of the burn area. These forest types consist of fire-resistant tree species, such as *Pinus ponderosa* Dougl. ex Laws. (ponderosa pine) and *Pseudotsuga menziesii* (Mirb.) Franco *(Douglas-fir)*, but also mesic tree species, such as *Abies concolor* (Gord. & Glend.) Lindl. *(white fir)*, *Populus tremuloides* Michx. *(aspen)*, *Abies bifolia* (Hook.) Nutt. *(subalpine fir)*, and *Picea engelmannii* Parry ex Engelm. (Engelmann spruce). The remaining 10% of the vegetation in the 416 Fire burn area is mostly (8%) mountain shrubland dominated by persistent re-sprouting shrubs and hardwood trees, such as *Quercus gambellii*_Nutt. (Gambel oak), *Almelanchier alnifolia* Nutt. (Nutt.) ex M. Roemer (serviceberry), *Prunus virginiana* L. (chokecherry), *Rosa woodsia* Lindl. (wild rose), *Symphoricarpos rotundifolius* Gray (serviceberry), *Berberis repens* Lindl. (Oregon grape), and others, including *Ribes* spp. The remaining two percent is Piñon-Juniper (P-J) woodlands and dominated by *Pinus edulis* Engelm. (piñon pine), *Juniperus scopulorum* Sarg. (Rocky Mountain juniper) and *Juniperus osteosperma* (Torr.) Little (Utah juniper). Mountain shrubland vegetation is also present in the understory of forests within the 416 Fire burn area, creating complex dynamics between tree species and shrubs [33,47]. The study area has never been logged and has a high proportion of large-diameter trees for all species present with many stands having old-growth characteristics [48]. In 2008, portions of the study area were burned in a broadcast-prescribed fire using aerial ignitions. Ten years later, in 2018, the study area was burned by an unplanned, artificial ignition that burned 54,130 acres (416 Fire). Suppression efforts focused on the wildland–urban interface, and no slurry drops, or direct attack measures were taken in the study area (Communication with Incident Section Chief).

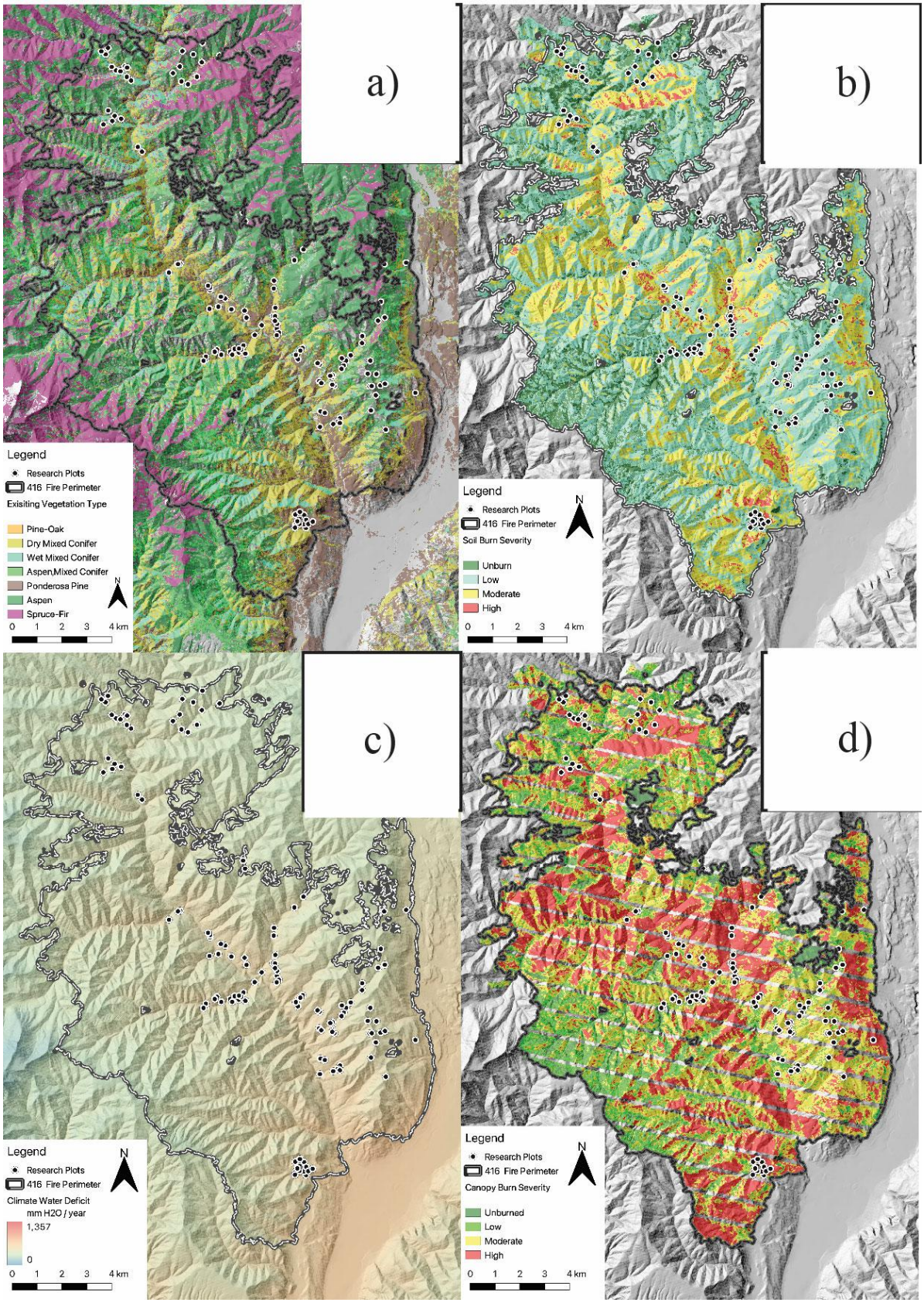

Figure 1. Map of (**a**) vegetation types, (**b**) soil burn severity, (**c**) Climate Water Deficit and (**d**) canopy burn severity for the 416 Fire.

2.2. Experimental Design

To collect detailed information on stand structure characteristics, we generated random points using QGIS with a minimum spacing distance of 100 m and within a mile buffer of existing trails to ensure accessibility to sites, given the steep slopes of the drainage. We then stratified these points across crown burn severities as determined by Monitoring Trends in Burn Severity (MTBS) data. Burn severities across the entire 54,130-acre fire in percent include: low (49.1%), moderate (24.4%), high (6%), and unburned (20.2%) [49]. We also sub-stratified these locations based on forest type from the existing vegetation type of the Landfire 2016 dataset [50]. Plots were established in ponderosa pine (PIPO), xeric-mixed conifer (XMC), mesic-mixed conifer (MMC), aspen-mixed conifer (AMC), Aspen, and spruce-fir (SF) forest types at unburned, low, moderate, and high crown burn severities, creating a total of 164 plots (Table 1). All plots were sampled in 2022, four years post-fire, and a subset of these plots was sampled in 2019, one year post-fire. It should be noted that Landfire classifies spruce-fir as either xeric spruce-fir or mesic spruce-fir; however, very little land area was represented by mesic spruce-fir, therefore we only refer to xeric-spruce-fir when we reference this forest type.

Table 1. Total plot numbers for each forest type and burn severity utilized in the sampling design. PIPO = ponderosa pine, XMC = xeric-mixed conifer, MMC = mesic-mixed conifer, AMC = Aspen-mixed conifer and SF = spruce-fir.

