



Extent of recent fire-induced losses of ponderosa pine forests of Arizona and New Mexico, USA

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ABSTRACT

Land management legacies coupled with climate change have led to shifts in western ponderosa pine (*Pinus ponderosa*) forest structure and fire regimes. A growing body of evidence suggests that under increasing area burned at high-severity, warming and drought, ponderosa pine forests are vulnerable to conversion to alternate forest types or non-forest vegetation. However, the extent and direction of recent fire-induced changes in southwestern US ponderosa pine forests have not been subject to region-wide evaluation. Here, we assess recent fire effects in ponderosa pine forests using long-term repeated samples of stand composition and structure from the US Forest Service's Forest Inventory and Analysis (FIA) program, combined with metrics of satellite-derived burn severity (predicted Composite Burn Index, CBI; and differenced normalized burn ratio, dNBR). We compiled and analyzed FIA plots dominated by ponderosa pine and associated species within the southwestern states of Arizona and New Mexico to quantify regional trends for ponderosa pine (e.g., forest losses or gains), link changes to wildfire severity, and characterize vegetation shifts.

Among 685 plots sampled three times between 1996 and 2017, 26% of plots burned at least once, with more than half of these burning at moderate to high severity. Plots that burned within the study period exhibited a net loss of 46% of ponderosa pine trees, but unburned plots also exhibited a net decline of 11%. While all tree size classes exhibited greater losses than gains, tree size was a positive predictor of post-fire survival. Satellite-derived burn severity (predicted CBI) was strongly related to tree mortality and shifts toward alternate post-fire vegetation types. Severely burned stands exhibited trajectories toward non-forest vegetation with high dominance by resprouting species, particularly Gambel oak (*Quercus gambelii*).

These findings contribute to an emerging understanding of the potential ecological outcomes of growing forest vulnerability to changing climate and disturbance regimes. Methods employed herein offer scalable opportunities to quantify changes across forest biomes using long-term monitoring data. As importantly, our findings inform regional and local land management efforts to sustain these valued forest types in an era of change. We highlight two key themes for management to promote the long-term persistence of ponderosa pine forests in the southwestern US: restoration of low-severity fire regimes and retention of large, fire-resistant trees.

1. Introduction

Ponderosa pine (*Pinus ponderosa*) forests have long been shaped by wildfire, yet recent changes in fire regimes and climate are raising concerns about the long-term persistence of this species in portions of its range in western North America. Abundant evidence demonstrates that historical fire regimes of ponderosa pine forests through the mid- to late-19th century were generally characterized by frequent, low-severity surface fires punctuated by infrequent, small, moderate- to high-severity patches (Brown and Sieg, 1999; Hessburg et al., 2000;

Stephens et al., 2015; Swetnam, 1996). Such fires reduced understory vegetation, removed surface fuels, maintained open stand structures, and created fine-scale spatial landscape heterogeneity (Allen et al., 2002). Ponderosa pine exhibits many fire adapted traits that endowed survival and regeneration under historical fire regimes (Fitzgerald 2005), including open crowns, thick bark, and tendency to self-prune limbs when mature, which reduces ladder fuels. Ponderosa pine is non-resprouting, non-serotinous, and dependent on nearby seed producing trees for regeneration (Moir et al. 1997, Allen et al. 2002, Fitzgerald 2005).

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Since the mid-to late- 19th century, Euro-American land use and fire management practices have driven major changes to the form and function of ponderosa pine forests. Fire suppression, livestock grazing, and selective harvest of large trees have produced forest structure and fire behavior considerably departed from historical conditions (Covington and Moore 1994, Allen et al. 2002, Battaglia et al. 2018). Without frequent surface fire, ponderosa pine forest landscapes have become denser and more homogeneous, with increased surface and ladder fuels to tree crowns (Hagmann et al., 2021; Hessburg et al., 2005). Consequently, increased fuel availability and continuity, now combined with warmer and drier fire seasons associated with anthropogenic climate change, have led to dramatic recent increases in the extent of high-severity fire in these systems (Miller et al. 2009, Westerling 2016, Abatzoglou and Williams 2016, Singleton et al. 2019).

Severe fire, coupled with warming and drying, can overcome ponderosa pine forest resistance and recovery mechanisms (Johnstone et al. 2016, Hessburg et al. 2019, Falk et al. 2022). Altered recovery dynamics associated with more and higher severity fire include increased distances to seed sources and short-interval reburning that hinder seedling recruitment and survival (Coop et al. 2016, Chambers et al. 2016, Haffey et al. 2018). Large, high severity wildfires can also alter soil properties, reducing seed germination and seedling survival (Kurth et al. 2013, Owen et al. 2019). Further, a warming climate can directly reduce the capacity of many tree species, including ponderosa pine, to re-establish following fire in warm and dry climate settings (Stevens-Rumann et al. 2018, Davis et al. 2019, Littlefield et al. 2020). Climate model projections of warming and increased aridity within the western US are expected to continue to drive increasing wildfire activity and reduced post-fire regeneration, increasing the vulnerability of ponderosa pine forest types (Parks et al. 2019a).

The ecological outcomes of the loss of forest resilience to changing climate and disturbance regimes includes forest losses and conversions to alternate and non-forest vegetation types (Coop et al. 2020). Palaeoecological records demonstrate that during past periods of rapid, directional climate change, wildfire triggered large-scale and enduring vegetative conversions, creating opportunities for new successional pathways leading toward outcomes that differed from the pre-fire vegetation (Crausbay et al. 2017). A growing body of research across western North America demonstrates that contemporary wildfires are similarly poised to catalyze lasting ecological shifts under climate change (Savage and Mast 2005, Coop et al. 2016, Haffey et al. 2018, Davis et al. 2019, Stevens-Rumann and Morgan 2019, Stanke et al. 2021). Within the intermountain western US, it is estimated that 6.6% of forested area is projected to be at risk of wildfire-induced conversion to non-forest by 2050, and within the southwestern US, 30% of forested areas are at risk, making this region particularly vulnerable (Parks et al. 2019a). Moreover, under a 2C warming scenario, 16% of ponderosa pine forests are at substantial risk of fire-catalyzed forest conversion (Davis et al. 2020, Rodman et al. 2020).

Despite a rapidly growing understanding of ponderosa pine forest vulnerability to changing fire activity and climate, landscape-scale quantification of the extent and direction of fire-induced forest changes is lacking. Here, we determine the extent of recent, fire-driven change in ponderosa pine forests of Arizona and New Mexico, based on data from the national USDA Forest Service Forest Inventory and Analysis (FIA) program. As data is collected annually across forest ecosystems in each state in the US, the FIA database allows for novel analyses and statistically rigorous estimation of change over large spatial scales (Bechtold and Patterson 2005, Shaw et al. 2017). We linked FIA vegetation data to satellite-derived burn severity, including the delta normalized burn ratio (dNBR) and predicted composite burn index (CBI). Both metrics are useful for characterizing fire effects across large spatial and temporal scales (Parks et al. 2018).

A closer examination of ponderosa pine forests within the southwestern US allows an assessment of current trajectories of change. Trends may serve as indicators of future effects of wildfire and drought

under intensifying climate change, thereby assisting researchers and land managers in prioritizing management interventions. Specifically, the objectives of this study were to: (1) assess recent wildfire activity (wildfires which occurred between 1996 and 2017) in southwestern ponderosa pine stands within the FIA plot network in Arizona and New Mexico, USA, (2) evaluate relationships between tree mortality and two metrics of satellite-derived burn severity (dNBR and predicted CBI), (3) quantify and contrast temporal patterns of tree mortality and regeneration among ponderosa pines with and without recent wildfire, and (4) characterize changes in vegetation composition associated with varying levels of burn severity.

2. Materials and methods

2.1. Forest inventory and analysis plot network

Data on recent forest change were assembled from the Forest Inventory and Analysis (FIA) program, a nationwide inventory of US forestlands maintained by the US Forest Service. The program is designed to assess status and trends of forests across all land ownerships and forest types. The network comprises permanent, geographically unbiased field plots at a density of approximately one per 2,403 ha (Bechtold and Patterson 2005, Burrill et al. 2018). As the FIA annual inventory program was being developed and implemented in the late 1990s, many earlier periodic inventory plots were carried over into a standardized annual inventory plot design with nationally consistent data collection protocols. Although the annual inventory started in 2000 across the interior western US, it was implemented in different years in different states. Now, two decades later, most western states are in a 10-year remeasurement cycle. All FIA data are freely available to the public and are deposited in the FIA database located at <https://apps.fs.usda.gov/fia/datamart/>. However, within the public database, plot coordinates are “fuzzed” to up to 1.6 km, with most being within 800 m of the actual location (Burrill et al. 2018).