	Burn Severity					Brief Description of the Forest Type
Forest Type	**Unburned**	**Low**	**Moderate**	**High**	**Total**	
PIPO	8	8	8	8	32	Ponderosa pine—Dominated by ponderosa pine, generally single-species stands. Frequent fire regime
XMC	8	8	8	8	32	Xeric-Mixed Conifer—Dominated by ponderosa pine and Douglas-fir. Mixed species stand with intermediate fire regime
MMC	8	8	8	8	32	Mesic-Mixed Conifer—Dominated by white fir, Douglas-fir and spruce species, intermediate-infrequent fire regime
AMC	8	8	8	8	32	Aspen-Mixed Conifer—Dominated by aspen, white fir, Douglas-fir and spruce species. Often the result of historic mixed-severity fire with groups of aspen intermixed with other species.
Aspen	5	5	5	5	20	Aspen—Dominated by Aspen with relatively infrequent fire, tends to be early successional to other forest types.
SF	4	4	4	4	16	Spruce-fir—Dominated by Englemann spruce and subalpine fir. Infrequent fire regime
Total:	41	41	41	41	164	

2.3. Field Methods

We quantified shrub cover at each plot to detect potential type conversion using a 30-m line intercept transect method along the steepest (aspect) environmental gradient to capture the greatest landscape diversity with 15 m of tape placed above and below the

center point creating a 30 m long transect. We recorded all shrubs that crossed the tape from their start to end location in centimeters on the tape as a proxy for shrub cover.

To quantify forest stand structure, we used a hypsometer to count all mature standing, dead or alive, conifers and trees taller than breast height (>2.64 m), using a 400 m^2 (11.37 m diameter) circle plot. We identified each tree to species and classified it as live or dead. To determine forest recovery in terms of species composition, we quantified conifer regeneration (trees < 2.64 m), using a 30 × 10 m belt transect overlaid on top of the shrub transect with 5 m on both sides of the transect (300 m^2).

We quantified plot slope, aspect, and elevation using a 10M digital elevation model (DEM) dataset, and Landfire Existing Vegetation Type (EVT) for each plot using ArcGIS. To quantify the 30-year average and 3-year post-fire climate in each regeneration plot and within each fire perimeter, we performed a statistical downscaling (following [30]) of 30-year monthly precipitation and temperature averages (i.e., 30-year normal). Using these data, we modeled actual evapotranspiration (AET) and climatic water deficit (CWD) using a modified Thornthwaite-type method [31]. CWD is the evaporative demand that is not met by available water and, therefore, is an index of the potential effects of drought stress on plants [32]. AET reflects the simultaneous availability of biologically usable energy and water and thus represents an index of site potential for productivity (USGS). We summed monthly values to calculate accumulated annual totals (by calendar year) of AET and CWD in each 30-m cell. We then developed predictors of 30-year annual average AET and CWD. While CWD provides an estimate of the intensity of drought stress because it estimates unmet atmospheric moisture demand, AET is an indicator of site productivity because high values are indicative of sites with high availability of both moisture and energy [31]. Burn severity was derived from satellite imagery comparing pre- and post-fire images and were field verified through reconnaissance and adjusted where needed to create a final soil burn severity map [51]. While soil burn severity is a useful metric for understanding potential watershed impacts and post-fire erosional dynamics, we chose to focus our analyses on the fire effects on overstory tree structure, and thus emphasize crown burn severity in our analyses.

2.4. LAI Raster Generation

Gridded LAI rasters were generated at a 30 m, monthly resolution for the 416 burn scar. One raster was generated for each month (July, August, September) over the years 2016–2021. These rasters were generated in Google Earth Engine following a random forest model approach described by [52]. This method produces 30 m LAI images from Landsat images (cloud filtered at 70%), that are consistent with remotely sensed LAI products from the Moderate Resolution Imaging Spectroradiometer (MODIS). Monthly point-based LAI values were extracted from monthly LAI rasters for each plot, using a 15 m buffer radius around each plot point.

2.5. Statistical Analysis

To test our first hypothesis that stand characteristics influenced burn severity and that soil burn and crown burn severity would differ from one another, we built two random forest models, one with soil burn severity and one with crown burn severity as a response variable. For each model, we predicted burn severity as a function of tree density from our plot data assuming all trees were alive to validate Landfire derived canopy cover and density estimates and then used topographic information including slope steepness, aspect, forest type, CWD and AET to predict burn severity.

To investigate the distinct and overlapping drivers of soil burn severity and crown burn severity, we employed a random forest model—a nonparametric ensemble learning method

that is well suited for ecological data characterized by complex non-linear relationships where one might expect multicollinearity [53]. We incorporated environmental covariates, including topographic indices, forest type, and stand density estimates to predict burn severity. To further compare the relationship between burn severity and LAI, we used a general linear mixed model (GLMM) framework, which accommodates diverse input data types, including continuous and discrete predictor variables [54].

To test our second hypothesis regarding the relationship between LAI and plot vegetation data, we used a piecewise multiple regression to determine which vegetation variables in plot data are related to remote-sensed LAI values. To test the third and fourth hypotheses, which focus on changes in LAI across forest types and burn severities, we used a repeated measures ANOVA test.

To test hypotheses about specific vegetation responses, including post-fire shrub dynamics and post-fire tree regeneration, we used a PERMANOVA approach to determine the shrub community across forest type and burn severity. We also used repeated measures ANOVA to determine differences in regeneration over time since fire and linear regressions to show the relationship between tree regeneration and climate by individual tree species.

3. Results

3.1. Burn Severity and Stand Structure

Contrary to our first hypothesis, which only had partial support, we observed that canopy and soil burn severity differed by forest type and from one another (Figure 2). We found that stand characteristics only sometimes accurately predicted crown burn severity and never predicted soil burn severity. We observed high variability in pre-burn tree densities within forest types, and within burn severities (Table 2). Stand characteristics varied by forest type, with aspen, aspen-mixed conifer, and mesic-mixed conifer having the highest densities. Soil burn severity was best predicted by slope aspect and crown burn severity was best predicted by slope steepness (Figure 3). The only forest type that showed a density-based relationship with crown burn severity was aspen, where moderate and high burn severity had higher densities than unburned and low burn severities (Table 2). Many stands exhibited irregular multi-aged diameter distributions more characteristic of old-growth forests (Figure 4 [48]). Shrub species also varied by forest type, with QUGA and AMAL being more common in ponderosa pine and dry mixed conifer forests, *Ribes* spp. and *Sambucus racemosa* L. (SARA) more common in spruce-fir forests, and SYRO being the most prevalent in aspen forests (Figure 5).

Table 2. Mean tree density (trees/ha) and (lower, upper) 95% Confidence Intervals for each forest type and burn severity with averages across all forest types. Asterisks indicate significant differences across rows; X indicate significant differences across columns. Data are derived from total tree density (live and dead) in plots four years post-fire.