All annual inventories and the most recent periodic inventory follow a nationally standardized, fixed-area, mapped-plot design. Each plot consists of four non-overlapping 7.3-m radius circular subplots which cover a total area of 0.7 ha. For all subplots, substantial forest mensuration data are collected on tally trees, which include conifer and hardwood species. Conifer tally trees are defined as species with a minimum diameter of 2.54 cm and height of 1.52 m. Conifer tree diameters are measured at breast height (DBH). Hardwood tally trees must be at least 2.54 cm diameter, measured at the ground line or at the stem root collar (DRC). The species identity, diameter, and height of every living and dead tally tree is measured and recorded. Within each subplot is a nested 2.1-m radius microplot for the measurement of tree seedlings. Tree seedlings are defined as trees with a diameter <2.54 cm and at least 15.24 cm tall for conifers and at least 30.48 cm tall for hardwoods. Species identity and a count of individuals per species are recorded for seedlings. All FIA plot data used in this study follow the most recent FIA protocol (Bechtold and Patterson 2005, Burrill et al. 2018).

Following the implementation of annualized inventory protocols, understory percent cover estimates are recorded for each sampled condition of the subplot within the subplot perimeter. Here, condition refers to a recorded FIA variable that characterizes substantial differences within a plot (i.e. differences in owner group, forest type, stand density). Percent cover is defined as the area of ground surface covered by a vertical projection of the canopy of a vascular plant. Estimates of percent cover are recorded by vegetation structure growth habit, layer height classes, and species. Growth habits include shrub, forb, and graminoid. Percentages by growth habit and layer classes are estimated to the nearest one percent (Bechtold and Patterson 2005, Burrill et al. 2018).

2.2. Dataset assembly and extent

Given our objectives, we required FIA plot data used in this study to

meet the following criteria: 1) located in the southwestern US states of Arizona and New Mexico, 2) sampled three times using comparable methodologies, and 3) contained at least one ponderosa seedling, sapling, or tree in at least one sample period. Plots were queried from late periodic inventory (1995–2000) and annual inventory (2000–2018) measured under the same sampling design. A total of 685 plots were ultimately included in this study (Table 1; Fig. 1). These plots were re-measured approximately 5–12 years apart. Elevations ranged from 1490 to 2963 m. Over half of the plots (65%) fell on USFS land, with the remaining on private/Native American, other federal, and state/local government land. Our study excluded plots within New Mexico’s Gila National Forest because they were only sampled twice under the annual inventory plot design.

Plots with any management treatment or lack thereof were included in the analysis. Approximately 5% of the selected plots had experienced management treatments since 1996, labeled primarily by FIA field crews as “cutting”. These included 30 plots in the first annual inventory (from 1996 to 2010) and 34 plots in the second annual inventory (from 2006 to 2017). Plots from periodic inventory listed “cutting” as the only treatment type and the treatment year went as far back as 1920 and up to 1998. More than 65% of the FIA plots in this study (458 plots) have experienced some timber harvest over the past century. Based on the FIA DSTRBCD variables, approximately 7% of plots exhibited insect damage and 18% of plots recorded disease damage over the study period. We consider the study area included in this analysis to represent contemporary conditions and processes found in ponderosa pine stands of the southwestern US.

To determine which plots had experienced recent fire activity, burn perimeters since 1984 from Monitoring Trends in Burn Severity (MTBS; Eidenshink et al., 2007) were overlaid on the exact “unfuzzed” FIA plot locations. To assess recent fire effects, we then determined which plots had at least one pre-fire inventory and at least one post-fire inventory. Plots that burned between the first inventory and second inventory, second and third inventory, or both, were categorized as “recently burned”. In total, 26% (n = 175) of plots burned at some time between the first and third inventory, 1996–2017 (Fig. 1). We hereafter refer to recent wildfires as fires that burned within our study area from 1996 to 2017. These 175 plots overlapped 88 distinct burns in the MTBS database (see Appendix Supplementary Data). The proportion of plots sampled in different fires is directly related to the area of ponderosa pine forest burned by these fires, thus our findings are expected to be broadly representative of changes to ponderosa pine across the study area.

Based on the MTBS fire names and IDs of these burns, we developed raster grids of differenced normalized burn ratio (dNBR) and predicted composite burn index (CBI) following the methods of Parks et al. (2018) and Parks et al. (2019b). Briefly, dNBR is computed with the normalized burn ratio (NBR) using near-infrared and short-wave infrared wavelengths from Landsat imagery. Post-fire NBR is subtracted from the pre-fire NBR to calculate burn severity. CBI is a frequently used field-based measure of fire severity and can be modeled as a function of multiple spectral indices, and variables representing spatial variability in climate (Parks et al. 2018, 2019b). Predicted CBI is based on the relationship between field-collected CBI and spectral indices such as NBR, climatic indices including climatic water deficit and actual evapotranspiration, as well as latitude and longitude. These gridded maps representing estimated CBI are considered more interpretable in terms of on-the-ground fire effects compared to non-standardized spectral indices

(Parks et al. 2019b). Unfuzzed FIA plot coordinates were then used to extract both fire severity metrics for each burned FIA plot.

2.3. Data analysis

Both dNBR and predicted CBI severity metrics were used to assess the effectiveness of each in predicting tree mortality and characterizing fire effects. Datasets of dNBR and CBI were categorized into discrete classes representing low, moderate, and high severity. Fire severity classes for dNBR include dNBR values ranging from 100 to 269 for low severity, moderate-low severity from 270 to 439, moderate-high severity from 440 to 659, and high severity from 660 to 1300 (Key, 2006). For CBI, low severity corresponds to values ranging from 0 to 1.24, moderate severity from 1.25 to 2.24, and high severity from 2.25 to 3.0 (Miller and Thode 2007, Parks et al. 2018). All ponderosa pine trees 12.7 cm or greater in diameter at breast height (DBH) were categorized into size classes as follows: small trees (12.7–25.3 cm DBH), medium trees (25.4–38.1 cm DBH), and large trees (greater than 38.1 cm DBH). Saplings were classified as trees < 12.7 cm. Seedlings were categorized the same as FIA size requirements (at least 15.24 cm tall). Basal area (m²) was calculated for each tree.

To assess changes in vegetation composition across the study area, a vegetation type was determined for each plot. Vegetation types were based on the presence/absence and composition of trees, seedlings, and understory vegetation recorded on the plot in the first and last inventory period, as follows. First, we grouped plots into two primary categories: plots that contained ponderosa pine trees or seedlings, and those that did not. Then, if trees and/or tree seedlings of any individual species were present, the plots were assigned to groups based on the top two dominant tree species. For example, a plot containing one ponderosa pine tree but dominated by two-needle pinyon (*Pinus edulis*) and Utah juniper (*Juniperus osteosperma*) could be assigned the ponderosa pine- pinyon/ juniper woodland group (Table 2). Plots containing any individual trees and seedling species were grouped into broad vegetation groups using the FIA variable “species group code” (SPGRPCD). FIA assigns a species group code to each tree and seedling. Within our plot selection, there were nine species group codes assigned to individual tree and seedling recordings. We refined these groups to reflect different species compositions, and contrasted this classification with an FIA forest typology, species group (Table 2).

If a plot contained no trees or seedlings, then the dominant understory growth type and species was used to form a vegetation group. FIA understory growth type categories include shrubs, forbs, and graminoids. The growth type with the highest percent cover was used to categorize the plot’s vegetation type. Forbs and graminoids were combined to the herbaceous category. If a plot contained more than one FIA field-determined condition, all trees, seedlings, or understory spanning across the entire plot was used to assign a vegetation group. Because we were interested in characterizing change from the beginning to end of our study period, just the first (cycle 1) and last inventory collections (cycle 3) were used for this portion of the analysis. Although periodic data (the first inventory cycle) collection did not include as detailed understory vegetation data, only two plots did not contain any trees or tree seedlings; these plots were excluded from this analysis.

To characterize recent patterns of wildfire in ponderosa pine stands across selected FIA plots, for each burned plot we extracted fire characteristics including fire type, size, and severity (dNBR and predicted CBI). To quantify forest loss and gain among ponderosa pines, we computed trends in FIA plots, including the total number and basal area (m²) of live ponderosa pine trees by size class and numbers of saplings and seedlings within each plot and across all samples. Differences in stand basal area (m²/ha) and number of trees/stems per hectare between each inventory period were tested using a one-way ANOVA, with a Tukey’s post-hoc test applied if the ANOVA indicated significant change.

To assess the relationships among tree mortality and fire severity, we

Table 1
Summary of attributes for selected FIA plots used in this study.