Forest Type	Mean Density (Trees/ha) in Unburned Stands	Mean Density (Trees/ha) in Low-Severity Stands	Mean Density (Trees/ha) in Moderate Burn Severity	Mean Density (Trees/ha) in High Burn Severity	Mean Density (Trees/ha) for Forest Type
Ponderosa Pine	138 (45, 180) N = 8	203 (75, 200) N = 8	211 (105, 273) N = 8	212 (108, 302) N = 8	191 (65, 210) N = 8
Xeric-Mixed Conifer	195 (110, 245) N = 8	194 (108, 246) N = 8	269 (205, 320) N = 8	311 (220, 412) N = 8	242 (123, 287) N = 8

Table 2. *Cont.*

Forest Type	Mean Density (Trees/ha) in Unburned Stands	Mean Density (Trees/ha) in Low-Severity Stands	Mean Density (Trees/ha) in Moderate Burn Severity	Mean Density (Trees/ha) in High Burn Severity	Mean Density (Trees/ha) for Forest Type
Mesic-Mixed Conifer	350 (280, 420) * N = 8	320 (276, 415) * N = 8	375 (282, 434) * N = 8	437 (331, 510) * N = 8	370 (293, 408) * N = 8
Aspen-Mixed Conifer	428 (350, 600) * N = 8	455 (362, 687) * N = 8	481 (401, 704) * N = 8	434 (387, 512) * N = 8	449 (371, 508) * N = 8
Aspen	242 (203, 315) * N = 5	312 (251, 401) * N = 5	707 (581, 1112) *X N = 5	532 (434, 912) *X N = 5	448 (267, 608) * N = 5
Spruce-fir	262 (245, 389) * N = 4	312 (289, 402) * N = 4	306 (255, 402) N = 4	291 (225, 396) N = 8	292 (263, 337) * N = 8
Average density for crown burn severity	269 (68, 343) N = 41	299 (109, 453) N = 41	391.5 (143, 536) N = 41	369 (160, 487) N = 41	

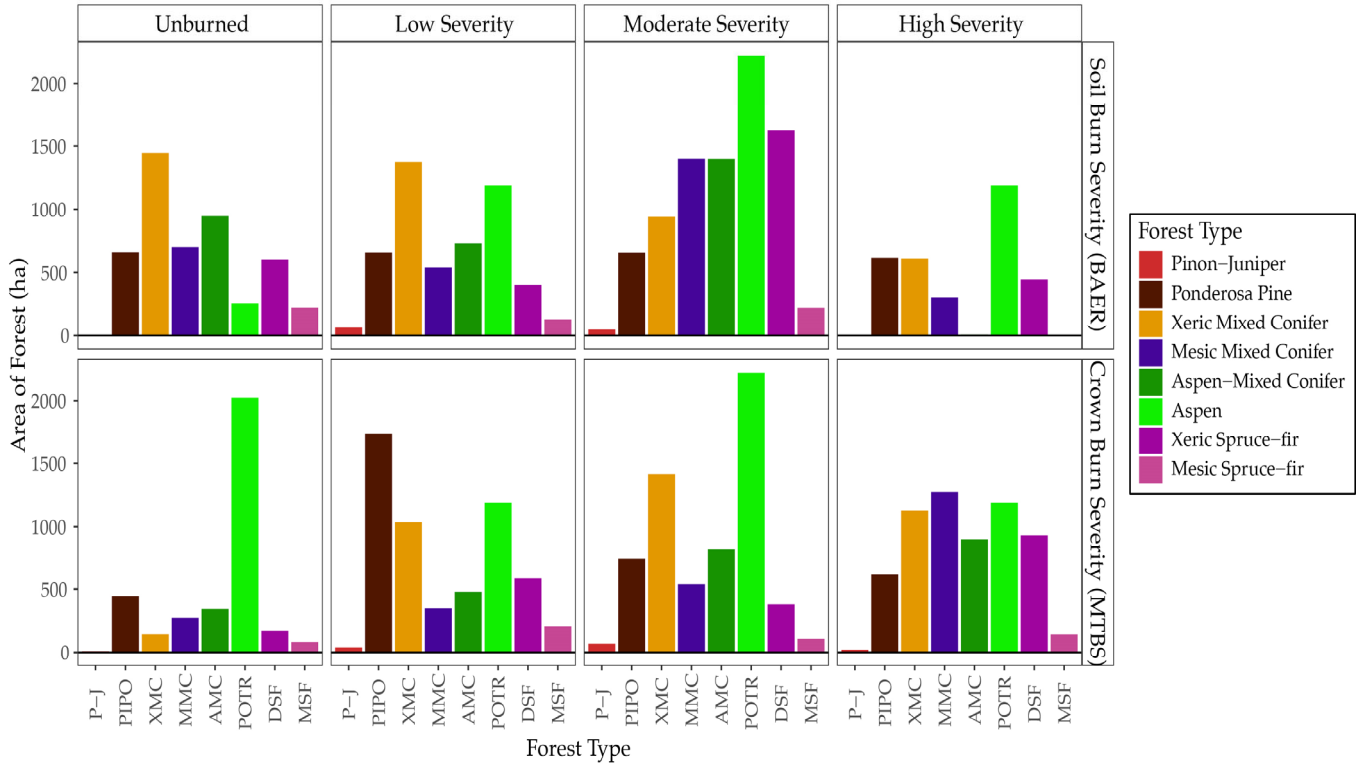

Figure 2. Area of forest burned (ha) for each forest type at each burn severity for both soil burn severity (BAER) and crown burn severity (MTBS). Data are derived from one year post-fire burn severity reports. PIPO = ponderosa pine, XMC = xeric-mixed conifer, MMC = mesic-mixed conifer, AMC = Aspen-mixed conifer.

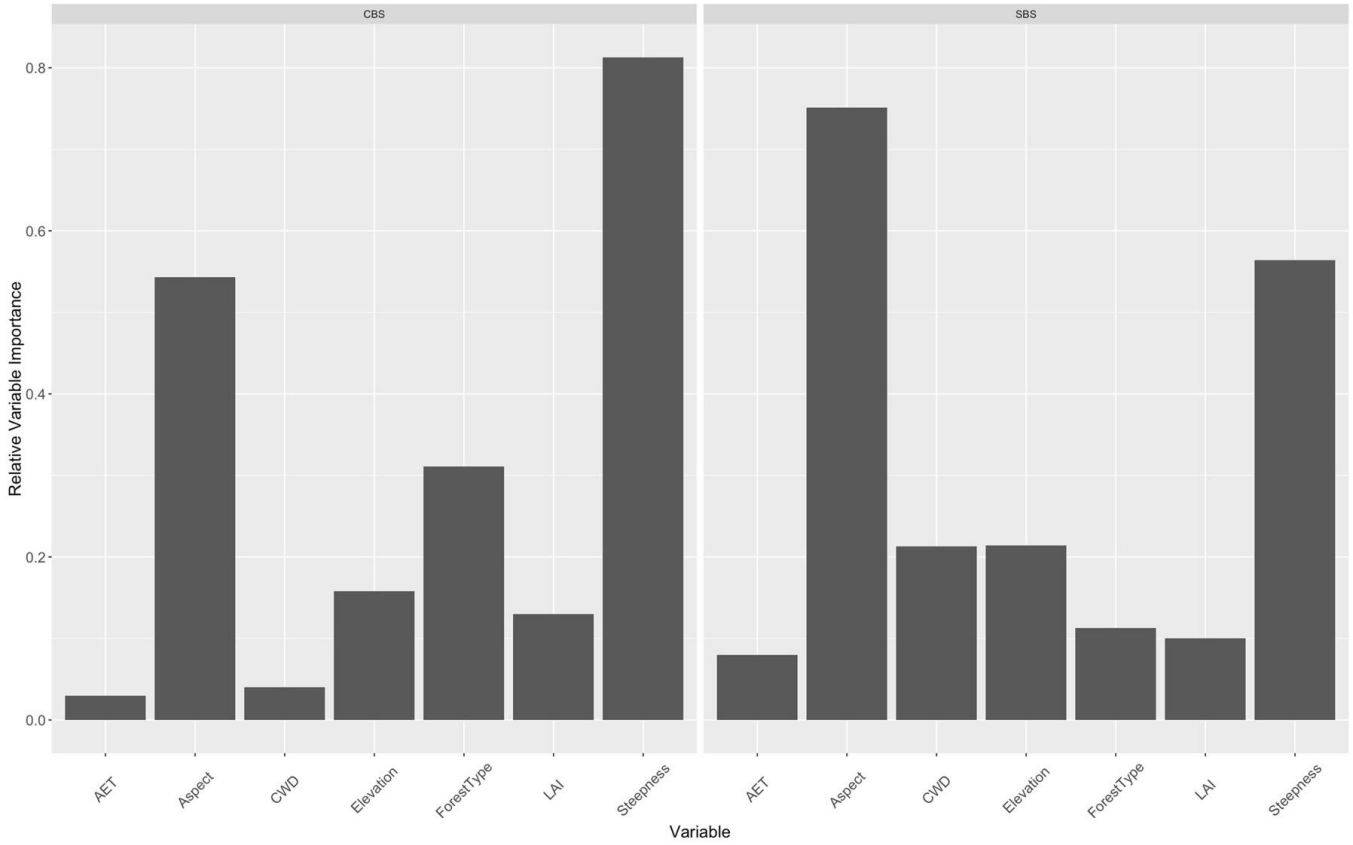

Figure 3. Relative Variable importance for Crown Burn Severity (**left**) and Soil Burn Severity (**right**) for all variables with greater than 1% relative importance.

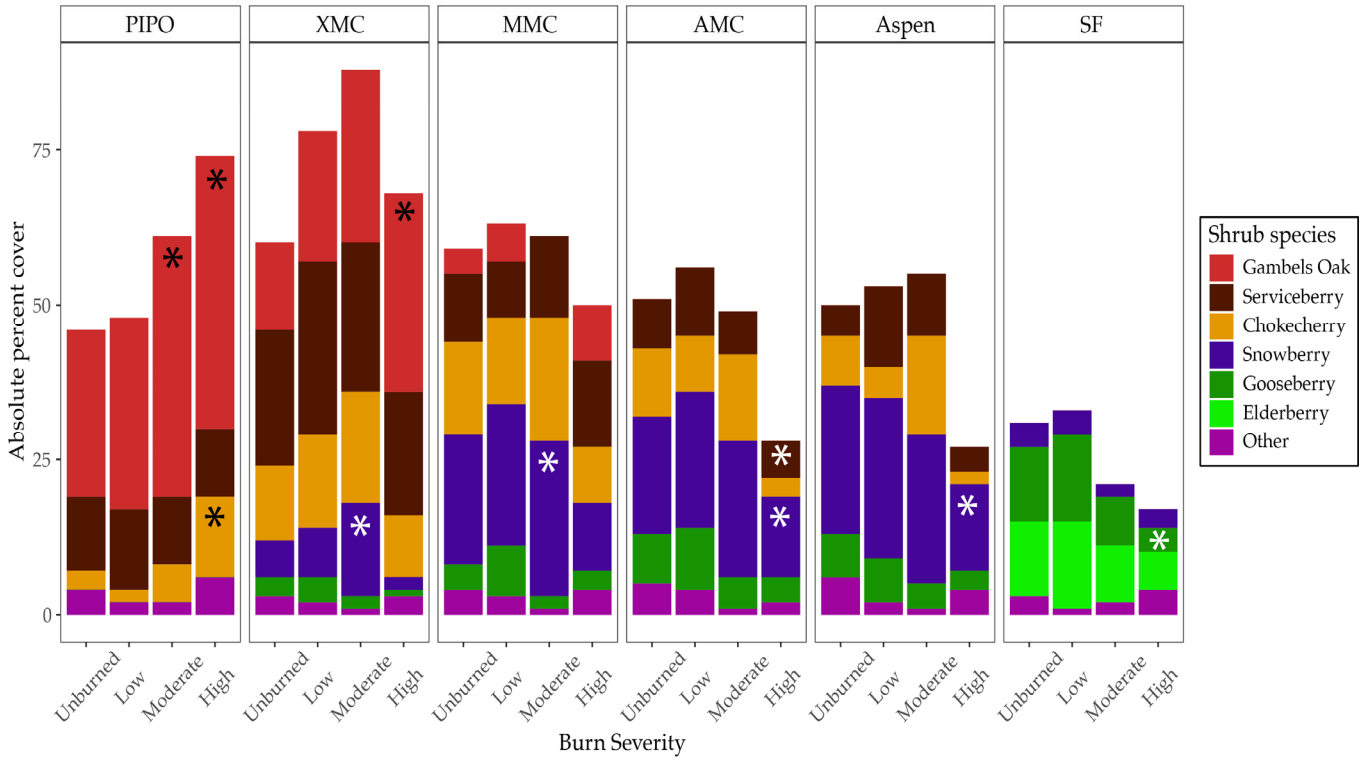

Figure 4. Tree density (trees/ha) for alive and dead tree species in each burn severity for each forest type. Data are derived from plot data collected 4 years post-fire. Asterisks represent significant differences relative to unburned shrub cover within each forest type.

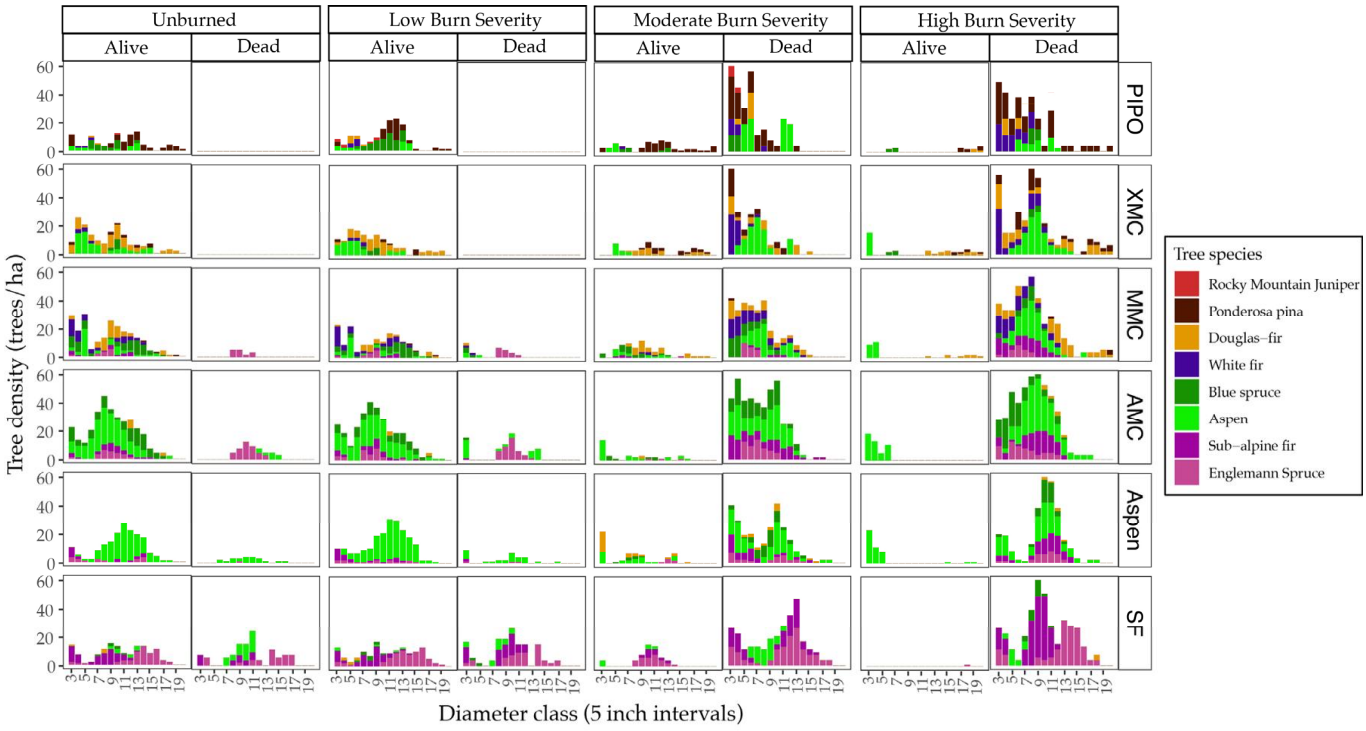

Figure 5. Absolute percent shrub cover for each forest type and burn severity four years post-fire.