Plot attributes	Arizona	New Mexico
Years of periodic data inventory	1995–1998	1996–2000
Years of annual data inventory	2001–2018	2008–2018
Number of plots	501	184
Total number of burned plots	149	26

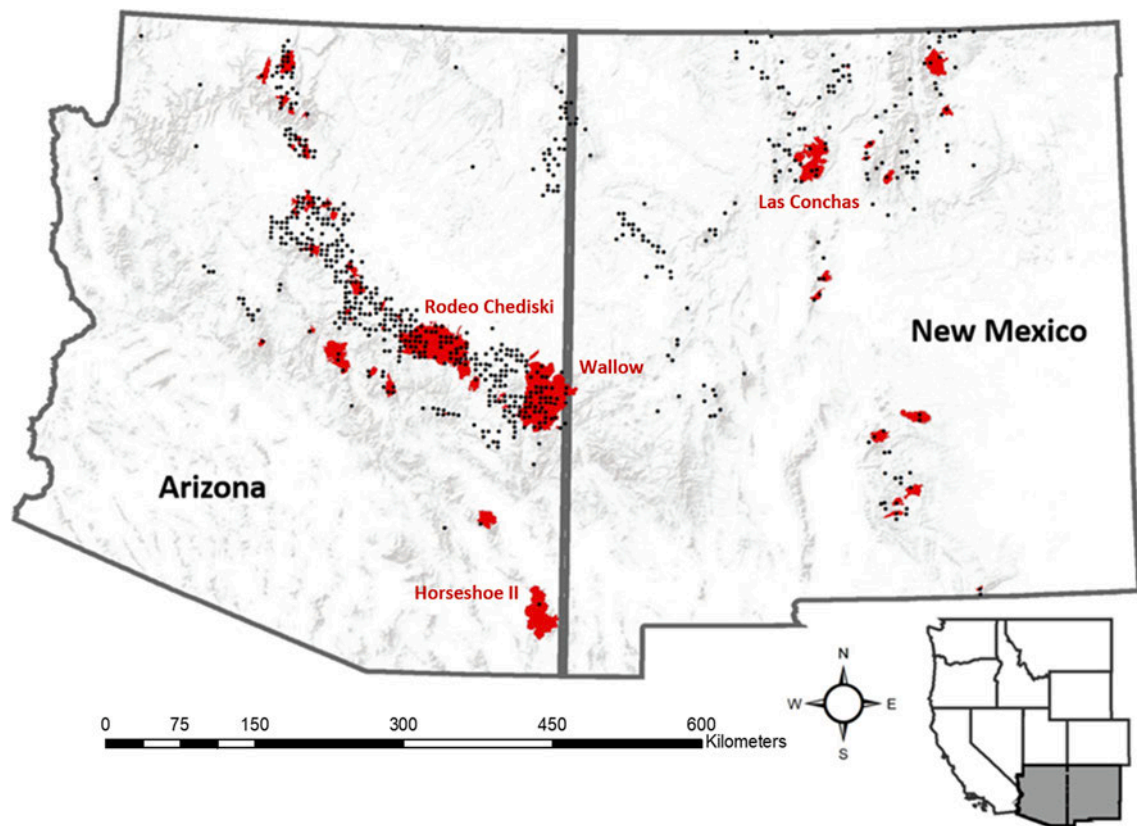


Fig. 1. Study area showing FIA plot locations (points) and study burn perimeters (red) in Arizona and New Mexico. Fires which burned more than 150,000 acres are labeled.

used binomial (logistic) generalized linear models. Logistic regression is appropriate for modeling mortality probability because its range is bounded by 0 and 1 (dead vs. alive). Probability of tree survival vs. mortality post-fire was predicted as a function of one fire severity metric (dNBR or predicted CBI) for each size class. The Akaike Information Criterion (AIC) was used to compare the relative quality of the dNBR and predicted CBI model to each other. The model with the lowest AIC value was considered to be a better fit. Negative binomial regression models were used to model the total number of ponderosa pine seedling and sapling stems as a function of fire severity. In all models, trees are defined as stems 12.7 cm or greater in DBH. Significance among all statistics was determined if p -values were <0.05 . To characterize changes in vegetation composition across the study area, we quantified proportional shifts among the assigned vegetation groups between the first and third sample cycle.

All data analysis was conducted in the program R (R Core Team, 2019). The packages *tidyr* (Wickham, 2021) and *dplyr* (Wickham et al., 2021) were used to clean and sort FIA and MTBS data. The packages *ggplot2* (Wickham, 2016), *circlize* (Gu, 2014), and *RColorBrewer* (Neuwirth, 2014) were used for all graphs. MASS (Venables and Ripley, 2002) was used to develop and test statistical models.

3. Results

3.1. Recent fire frequency and severity in southwestern US ponderosa pine stands

A total of 88 recent fires ranging in fire severity overlapped with FIA ponderosa pine plots across the Arizona and New Mexico study area during the period of analysis (see Appendix in Supplementary Data). Many of the fires spanned large geographical areas and burned more than one plot; including two megafires, the Rodeo-Chediski and Wallow

fires. These two fires burned 46% (80 plots) of the plots that burned recently. In total, 26% (175 plots) of our sampled FIA plots experienced at least one fire between 1996 and 2017. Fire types included prescribed burns, wildland fire use, and wildfires. A total of 83 plots burned in selected ponderosa pine FIA plots between cycle 1 and 2 (68 in AZ and 15 in NM), 3 of them burned twice during this period, and one plot burned two more times between cycle 2 and 3. Between cycle 2 and 3, 92 other plots burned (82 in AZ and 10 in NM), and 3 of them burned twice during this period. A total of 6 other plots burned twice across the interval periods, yielding a total of 13 plots which burned more than once from 1996 to 2017.

Of the plots that burned once during our study period, 41% burned at low severity (CBI values 0–1.24), 31% burned at moderate severity (CBI values 1.25–2.24) and 28% burned at high severity (CBI values 2.25–3.0) (Fig. 2). Of the plots that burned twice, 75% burned at low severity the first interval and 83% burned at low severity the second interval. The plot that burned three times from 1996 to 2017 burned at low severity each time. As of the last measurement of this study in 2017, 74% of plots (510) had not experienced any recent fire.

3.2. Tree mortality and burn severity

Both predicted CBI and dNBR were significant predictors of post-fire tree mortality, but the predicted CBI fire severity metric produced the lowest AIC model, as follows: where p is probability (survival), $\log(p/1-p) = 3.375 - 1.949 \cdot \text{CBI}$ ($p < 0.001$, $df = 2325$, $\text{AIC} = 2014$). In contrast, the dNBR model was $\log(p/1-p) = 2.759 - 0.011 \cdot \text{dNBR}$ ($p < 0.001$, $df = 2325$, $\text{AIC} = 2067$). The probability of individual tree mortality within each size class was further modeled as a function of CBI. We found strong relationships between tree mortality and predicted CBI among small trees ($p < 0.001$, $df = 1326$), medium trees ($p < 0.001$, $df = 643$), and large trees ($p < 0.001$, $df = 352$). Fig. 3 illustrates the models predicting

Table 2

Vegetation types classified for this study. The dominant species found within the study sample's FIA Species Group is listed where applicable. Vegetation types are grouped by those containing ponderosa pine and others in the associated Species Group, plots containing no ponderosa pine but other dominants from the Species Group, and non-forest (dominated by grass, forbs, or shrubs).

Vegetation Type	FIA Species Group	Dominant Species Found Within Selected Plots
Ponderosa pine forests		
Pure ponderosa pine	Ponderosa and Jeffrey pines	<i>Pinus ponderosa</i>
Ponderosa pine-oak	Ponderosa and Jeffrey pines, Woodland hardwoods	<i>Pinus ponderosa</i> , <i>Quercus gambelii</i> , <i>Acer grandidentatum</i> , <i>Quercus arizonica</i> , <i>Quercus emoryi</i>
Ponderosa pine-mixed conifer	Ponderosa and Jeffrey pines, Douglas-fir, true fir, Engelmann and other spruces, Other western softwoods	<i>Pinus ponderosa</i> , <i>Pseudotsuga menziesii</i> , <i>Abies concolor</i> , <i>Picea engelmannii</i> , <i>Picea pungens</i> , <i>Pinus strobiformis</i> , <i>Pinus flexilis</i> , <i>Cupressus arizonica</i> , <i>Pinus leiophylla</i>
Ponderosa pine-Pinyon/juniper woodland	Ponderosa and Jeffrey pines, Woodland softwoods	<i>Pinus ponderosa</i> , <i>Juniperus deppeana</i> , <i>Juniperus osteosperma</i> , <i>Juniperus scopulorum</i> , <i>Juniperus monosperma</i> , <i>Pinus edulis</i>
Ponderosa pine-aspen	Ponderosa and Jeffrey pines, Cottonwood and aspen	<i>Pinus ponderosa</i> , <i>Populus tremuloides</i> , <i>Populus fremontii</i> , <i>Populus angustifolia</i>
Forests lacking ponderosa pine		
Mixed conifer	Douglas-fir, true fir, Engelmann and other spruces, Other western softwoods	<i>Pseudotsuga menziesii</i> , <i>Abies concolor</i> , <i>Picea engelmannii</i> , <i>Picea pungens</i> , <i>Pinus strobiformis</i> , <i>Pinus flexilis</i> , <i>Cupressus arizonica</i> , <i>Pinus leiophylla</i>
Pinyon/juniper woodland	Woodland softwoods	<i>Juniperus deppeana</i> , <i>Juniperus osteosperma</i> , <i>Juniperus scopulorum</i> , <i>Juniperus monosperma</i> , <i>Pinus edulis</i>
Non-forest		
Oak	Woodland hardwoods	<i>Quercus gambelii</i> , <i>Acer grandidentatum</i> , <i>Quercus arizonica</i> , <i>Quercus emoryi</i>
Mixed shrub	NA	<i>Robinia neomexicana</i> , <i>Acer pungens</i> , <i>Rosa woodsii</i>
Herbaceous	NA	<i>Poa fendleriana</i> , <i>Muhlenbergia straminea</i>

probability of mortality as a function of predicted CBI for each size class.