3.2. LAI and Plant Cover

In support of our second hypothesis, we found a strong linear relationship in a multiple regression with shrub cover (SC) and tree density (TD) as predictors for LAI (R2 = 0.70, f = 102.2 $p < 0.011$, Figure 6). This linear regression has the following formula.

$$LAI = 48.37 + 0.6(TD) + 0.67(SC) - 0.003(TD * SC)$$

Other metrics, including tree regeneration density, did not improve model fit, and the above formula represents the best-fitting model from a series of stepwise linear regressions.

LAI varied by time since fire (recovery) and forest type, showing a significant decrease in areas with high crown burn severity (Figure 7). LAI was similar across burn severities in pre-fire conditions for all forest types. For ponderosa pine, LAI in all burn severities, including unburned, was significantly lower one year post-fire, with unburned and low severity recovering to pre-fire values three years post-fire and moderate severity recovering by year 4 post-fire. For the xeric-mixed conifer, moderate and high-severity burn severities reduced LAI one year post-fire, with moderate recovery three years post-fire and high recovery four years post-fire. Mesic-mixed conifer forests at low, moderate, and high burn severities all experienced decreased LAI one year post-fire, with low recovery in 3 years and moderate recovery in 4 years post-fire. Aspen-mixed conifer had reduced LAI in moderate and high burn severities 1 year post-fire, but both had recovered by year 3 and exceeded pre-fire LAI by year 4 post-fire. Aspen had reduced LAI in unburned, moderate, and high burn severities one year post-fire, but higher LAI in low-severity fire one year post-fire. By year three post-fire, moderate and high burn severities recovered to pre-fire levels, and by year four post-fire, all burn severities except unburned exceeded pre-fire LAI values. Xeric spruce-fir experienced reduced LAI values across all burn severities except unburned in one year post-fire, with low severity recovering to pre-fire values by year three and moderate severity recovering by four years post-fire. Mesic spruce-fir had reduced LAI in moderate and high burn severities one year post-fire, and these remained reduced through year four post-fire.

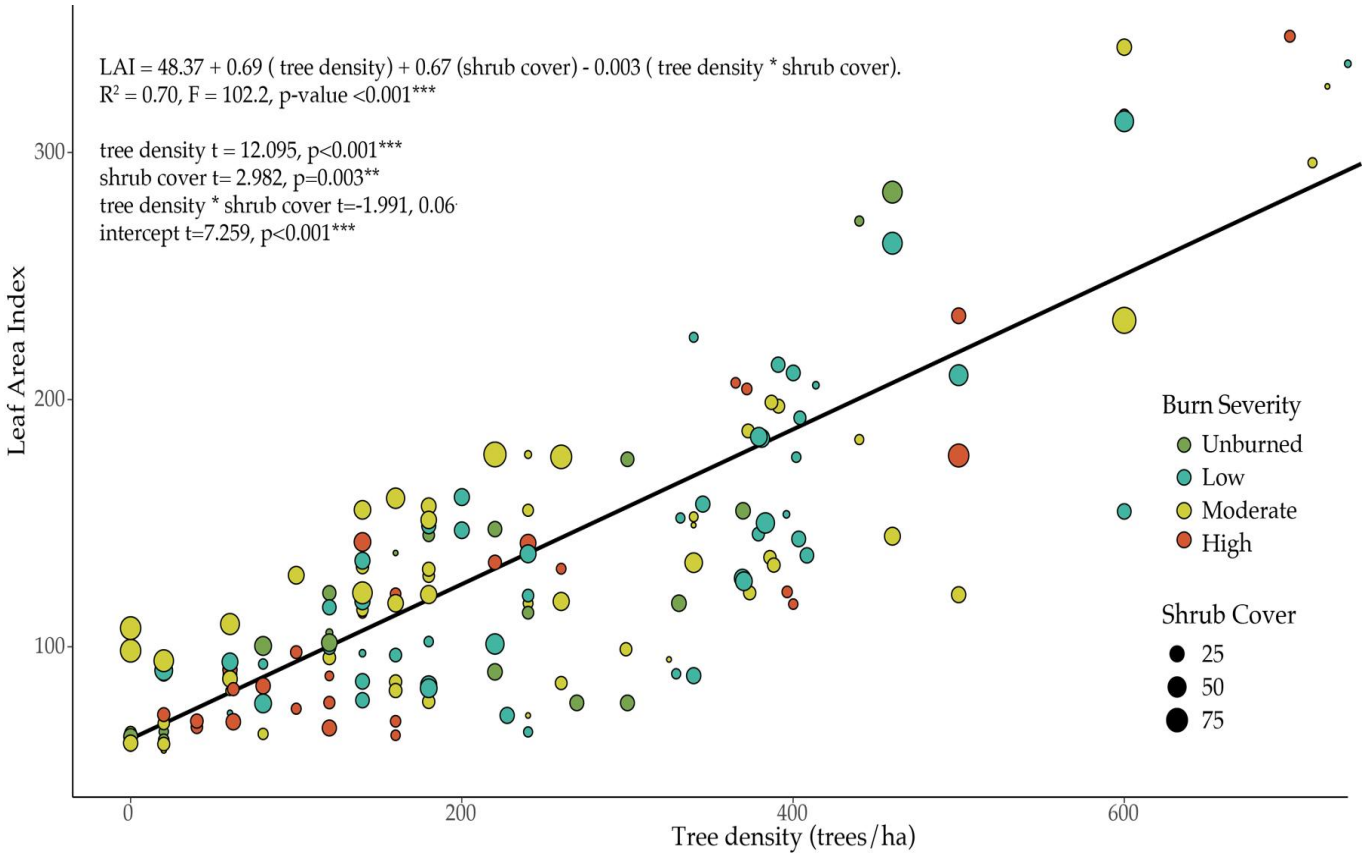

Figure 6. Correlation between Leaf Area Index and living tree density (trees/ha) and absolute shrub cover (percent). Each point represents a sampling point four years post-fire where points are colored by burn severity and the size scale represents shrub cover. Both shrub cover and tree density have positive effects on observed LAI. Model coefficient significance is represented by * where $p < 0.05$, ** where $p < 0.01$ and *** where $p < 0.001$.

3.3. Understory Shrubs, Regeneration and Climate

Shrub species abundance varied by forest type and burn severity, with Gambel's oak being more abundant in PIPO and XMC forest types, and snowberry, gooseberry, and elderberry being more common in AMC, Aspen, and SF forest types (Figure 5). In PIPO and XMC forest types, we saw increasing shrub cover under moderate and high severity, whereas in AMC, Aspen, and SF, we saw an overall decrease in shrub cover under high-severity fire (Figure 5).

We observed regeneration in all forest types in 2022, four years post-fire, with aspen being the most observed regenerating species (Figure 8). Besides aspen, subalpine fir was the next most observed regenerating tree species. For aspen, tree regeneration was highest in moderate and high severities with no difference between the two. For subalpine fir, regeneration was highest in the spruce-fir forest type and was highest in unburned and low-severity fire. For other conifers, there was little regeneration observed at moderate and high severity, except for in the mesic-mixed conifer forest type (Figure 9).

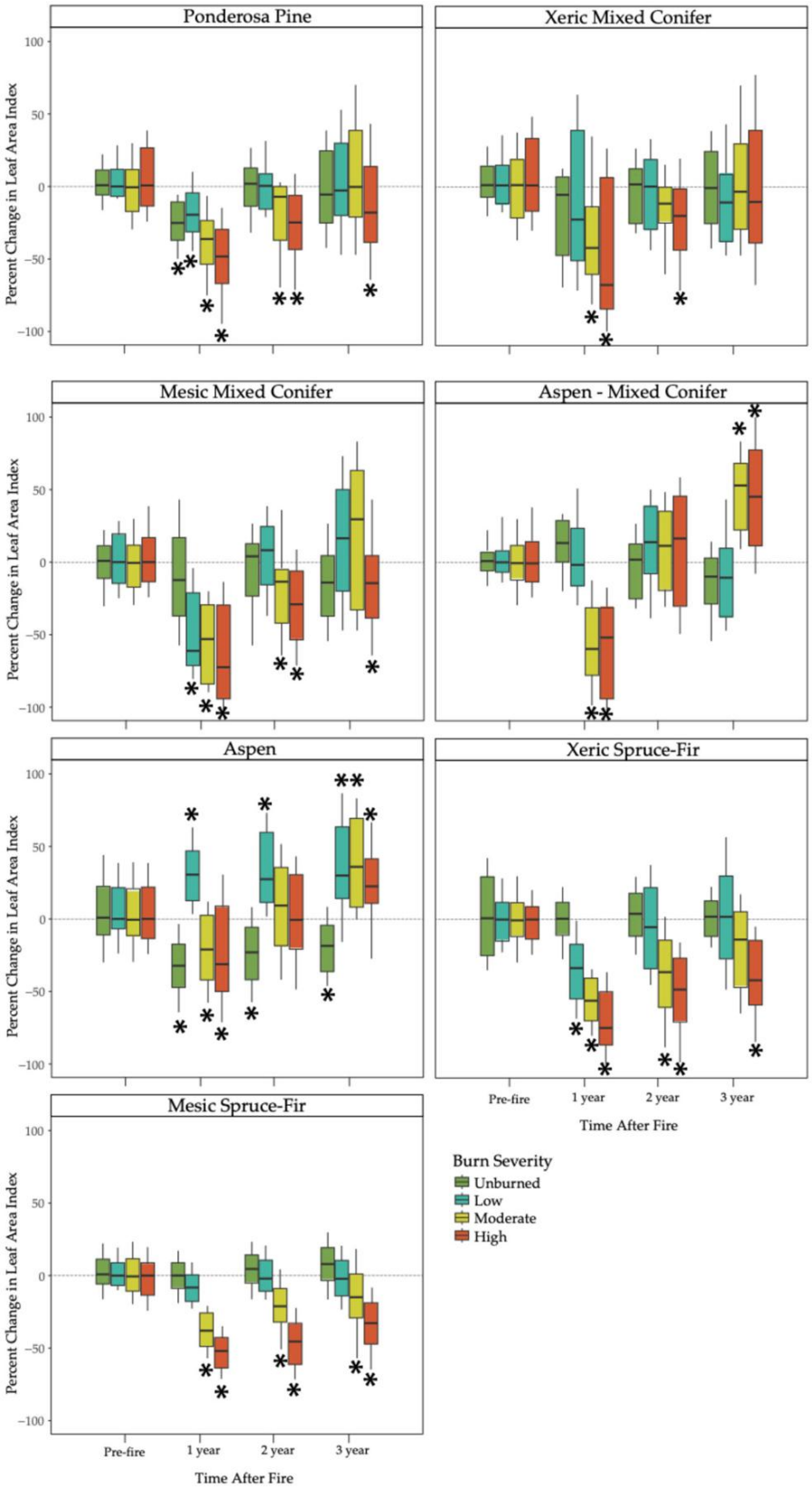

Figure 7. Percent change in Leaf Area Index compared to the pre-fire year median for each forest type and burn severity over time. Values are derived from LAI pixel values for each year. Box and whisker plots represent min, 25th quartile, median, 75th quartile and maximum pixel values. Asterisks represent significant differences within groups relative to pre-fire.

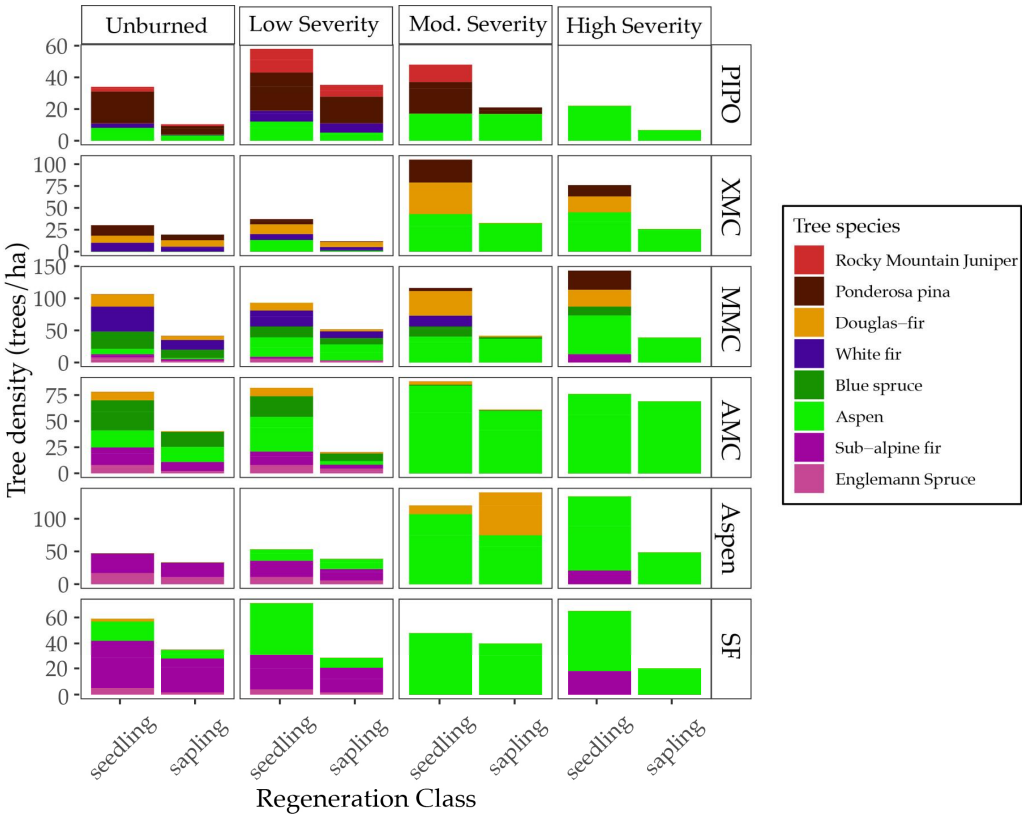

Figure 8. Seedlings and saplings (trees/ha) for each forest type. We observed seedlings and saplings four years post-fire in each forest type.