3.3. Decreases in inventoried ponderosa pine trees

Below, we first report changes across the entire sample, then report significance of changes in mean plot basal area and density, and lastly contrast changes in burned vs. unburned plots. Across the entire sample, the total number of live ponderosa pine trees decreased by 21% (from 10,154 to 8,010), and total inventoried ponderosa pine basal area declined by 7% (from 620.81 m² to 578.23 m²) over the study period. The number of plots containing any live ponderosa pine decreased by 10% (from 675 to 608). Of the plots that contained ponderosa pine at the beginning of the sample period, 11% of plots (77 of 685) experienced 100% ponderosa pine tree mortality. In contrast, only 1% of plots (10 out of 685) did not contain ponderosa at the beginning of the sample period but did by the end.

A total of 175 out of 685 plots burned over the study period. In the plots that burned, the number of plots containing ponderosa pine decreased by 32%, the number of ponderosa pine trees decreased by 46%, and the basal area decreased by 34%. These changes differed among size classes (Fig. 4). The number of small-sized ponderosa pine trees (12.7–25.3 cm DBH) decreased by 57% and the basal area decreased by 54%. The number of medium-sized ponderosa pine trees (25.4–38.1 cm DBH) decreased by 31% and the basal area decreased by

29%. The number of large-sized ponderosa pine trees (greater than 38.1 cm DBH) decreased by 25% and basal area decreased by 27%. Among the 77 plots that exhibited 100% tree mortality, 57 had experienced wildfire during the sample period. The cause of ponderosa pine loss in the other 20 plots is not certain; some were given an FIA disturbance code of insect damage (4 plots), disease (2 plots), drought (1 plot), human caused (1 plot), fire (4 plots), and no code listed (8 plots). The four plots with a fire disturbance code were not picked up in the MTBS database, perhaps due to small fire size.

In the plots that did not burn across the study period, the number of plots containing ponderosa pine decreased by 3%, the number of ponderosa pine trees decreased by 11%, but basal area increased by 5%. Across the plots that did not burn recently, these changes also differ among size classes (Fig. 4). The number of small-sized ponderosa pine trees decreased by 24% and their basal area decreased by 21%. The number of medium-sized ponderosa pine trees increased by 5% and their basal area increased by 8%. The number of large-sized ponderosa pine trees increased by 22% and their basal area increased by 22%.

Significance tests were used to characterize plot-scale changes in ponderosa pine basal area and density. The data were log transformed to meet the assumptions of normality. We found significant declines among the burned plots in mean basal area (m²/ha) [ANOVA $P < 0.001$] and mean number of trees (per hectare) [ANOVA $P < 0.001$] across the inventory cycles. There were no significant differences among the unburned plots in mean basal area and the number of trees across the inventory cycles.

The mean stand basal area (m²/ha) was significantly different between cycles one and three ($P < 0.001$, 95% C.I. = [−0.49, −0.22]) and decreased in cycle three on average by 5.52 m²/ha (or 34%) from cycle one. Stand basal area (m²/ha) was also significantly different between cycles one and two ($P < 0.01$, 95% C. I. = [−0.33, −0.07]), decreasing in cycle two on average by 3.32 m²/ha (20%), and between cycles two and three ($P < 0.05$, 95% C. I. = [−0.28, −0.02]), decreasing by 2.2 m²/ha (17%).

The mean number of trees (per hectare) was significantly different between cycle one and three ($P < 0.001$, 95% C.I. = [−0.98, −0.54]) and decreased in cycle three on average 117.61 (or 46%). Similarly, the mean number of trees was significantly different between cycles one and two ($P < 0.001$, 95% C.I. = [−0.65, −0.21]) and decreased in cycle two on average 72.74 (28%), and was also significantly different between cycles two and three ($P < 0.01$, 95% C.I. = [−0.55, −0.11]), decreasing by 44.87 (25%).

3.4. Changes in tree regeneration densities

Across all samples, the total number of plots containing ponderosa pine seedlings and saplings decreased by 27% (from 364 to 265) and the number of ponderosa pine seedlings and saplings decreased by 21% (10,154 to 8,010 stems; Fig. 5). In the plots that burned, the number of plots containing ponderosa pine seedlings decreased by 41% vs. 22% in unburned plots. The number of plots containing saplings also decreased in both recently burned plots by 57% and unburned plots by 22%. Seedling counts decreased 26% in recently burned plots while seedling counts increased by 9% in unburned plots. Sapling counts decreased 64% in recently burned plots and sapling counts decreased by 15% in unburned plots. However, we did not find significant differences in plot means for seedling or sapling density across inventory periods.

Among recently burned plots, 59 plots contained seedlings and saplings in the third inventory, and three of those plots burned more than once within our sample period. Fire severity and time since fire for the most recent fire were used for the analysis in the three plots which burned more than once. Of those 59 plots, 44 plots contained seedlings and 31 plots contained saplings in the third inventory. Recently burned plots that experienced severity values between 0 and 1.58 CBI (low to moderate severity) showed the most ponderosa pine regeneration among seedlings and saplings (Fig. 6A). Fewer seedlings and saplings

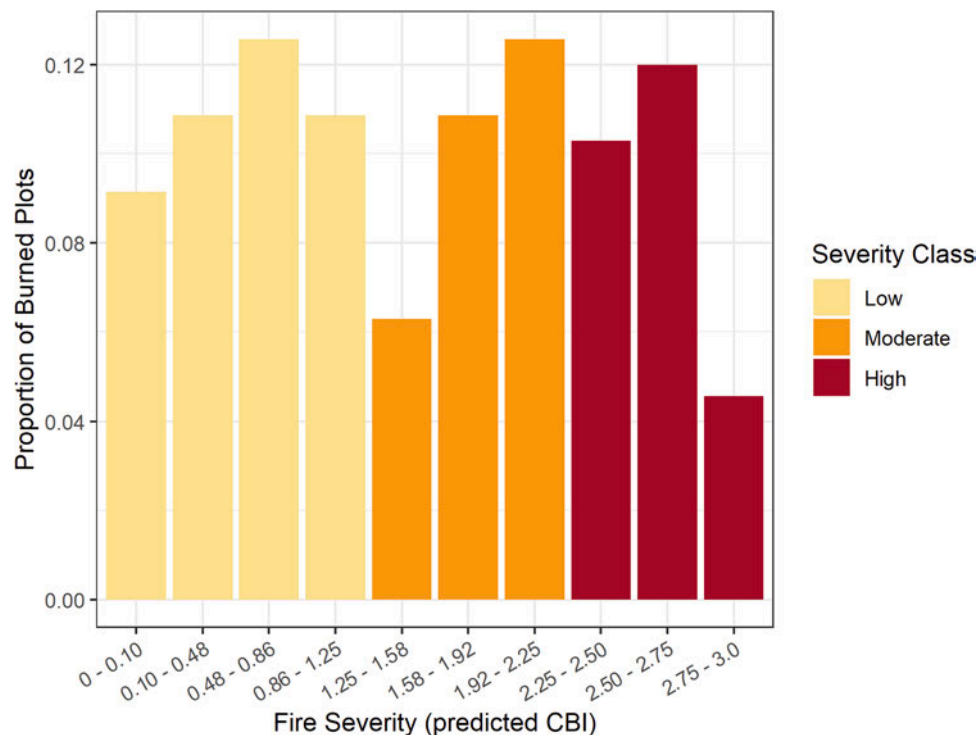


Fig. 2. Among the sample of FIA plots, the proportion of burned plots ($n = 175$) that burned at predicted composite burn index (CBI) values: low, moderate, and high severity from 1996 to 2017. Of the plots that burned more than once, the fire severity of the first fire was used. Predicted CBI low severity corresponds to values ranging from 0 to 1.24, moderate severity from 1.25 to 2.24, and high severity from 2.25 to 3.0.

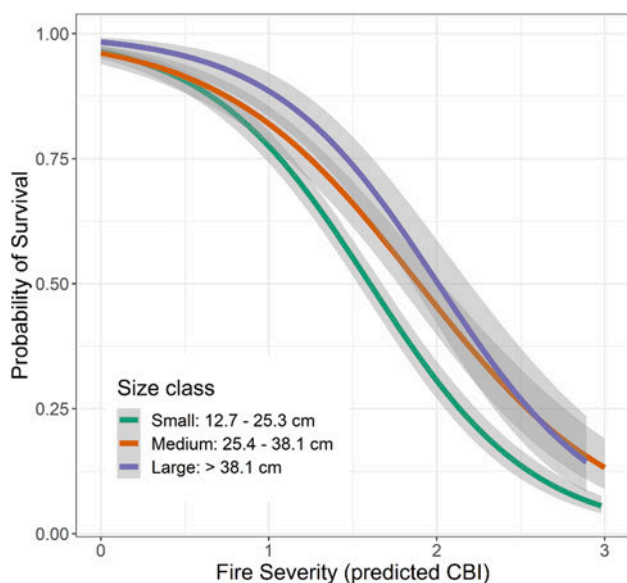


Fig. 3. Probability of postfire survival for ponderosa pine trees as a function of fire severity expressed by CBI for small trees (12.7–25.3 cm), medium trees (25.4–38.1 cm), and large trees (greater than 38.1 cm). The predicted probability is expressed by the colored line among each size class. A 95% confidence band for each size class is expressed in grey. The confidence intervals are as follows: small trees 95% CI 0.10–0.16, medium trees 95% CI 0.14–0.24, and large trees 95% CI 0.08–0.20.

regenerated in plots that burned at values higher than 1.58 CBI (moderate to high severity). Across all plots that burned among various fire severities, 75% of seedlings (132 stems) were recorded between 12 and 18 years post-fire (Fig. 6B). The total number of ponderosa pine stems were modeled as a function of fire severity and time since fire separately

for seedlings and saplings. Predicted CBI [$P < 0.001$] and time since fire [$P < 0.01$] were both significant predictors of seedling stem counts.