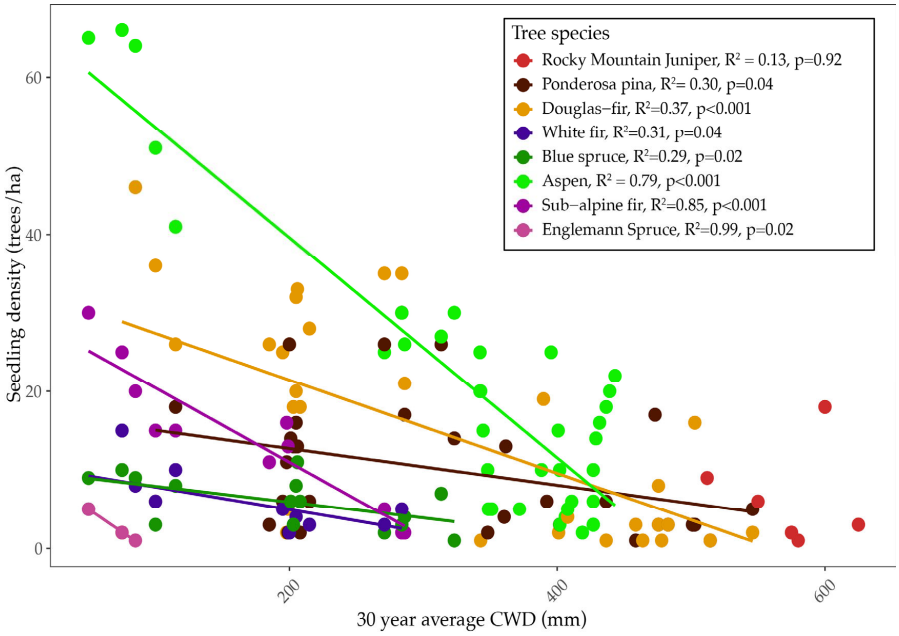

Figure 9. Linear relationships between seedling density and 30-year average CWD (mm) for each species for which regeneration was documented.

For all observed tree species, except for Rocky Mountain juniper, we observed a negative linear relationship between seedling density and 30-year average climate water deficit (mm) (R^2 = 0.13, p = 0.92; Figure 8). Some species, like Engelmann spruce, only had three plots where regeneration was observed, but for all species higher regeneration counts were observed at sites with lower CWD.

4. Discussion

We did not find support for our first hypothesis that higher stand densities would result in higher burn severities. Instead, we found that all forest types had variable tree densities and that stand conditions were highly variable. On average, there were slightly higher densities in ponderosa pine forests and xeric-mixed conifer forests that burned at high severities. Still, the range of densities was highly variable and overlapping for each burn severity. We did find that wetter forest types, particularly mesic-mixed conifer, aspen-mixed conifer, and aspen forests, had higher tree densities than other forest types. This is likely because of the strong presence of sprouting aspen and frequent small-scale, within-stand disturbances in these stands [16]. Our stand structure data demonstrate that these forests have higher mortality rates in low and unburned burn severities than other forest types, likely from spruce bark beetle or aspen-related mortality. However, this mortality is unlikely to influence fire severity [55]. In aspen, moderate and high burn severities were associated with higher stand densities. This could result from aspen's sensitivity to fire, where many stems result in high mortality. Some studies have demonstrated that aspen stands can moderate fire severity, but here we found this is perhaps more likely when stem density is lower [56]. We also found that in spruce-fir forests, stand density was slightly lower in stands that burned at moderate and high severity. This could result from these stands being more susceptible to drought from increased solar radiation and lower shade in stands with more gaps and lower densities [57,58]. We demonstrated that soil and crown burn severity are distinct metrics associated with forest stand characteristics and abiotic variables. Crown burn severity only sometimes had a strong relationship with stand characteristics and, in general, was explained by slope steepness, which is a consistent finding in areas with steep slopes where topography strongly influences fire behavior [59–61]. Soil burn severity was most predicted by aspect, which could be confounded with surface fuel loads and surface fuel moisture availability [36,62,63]. Given the relatively natural and unlogged mature forest condition of these stands, it is possible that pre-fire stand density played a lesser role in burn severity because of the variable stand structure [64,65]. An important takeaway from these two burn severity metrics is their ecological distinction, which matters regarding fire recovery [41,42]. In this study, we focused on forest recovery and, therefore, on crown-fire severity; however, given detectable differences in these metrics, research focused on mechanisms of post-fire recovery may want to distinguish changes to the soil environment vs. changes to the overstory canopy condition. Together, these results show the complexity of assumptions regarding canopy fuel densities and their contribution to observed fire effects. These findings support the idea that many variables determine how forest structure will interact with topography and weather to influence fire effects on ecosystems [66].

Our second hypothesis was well supported: LAI correlated with forest stand characteristics of living overstory trees and shrub cover, even over a large area with complex topography. In some instances, we found that even unburned areas experienced decreased LAI in the year following the fire. This pattern occurred in aspen and ponderosa pine forests, which may result from leaf drop due to drought [67,68]. There was no difference between low burn severity and unburned forests in ponderosa pine forests in the first year following the fire, providing partial support to our third hypothesis. In other forest types, particularly xeric-mixed conifer, aspen-mixed conifer, and mesic spruce-fir, there was no change in LAI in low-severity fire. This could result from minimal tree mortality in low-severity fires in these forest types or the response of increasing shrub cover because of sprouting following low-severity fires. These results demonstrate the resistance of these forest types to low-severity fires, where minimal changes occur following a low-severity fire [69]. In mesic-mixed conifer forests and xeric spruce-fir, low-severity

fire significantly reduced leaf area index relative to unburned forests, demonstrating the lack of resistance to these low-severity disturbances. This could result from slow growth in these systems and a lack of moisture during drought to facilitate regrowth following the disturbance [70]. These findings show a more nuanced perspective to our third hypothesis than we anticipated, which could be due to the complex interacting variables that influence post-fire trajectories, including climate and post-fire-related mortality associated with tree injury or insect outbreaks. These results indicate that LAI may be useful for considering recovery post-fire or other landscape-scale disturbances. Some studies have demonstrated that LAI is variable based on forest type and topographic features [20,23,27]. Here, by demonstrating the relationship of LAI to stand characteristics, we demonstrate how a decrease in LAI from overstory mortality may increase LAI from shrub cover. Thus, LAI is a valuable metric with ecological relevance. However, relating a singular metric, like LAI, to forest recovery requires more perspective on resilience and the desired conditions of the setting in which a disturbance occurs [71–73]. For example, increases in LAI, regardless of species, may prevent erosion and mitigate post-fire flooding. In contrast, increases in shrub cover simultaneously provide competition to tree seedlings and slow or inhibit forest recovery [74,75]. In this way, it is unclear if LAI strongly represents "recovery" or simply revegetation after a disturbance, which could represent recovery or reorganization [76]. Furthermore, our study is limited in spatial scale, as we used a 30 m spatial resolution for our rasters, which represents a coarse value that excludes microsite variation. While our plot data may capture the variation across microsites, the temporal scales of recovery also matter, given that burned trees falling from the fire preclude any potential for microsites that regenerate faster than the surrounding areas. Temporal scales of recovery also matter, given that burned trees falling from the fire will eventually serve as microsites for conifer seedlings. Shrubs may also serve as essential microsites, manipulating early successional species. Thus, forest recovery trajectories may be in the order of centuries, regardless of initial responses [31,77–79]. Climate and other abiotic factors likely have a stronger control on post-fire recovery regarding species composition and stand structure [70,80–84].

Our fourth hypothesis was well supported in that moderate and high-severity fires consistently reduced LAI throughout our study. Only xeric-mixed conifer systems recovered to pre-fire LAI values after high-severity fire 4 years post-fire. However, every forest type in our study system recovered to pre-fire LAI levels after experiencing a moderate-severity fire. This could result from different forest stand gap sizes in high relative to moderate severity fires [85]. The ability of xeric-mixed conifer to recover to pre-fire LAI values in high-severity fire may result from increased shrub cover in the system that vigorously sprouted and took advantage of the openings created by total canopy removal [86,87]. In this case, recovery may only be an appropriate term given the plant cover's functions, but the forest could still be susceptible to type conversion to shrub fields. Below, we discuss some of the key regeneration patterns observed to reflect on the trajectory of these post-fire ecosystems. In moderate and high-severity fires in xeric-mixed conifer forests, surviving large fire-resistant trees exist on the landscape and could provide potential seed sources [88–90]. The forests in our study area are unique from other forests in the region because of the stand structure of large trees and uneven-aged stand structure, and this could be a contributing factor to why there are survivors in high-severity fire patches [7,15,91,92]. In aspen forests and aspen-mixed conifer forests, LAI was increased relative to pre-fire in low-severity fire, and by four years post-fire, LAI is higher in moderate and high-severity fire areas relative to pre-fire conditions or unburned conditions. This represents the disturbance response of aspen that proliferates following stem disturbance, demonstrates the resilience of aspen stands to the fire of all severities, and supports findings that aspen is favored by fire [93,94]. Interestingly, aspen in unburned stands experienced reduced LAI values

and never recovered to pre-fire values. This could result from drought stress in aspen stems that do not receive above-ground disturbance and could contribute to eventual aspen mortality [95,96]. Spruce-fir systems showed the most significant reductions in LAI in high-severity fires and the slowest responses, likely because of short growing seasons and cold conditions at high elevations that limit recovery of spruce-fir forests or the trajectory of spruce-fir forest regeneration being dominated by subalpine fir instead of spruce [79]. This also demonstrates that our fifth hypothesis was not supported in that shrub cover was lowest in spruce-fir forests that are adapted to high-severity fire and highest in xeric-mixed conifer forests that experienced moderate burn severities or ponderosa pine forests that experienced high-severity fire. These results indicate that shrub cover following fire may not be an indicator of recovery, but instead could be an indicator of type conversion or change, even if functional recovery in terms of vegetative cover is observed.

Our sixth hypothesis was supported in that regeneration of seedlings tended to occur at wetter sites regardless of specific forest types. CWD was the primary predictor for tree regeneration for all species, with regeneration generally occurring at sites with lower CWD. This implies CWD was more important than tree density in predicting regeneration which could be the result of the 416 being a mixed-severity fire where large areas without living trees are less common. Average densities of tree regeneration were low relative to seedling densities needed to recreate pre-fire stand conditions [97]. In some instances, we observed tree regeneration of dry-adapted species in more mesic sites, such as ponderosa pine recruitment in mesic-mixed conifer forest types. This pattern could represent the natural upward leaning of forest types; however, it is difficult to make any general assertions given the limited regeneration observed in our study [98]. Many studies have documented the lack of conifer regeneration following uncharacteristically high-severity fires and have inferred that, at least in part, these patterns are related to unfavorable climatic conditions and/or human-altered fuel scapes that result in ecosystem conversion following wildfire [70,80,99]. Alternatively, lack of regeneration following high-severity fire could result from the loss of microsites needed for tree regeneration [100]. One challenge in these studies is that forested ecosystems operate on longer time scales and are dependent on ideal weather conditions for regeneration to occur, and this is sometimes episodic based on the climate following the disturbance [101]. One realm of uncertainty is the need for more understanding of successional dynamics following stand-replacing events, particularly in ecosystems adapted to frequent low-severity disturbances and only occasionally experiencing a high-severity disturbance, such as ponderosa pine or mixed conifer ecosystems [16]. Some studies have demonstrated how shrub species, such as *Quercus gambelii*, may serve as early successional species in these systems, eventually serving as nurse plants facilitating conifer seedling establishment and growth during dry periods [78,102]. This leads to uncertainty in the future state of ecosystems, prompting a challenging and perhaps philosophical question regarding the status of ecosystem recovery. Importantly, since we showed negative relationships between seedling density and climate water deficit, it seems likely that wetter than average years or wetter sites will still favor regeneration of trees, and these sites are also often associated with fire refugia [103]. These fire refugia can contribute to forest resilience and provide seed sources to areas lacking surviving trees [104]. Taken together with LAI values for these forest types, we demonstrate optimism in this specific fire amid the narrative of forest loss due to climate change and mega-fires [105,106]. It is important to note that tree regeneration did not have a relationship to LAI and therefore information about regeneration is difficult to capture in remotely sensed data. Further, because both shrub cover and living tree density are explanatory variables of LAI, it is difficult to interpret whether LAI is capturing structural vs. functional recovery. While our study offers a metric of forest recovery using LAI, we are not able to assert whether forests have recovered in terms of structure and

species composition or function (i.e., vegetation cover) with LAI alone. This finding is important because while LAI may offer a useful remote-sensed tool to ascertain whether or not ecosystem function is recovering, plot-based data are still needed to determine the direction of recovery in terms of species composition and structure. This demonstrates the importance of considering individual forest types within individual fires rather than making blanket conclusions regarding fire effects on ecosystems.

5. Conclusions

Our study provides a detailed example of how soil burn severity and crown burn severity differ and are not necessarily predicted by tree density. We also provide a linear regression model that connects a remotely sensed value of the Leaf Area Index to stand structure components, specifically demonstrating that LAI is best explained by living tree density and shrub cover and that LAI varies by forest type and burn severity in the years since the fire. This study helps connect remote-sensed data to useful plot-based data and demonstrates some limitations in the perspective of structural recovery vs. functional recovery in using a remote-sensed LAI value to assess forest recovery following a fire.

Given the relationship between plant cover and erosion, we provide an interesting narrative on forest recovery by forest type and burn severity. The above forest responses demonstrate that mixed-severity fire generally results in forest recovery within 4 years of fire and thus has important links to the socioeconomic concerns regarding erosion from fire effects and forest recovery. By examining conifer regeneration, we can consider ecosystem recovery as the product of plant cover and sufficient regeneration of desired tree species to maintain or recover pre-fire stand conditions. We demonstrate that LAI is a valuable metric of recovery given its relationship with plant cover; however, from an ecological perspective, it becomes unclear whether LAI represents forest recovery or reorganization. Our study demonstrates that LAI can be used as an adaptive management tool in post-fire environments, especially when paired with, plot-based observations on tree regeneration to emphasize functional recovery from a wildfire. We specifically demonstrate that land managers can utilize LAI as a metric to represent post-fire vegetation cover, encompassing both shrub and living tree cover, to estimate when a burn area spanning diverse forest types may recover to pre-fire LAI values. Despite this, land managers may need additional information to determine whether recovery towards similar community composition and structure is occurring by collecting regeneration data in the field.

Our study was conducted in a forested ecosystem that resembles old-growth characteristics across much of the study area and provides some important considerations for both pre-fire planning and post-fire actions. We found that tree density was not higher in moderate or high burn severities and that large fire-resistant Douglas-fir and ponderosa pine trees survived moderate and high-severity fires. These results demonstrate the importance of maintaining large trees in the landscape to promote fire resilience [88]. Additionally, tree density manipulations may not always reduce fire behavior, especially in areas where large trees exist and tree densities are generally lower than in the regions that had been previously clear-cut or plantation-logged [65]. This is particularly true in a forested ecosystem with little to no wildland–urban interface (WUI) or human structures built on the landscape, and mixed-severity fire can be tolerated. Importantly, to coexist with mixed-severity fire, post-fire erosion is inevitable and is likely to persist for at least four years following the fire [107–109]. Natural forest recovery can prevent long-term erosional patterns; however, post-fire erosional structures may be needed immediately after the fire to reduce sediment loads in ditches and rivers. Further silvicultural interventions may be required to achieve desired recovery outcomes, particularly if land managers are concerned about losing ecosystem function because of conversion to non-forested ecosystems. These

actions could include target plant-based reforestation, particularly using planting methods to enhance seedling survival [97,110,111].

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