3.5. Shifts in vegetation associated with fire

Among the plots that did not burn within the study period (510 plots), 82% (420 plots) remained in the same vegetation type classification from the first inventory cycle to the last. The largest shifts were from the ponderosa pine-oak group to ponderosa pine-pinyon/juniper woodland group (26 plots) and ponderosa pine-pinyon/juniper woodland to ponderosa pine-oak (16 plots). A total of 16 plots transitioned from forest type groups containing ponderosa pine in the first inventory to types not containing ponderosa pine by the third inventory. Among those, nine plots shifted to the non-forest oak group, one plot transitioned to mixed conifer without ponderosa pine, and four plots transitioned to pinyon/juniper woodland without ponderosa pine.

Of the 175 plots that burned, only 48% (84 plots) persisted as the same vegetation type in the last inventory cycle. The remaining 52% transitioned to a different forest type or non-forest (Fig. 7). Among those that persisted as the same vegetation, 23% remained as ponderosa pine-oak, 9% remained as ponderosa pine-mixed conifer, 8% remained as ponderosa pine-pinyon/juniper woodland, 6% remained as pure ponderosa pine, and 1% remained as ponderosa pine-aspen. Of the 52% (91 plots) that transitioned to a new vegetation type in the third inventory cycle, plots that still contained ponderosa pine (24%) consisted of 8% pure ponderosa pine, 7% ponderosa pine-oak, 3% ponderosa pine-pinyon/juniper woodland, 3% ponderosa pine-aspen, and 2% ponderosa pine-mixed conifer. In contrast, 28% (49 plots) contained no ponderosa pine in the last inventory. Approximately 5% shifted to different forest or woodland types lacking ponderosa pine, consisting of 4% mixed conifer and 1% pinyon/juniper woodland. The remaining 23% (41 plots) of plots transitioned to non-forest vegetation consisting of 17% oak, 5% herbaceous, and 1% mixed shrubs.

Our results show fire severity varied by pre-fire vegetation type and was also a determinant of vegetation change. Plots that were pure

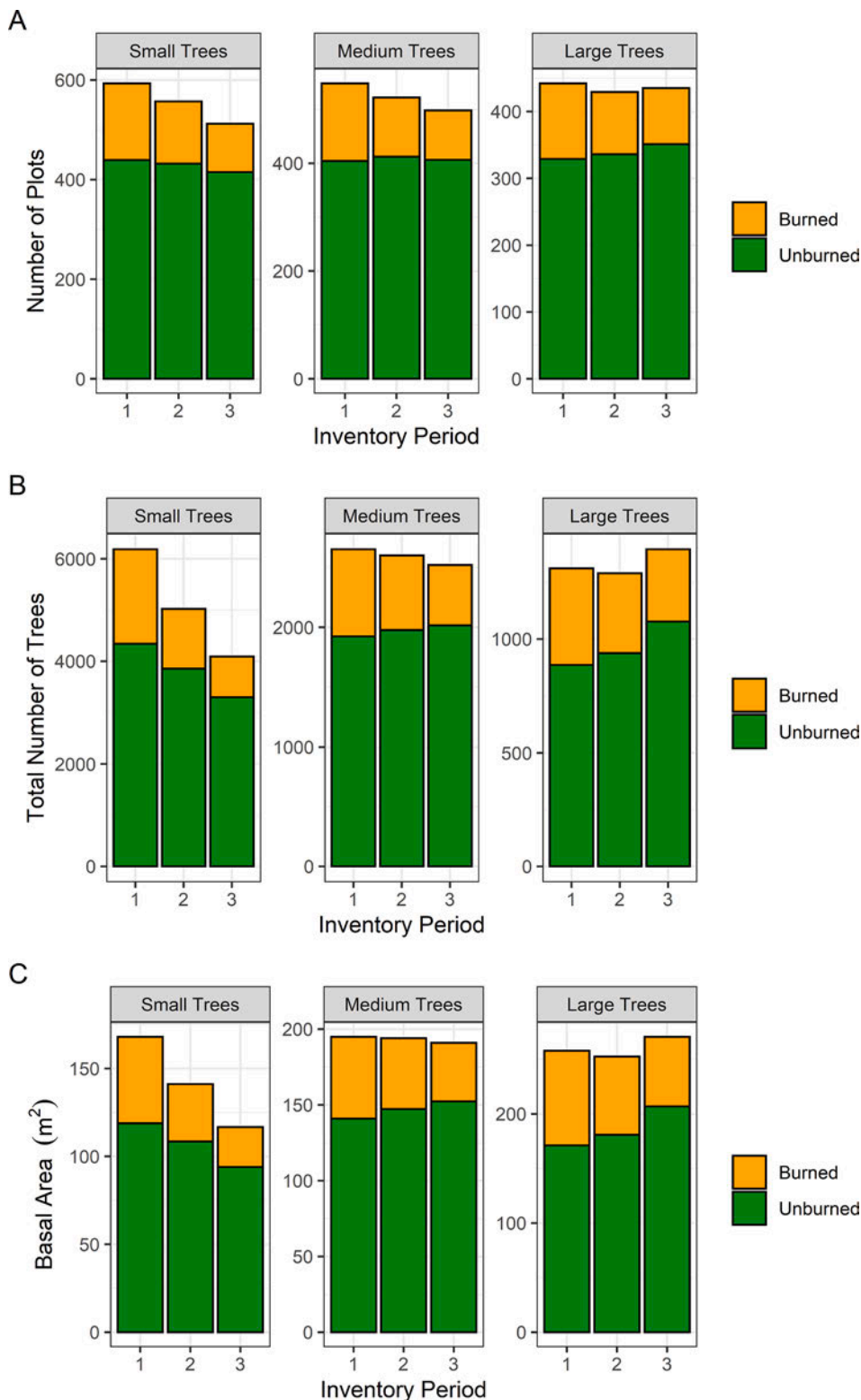


Fig. 4. Across the sample period (1995–2018), trends in (A) the total number of plots containing live ponderosa pine greater than 12.6 cm diameter, (B) the total number of live ponderosa pine greater than 12.6 cm diameter within each plot, and (C) the total basal area (m²) of live ponderosa pine greater than 12.6 cm diameter. Small trees are 12.7–25.3 cm DBH, medium trees are 25.4–38.1 cm DBH, and large trees are greater than 38.1 cm DBH. Inventory period 1 is from 1995 to 2000, inventory period 2 is 2001–2012, and inventory period 3 is 2011–2018. Each plot was remeasured three times, approximately 5–12 years apart. Plots that burned in between the first and third inventory cycle are categorized as Burned. Plots that did not burn within the sampling period are categorized as Unburned.

ponderosa and ponderosa pine-aspen pre-fire (in the first inventory cycle) burned at low severity; all other pre-fire ponderosa pine types burned at moderate-high severity (Table 3). The likelihood and direction of post-fire transitions to other vegetation types were also influenced by fire severity (Table 4, Fig. 7b). Burn severity of plots that retained ponderosa pine (among all ponderosa pine forest types) after fire was low, 1.18 CBI units on average. In contrast, burn severity of plots that

transitioned to forests lacking ponderosa pine (mixed conifer and pinon/juniper woodland) was moderate, 1.93 CBI units on average, and plots that transitioned to non-forest (oak, mixed shrub, and herbaceous) was high, 2.34 CBI units on average. Plots that remained or transitioned to pure ponderosa pine stand post-fire burned at the lowest severity, 0.93 CBI units on average, while plots that transitioned to shrubs and herbaceous vegetation burned at the highest severities, 2.95 and 2.41

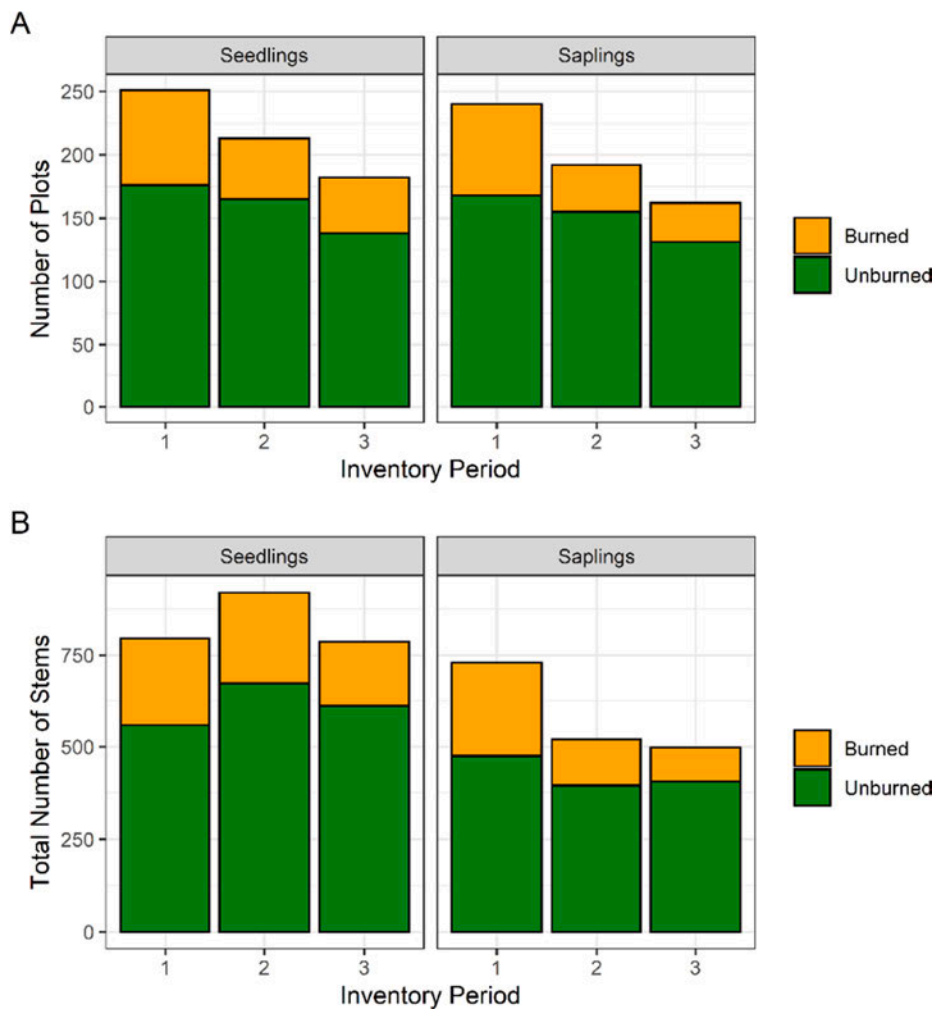


Fig. 5. Regeneration (seedling and sapling) trends across the sample period (1995–2018) in (A) the number of plots containing live ponderosa pine stems and (B) the total number of stems. Seedlings are at least 30.48 cm tall and <2.54 cm diameter. Saplings are between 2.54 cm and 12.6 cm diameter. Plots were remeasured three times, approximately 5–12 years apart. Plots that burned in between the first and third inventory cycle are categorized as Burned. Plots that did not burn within the sampling period are categorized as Unburned.

CBI units on average, respectively. Among those that underwent a transition to a type that contained no ponderosa pine in the third inventory (49 plots), 33 plots burned within two megafires, the Rodeo-Chediski and Wallow fires.

4. Discussion

Here, we report major losses and changes to southwestern ponderosa pine forests associated with recent burning. Wildfire is an integral part of the landscape in the southwestern US and has shaped ponderosa pine forests for millennia. However, large and severe fires have driven significant reductions of ponderosa pine forests over the past three decades. Losses of ponderosa pine forests in our study area were closely tied to satellite-derived measures of burn severity. Prior to 1900, fire regimes in ponderosa pine forests specific to the southwestern US were characterized by high-frequency, low severity surface fires (Falk et al. 2011), and high severity fires were rare (Swetnam, 1996). Among our study plots, 26% of plots burned at least once since 1996, with more than half of these burning at moderate to high severity, representing a considerable departure from historical fire regimes. Because FIA plots occur in direct proportion to the spatial extent of different conditions on the landscape, we are confident that our sample is broadly representative of recent ponderosa pine dynamics in both burned and unburned settings across the study area.

While most of the recent wildfires in our sample burned only a few (1–5) FIA plots, two megafires, Rodeo Chediski and Wallow, together impacted nearly half of all the burned plots. This finding is consistent

with an emerging understanding of the outsized effects of particularly large fire events in driving spatial and temporal patterns of fire effects (Duane et al., 2021). As of 2019, approximately 4.1 million hectares have burned in all vegetation types in the past three decades in Arizona and New Mexico, and the largest fires historically documented have occurred since 2000 (Singleton et al. 2019).

Our findings are consistent with previous, but localized studies demonstrating that these forests are vulnerable to persistent fire-driven conversion to a different forest type or non-forest vegetation following anomalously high-severity fire (Savage and Mast 2005, Owen et al. 2017, Haffey et al. 2018, Singleton et al. 2019, Rodman et al. 2020). Building on these findings, the results of our field vegetation data and remote sensing-based analysis demonstrate the widespread extent of fire-induced ponderosa pine forest loss in Arizona and New Mexico since 1995. Fire-induced losses in southwestern ponderosa pine forests in our study area were in part modulated by tree size, associated with fire resistance but also representative of other stand conditions that may promote or impede burning (Moir et al. 1997, Fitzgerald 2005). The number of live ponderosa pine trees in recently burned plots decreased by at least 25% among all size classes, with the most considerable loss among small trees (57%). Although decreases among small diameter trees may be expected in low-moderate severity fires or considered standard for gradual stand development, mortality among this size class can also create open areas for other species to establish. Further, more than a quarter of large trees died in burned plots since 1995. During historical fire regimes, the largest trees would have survived most low and moderate severity fires, but are now experiencing relatively high

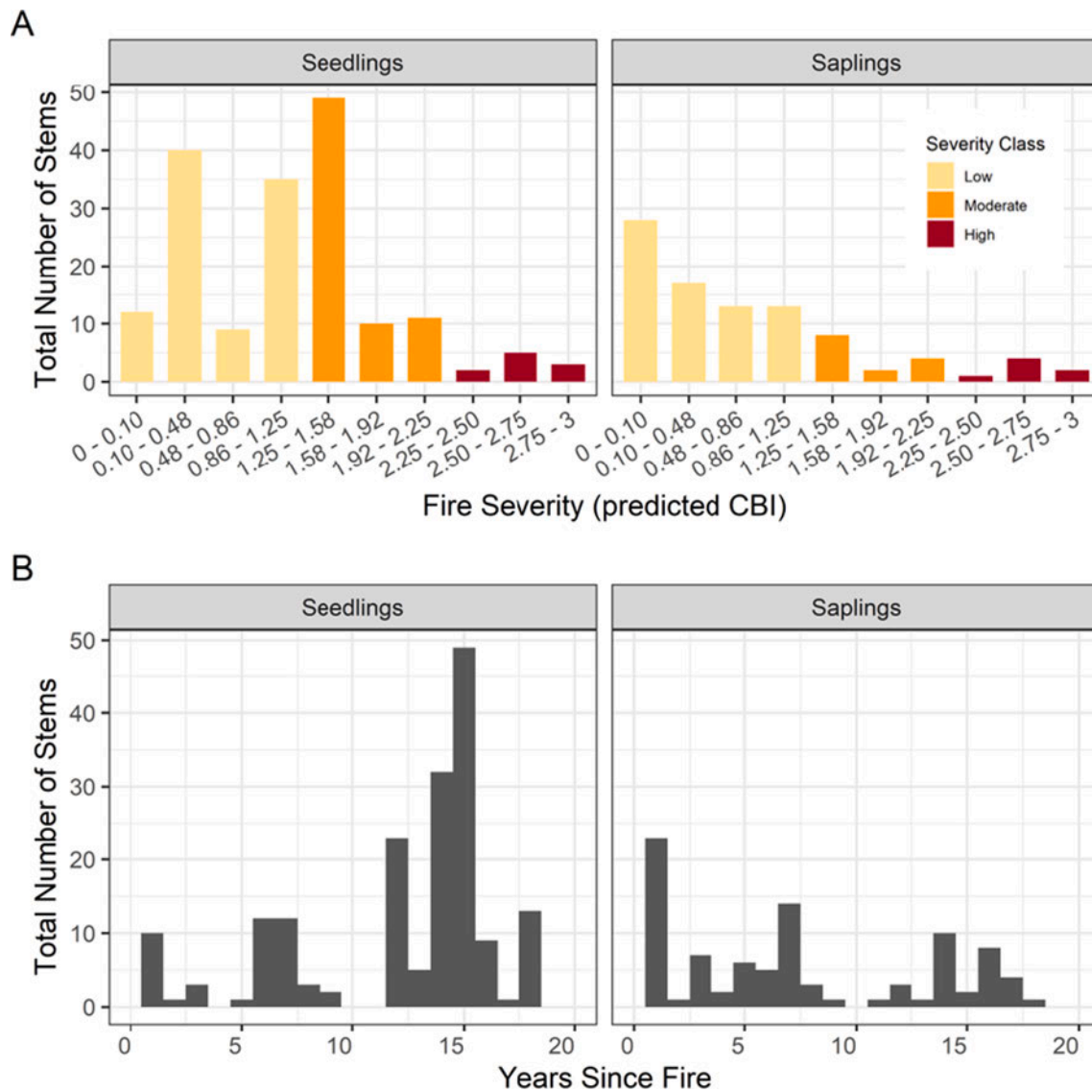


Fig. 6. Differences in total number of ponderosa pine seedlings and saplings recorded in the third inventory period among plots that burned recently by (A) fire severity (predicted CBI) and (B) time since fire (years). Seedlings are at least 30.48 cm tall and <2.54 cm diameter. Saplings are between 2.54 cm and 12.6 cm diameter. Predicted CBI low severity corresponds to values ranging from 0 to 1.24, moderate severity from 1.25 to 2.24, and high severity from 2.25 to 3.0.

rates of mortality. Large diameter trees are essential to the long-term persistence of this species and offer many critical components to the ecosystem, including modulating microclimates, influencing the rate and pattern of tree regeneration, carbon storage and other nutrients, and offering wildlife habitat (Kaufman et al. 1992, Mast et al. 1999).

The structure and function of post-fire ponderosa pine communities that develop following wildfires is highly contingent on patterns and rates of tree regeneration (Korb et al. 2019). Our findings are consistent with declining rates of post-fire tree regeneration across the southwestern US (Stevens-Rumann and Morgan 2019, Davis et al. 2020). In plots that burned within the past three decades, seedling counts decreased by 25% and sapling counts decreased by 64%. We found that 82% of counted seedlings (from only 27 plots) appeared more than 12 years after a fire. This may suggest it is too soon to determine whether regeneration failed at these sites, but successful tree reproduction depends on many factors. Because ponderosa pines are non-resprouting and non-serotinous, regeneration relies on nearby seed producing trees (Korb et al. 2019). Ponderosa pine seedlings are found to be most abundant at distances <50 m from a seed source and large patches without large trees or seed sources are particularly limited to natural

post-fire regeneration (Chambers et al. 2016, Haffey et al. 2018, Korb et al. 2019). Ponderosa pine refugia, or trees that survive fires, are a critical component for these forests to recover from wildfires (Coop et al. 2019).

Southwestern US ponderosa pine forests can contain a mix of conifer and broadleaf species, shrubs, and herbaceous understories, all of which influence fire severity and post-fire outcomes (Moir et al. 1997, Graham and Jain 2005). The composition and/or structure of surface fuels, ladder fuels, and crown fuels among different forest types can influence wildfire behavior (Hessburg et al. 2005, Agee and Skinner 2005, McKinney, 2019). Our results show fire severity varied as a function of pre-fire vegetation type, likely due to differences in fuel structure, quantity, and type. Pure ponderosa pine plots burned at a relatively low severity, likely due to low abundance of ladder fuels that can transition fire from the surface to the forest canopy. Ponderosa pine-oak and ponderosa pine-mixed conifer groups tended to burn at moderate to high severity, a probable outcome of greater ladder fuel abundance. Fire severity also shaped post-fire vegetation type, with low severity fire allowing ponderosa pine persistence, and higher severity fire, associated with greater probability of tree mortality, driving transitions toward

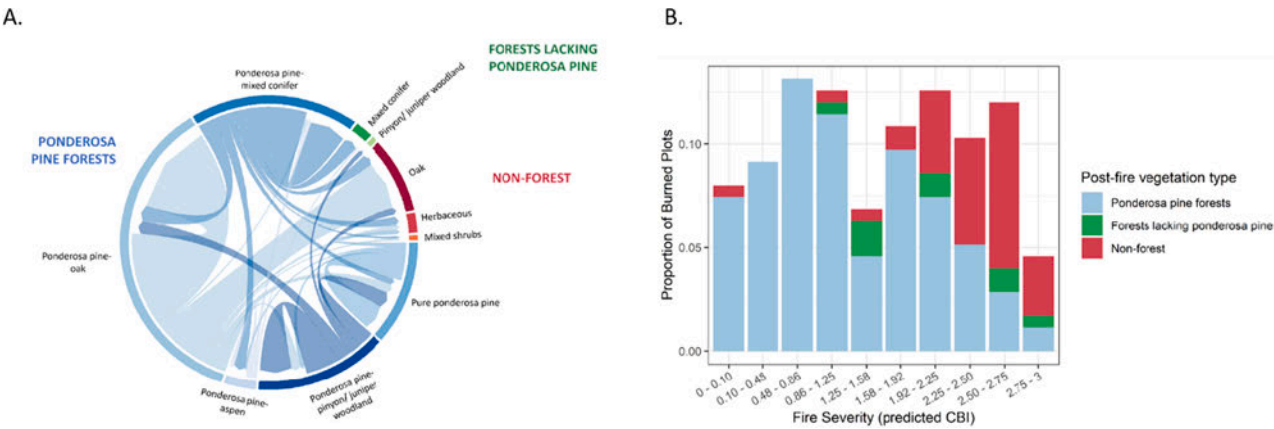


Fig. 7. A. Vegetation type changes across all plots that experienced fire between the first and third inventory. Vegetation types containing ponderosa pine are in blue, forest and woodland types lacking ponderosa pine are in green, and non-forest types are in orange. The arrows are directional, linking pre-fire vegetation groups (flat ends) to postfire replacing vegetation groups (pointed ends). The link widths are proportional to the number of plots represented by that pathway. B. Among the sample of burned FIA plots ($n = 175$), the proportion of plots that burned at predicted composite burn index (CBI) values and the corresponding post-fire vegetation type. Post-fire ponderosa pine forests include pure ponderosa pine, ponderosa pine with mixed conifer, ponderosa pine with pinyon/juniper woodland, and ponderosa pine with aspen. Forests lacking ponderosa pine contain mixed conifer and pinyon/juniper woodland; non-forest contains oak, mixed shrub, and herbaceous. Low severity CBI corresponds to values ranging from 0 to 1.24, moderate severity from 1.25 to 2.24, and high severity from 2.25 to 3.0.

Table 3
Subsequent fire severity (predicted CBI) of pre-fire classified vegetation types.

Pre-fire vegetation type	Subsequent fire severity (predicted CBI)
Ponderosa pine forests	
Ponderosa pine- aspen	0.79 ± 0.66
Pure ponderosa	0.98 ± 0.82
Ponderosa pine- pinyon/juniper woodland	1.34 ± 0.98
Ponderosa pine-oak	1.52 ± 0.95
Ponderosa pine-mixed conifer	1.72 ± 0.81

Notes: Predicted CBI low severity corresponds to values ranging from 0 to 1.24, moderate severity from 1.25 to 2.24, and high severity from 2.25 to 3.0. Values of predicted CBI are mean $\pm$ one standard deviation. There are no vegetation types of forests lacking ponderosa pine or non-forest because these groups were not present within our sample pre-fire.

Table 4
Prior fire severity (predicted CBI) of each post-fire vegetation type.

Post-fire vegetation type	Preceding fire severity (predicted CBI)
Ponderosa pine forests	
Pure ponderosa	0.93 ± 0.82
Ponderosa pine- pinyon/juniper woodland	1.01 ± 0.76
Ponderosa pine-oak	1.29 ± 0.91
Ponderosa pine-mixed conifer	1.33 ± 0.74
Ponderosa pine- aspen	1.40 ± 0.59
Forest lacking ponderosa pine	
Mixed conifer	1.88 ± 0.68
Pinyon/juniper woodland	2.09 ± 1.02
Non-forest	
Oak	2.29 ± 0.63
Herbaceous	2.41 ± 0.24
Mixed shrub	2.95 ± 0.08

Notes: Predicted CBI low severity corresponds to values ranging from 0 to 1.24, moderate severity from 1.25 to 2.24, and high severity from 2.25 to 3.0. Values of predicted CBI are mean $\pm$ one standard deviation.

alternate vegetation types. Of the burned plots, 28% no longer contain ponderosa pine and shifted to vegetation types dominated by resprouting shrubs, alternate tree species, or non-forest vegetation in the last inventory cycle. Our results show that a fire severity threshold near 1.92 CBI may be associated with sharp increases in the likelihood of conversion toward non-forested vegetation types. This threshold could potentially be used to predict tree mortality in future fires and

characterize ongoing or simulated changes in the study area, including the likelihood of type conversions under a future climate and wildfire activity.

Major shifts in species composition coupled with barriers to recovery by pre-fire forest species can result in a conversion of the pre-fire forest to a persistent alternate state (Johnstone et al. 2016, Hessburg et al. 2019, Coop et al. 2020, Davis et al. 2020, Falk et al. 2022). Here, we document fire-associated shifts from ponderosa pine-dominated forests toward a suite of vegetation types lacking ponderosa pine, instead composed of other forest and woodland trees, and resprouting shrubs and herbaceous vegetation. These findings are aligned with a growing body of research that ponderosa pine forests are not resilient to contemporary fire regimes, and resprouting species are expanding in these landscapes (Fitzgerald 2005, Savage et al. 2013, Shaw et al. 2017, Davis et al. 2020). It is well documented that Gambel oak (*Quercus gambelii*) vigorously resprouts from extensive root systems after disturbances kill above-ground stems (Abella 2008). Fires can result in sharp increases in densities of small-diameter oak, and once established can impede ponderosa pine regeneration (Abella 2008, Singleton et al. 2021). In our study, plots shifted to resprouting oak dominance more than any other non-forest vegetation type. Once established, resprouting oak scrub vegetation in the southwestern US appears to be resilient to future fire and drought, and able to stabilize over centuries (Savage and Mast 2005, Coop et al. 2016, Guiterman et al. 2018, Roos and Guiterman, 2021). Thus, under some conditions, shifts from conifer forest toward resilient, re-sprouting vegetation types may better reflect altered fire regimes and future climate.

Changes observed among the plots that burned foreshadow likely outcomes of fire in sites that have not yet burned. We anticipate increases in ponderosa pine forest loss and increases in non-forest or shrub-dominated ecosystems in the future. Throughout our study period, 11% of plots lost ponderosa pine entirely, in contrast to 1% of plots that contained no ponderosa pine in the beginning of the sample period but gained it by the end. Given the increase in wildfires in this area since 2017, these unbalanced percentages are likely to have increased in the study area since 2017. Further, the longer these stands go without a disturbance, the more shade-tolerant and less fire-tolerant species are likely to increase, thereby increasing tree canopy connectivity and ladder fuels, and increasing the probability of surface fire transitioning to a crown fire when they burn (Covington and Moore 1994, Agee and Skinner 2005). Within the southwestern US, 30% of forested area may be vulnerable to fire-driven conversion and on the

Kaibab Plateau of northern Arizona, up to 49% of the landscape is predicted to be non-forest by 2090 (Flatley and Fulé 2016, Parks et al. 2019a). In a time of rapid ecological change, management both pre- and post-wildfire at large scales is needed.

4.1. Management implications

The long-term undesirable consequences resulting from altered fire regimes within our study area bring attention to an increasingly urgent question: how can management best support and enhance the resiliency of southwestern ponderosa pine forests? Contemporary southwestern ponderosa pine forest management practices generally focus on resisting change in the form of restoring historical stand structure and function (Allen et al. 2002). While recognizing that restoration of historical conditions and processes may not always be appropriate, our study points toward two important considerations for southwestern ponderosa pine persistence in Arizona and New Mexico: restoring recurrent, low-severity fire and sustaining large, fire-resistant trees. Both principles are already understood as foundational for dry forest restoration efforts (Allen et al., 2002; Prichard et al., 2021). Restoring low-severity fire that reflects historical fire regimes and introducing prescribed fires can promote key ecological benefits to wildlife and humans (Pausas and Keeley 2019). Frequent, low-severity surface fires can reduce the severity of subsequent fires, increase resistance to drought, and reduce the costs associated with fire suppression (Stoddard et al. 2021). Thinning and prescribed fire treatments prior to Arizona's 2002 Rodeo-Chediski Fire reduced fire severity and significantly increased ponderosa pine regeneration, compared to untreated areas (Shive et al. 2013, Owen et al. 2017).

Management that retains and promotes large, fire-resistant trees may also be critical for sustaining contemporary forests and fostering regeneration thus creating long-term resilience. Large and old trees, particularly those established before ecosystem disruption by Euro-American settlement, are of high ecological significance and difficult to replace (Allen et al. 2002). In many parts of the world, large old trees are rapidly declining and pose a threat to ecosystem integrity and biodiversity (Lindenmayer et al., 2012). Thinning from below, also known as low thinning, leaves the larger, older, and more fire resistant trees, and removes trees in subordinate lower crown classes (Graham et al. 1999, Fitzgerald 2005). Retention of these fire-resistant trees can enhance ecological resilience: even small patches of trees that survive subsequent, severe fire can provide important critical functions and support landscape forest recovery (Coop et al. 2019). Undoubtedly, management will require context-specific approaches. For example, reducing tree density and ladder fuels through thinning and prescribed burns may be needed before reintroducing low-severity surface fires (Allen et al. 2002, Agee and Skinner 2005, Walker et al. 2018). Treatment costs, public support, and topographic constraints can limit the pace and scale of these projects (Hessburg et al. 2019).

While it may not always be feasible or desirable to restore exact reference compositions and structures, restoration of key compositional and structural elements on a site-by-site basis can enhance the resiliency of these forests (Reynolds et al. 2013). Given the urgent need for more informed management in the 21st century, a timely paradigm shift from strategies favoring fire suppression to those favoring fire-adapted forests and communities is needed (Hagmann et al. 2021). However, where severe fire has already overcome ecological resistance and resilience in ponderosa pine forests, post-fire landscape management is called for (Stevens et al. 2021). This can include resistance strategies (e.g., replanting), but also accepting or directing change (Schuurman et al. 2021). Directing or accepting changes such as those reported here lack the research that resisting change has developed in recent years. There are many ecological and ethical questions associated with targeted tree-planting and assisted migration, though under this framework managers can proactively plan for future conditions under shifting fire and climate regimes (Stevens et al. 2021). Data networks such as the FIA data used

here may be useful to inform strategies around resisting or directing change, for example by highlighting regional trends in species compositional shifts, such as increases in dominance by particular life forms (e.g., shrubs) or non-native species. For example, transitions from ponderosa pine to aspen may be more widely accepted than shifts to shrublands or annual grasses.

4.2. Study limitations and directions for further research

The FIA program provides the most comprehensive forest database currently available in the US, and is spatially and temporally robust. FIA data are widely used by managers, researchers, and policymakers because of the nationwide coverage, consistent data collection protocols, and publicly available datasets (Hoover et al. 2020). The use of FIA data to address contemporary and future research questions is likely to increase with the onset of annual inventory protocols and all states being in a remeasurement cycle (Shaw et al. 2017). Recent applications of FIA data include informing forest plan revision processes and supplying managers with timely information on important forest attributes at stand- and landscape- scales (Hoover et al. 2020). Yet many studies mention the database's complex structure and that it can be difficult for non-expert FIA users to construct database queries needed to obtain information not available in a standard report (Tinkham et al. 2018, Hoover et al. 2020).

In addition to the database's steep learning curve, there are additional limitations to the use and interpretation of FIA data that may be important to note. Though periodic data collection ran for approximately 70 years (beginning in 1930) much of this dataset is publicly unavailable, follows different protocols from annual inventory, and is inconsistent with the type of measurements taken in annual inventory. Due to our plot selection criteria (sampled three times between 1995 and 2018), there are additional ponderosa pine forests of Arizona and New Mexico ponderosa pine samples that could not be included in this study. Plots from the states of Colorado and Utah were not considered in this study because none of the periodic data collection was completed under the annual inventory methodologies, yielding only two rounds of methodologically-consistent inventory rather than three. We note that while earlier study findings from Arizona and New Mexico have been considered representative of southwestern ponderosa pine (e.g., Savage and Mast 2005; Haffey et al. 2018), different patterns could emerge if a broader geographic range were considered. However, consistent with our findings, major losses of ponderosa pine forest, strongly limited regeneration, and shifts to shrub- and grass-dominated states have also been extensively documented in recent burns in the Colorado Front Range (e.g. Battaglia et al., 2018). Our study excluded plots within New Mexico's Gila National Forest because the first inventory period did not follow the new annual inventory plot design, and these plots were only sampled twice under the annual inventory plot design. Much of this area has experienced recent wildfires. Follow up studies may thus be able to achieve broader geographic representation across the FIA plot network, though at the cost of temporal depth (two sample periods vs. three).

We also found challenges to using the understory species percent cover data, including apparent systematic increases in percent cover by many species that did not seem ecologically plausible. Such variations across the database may present limitations to more detailed analysis of compositional shifts across large regions, such as have been conducted within particular burns (e.g. Coop et al. 2016).

Nevertheless, there are abundant research opportunities within the FIA database to continually study forest structure and composition, woody fuels, understory vegetation, and wildlife habitat at large spatial scales (Shaw et al. 2017, Burrill et al. 2018, Tinkham et al. 2018). Successful management and conservation in an era of rapid and widespread ecological change requires land managers and researchers to collaborate at large scales and across jurisdictions. Further, FIA data have the potential to be linked to other publicly available large regional databases. For example, MTBS or other remotely sensed databases could

be used to provide a suite of satellite-derived measures of disturbances, drought, and climate variation to exact FIA plot locations (Shaw et al. 2017). The methods we employ in this study are transferable and scalable to other kinds of disturbances, tree species, and geographic regions, with the potential to strongly improve our understanding of the causes and consequences of forest ecosystem change in the US.

CRedit authorship contribution statement

Ashley M. Woolman: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Project administration, Visualization, Writing – original draft, Writing – review & editing. **Jonathan D. Coop:** Conceptualization, Formal analysis, Funding acquisition, Methodology, Supervision, Validation, Visualization, Writing – original draft, Writing – review & editing. **John D. Shaw:** Conceptualization, Data curation, Methodology, Resources, Writing – review & editing. **Jennie DeMarco:** Conceptualization, 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.

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