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Extent of Recent Fire-induced Losses of

Ponderosa Pine Forests of the Southwestern US

by

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EXTENT OF RECENT FIRE-INDUCED LOSSES OF PONDEROSA PINE FORESTS OF THE SOUTHWESTERN US

by

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Thesis

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ABSTRACT

Fire has shaped western ponderosa pine (*Pinus ponderosa*) forest landscapes for millennia. Yet, contemporary land management coupled with warming and drought has led to shifts in forest structure and severe wildfires. A growing body of evidence suggests that under altered fire regimes and climate change, ponderosa pine forests may be vulnerable to fire-driven conversion to a different forest type 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, our objective was to 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 and satellite-derived burn severity (predicted Composite Burn Index; CBI and difference 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 changes. Among our 685 plots, we found 26% of plots burned at least once from 1996-2017. Plots that burned within the study period exhibited a 46% loss of ponderosa pine trees and plots that did not burn decreased by 11%. Small ponderosa pine trees (12.7-24.5 cm diameter) exhibited the greatest declines in the number of trees and basal area compared to trees greater than 24.5 cm. Overall regeneration rates decreased over time, and approximately 11% of plots lost all ponderosa pine. Satellite-derived burn severity (predicted CBI) was a strong predictor of tree mortality and more than half of burned plots burned at moderate-high severity levels. Post-fire vegetation was influenced by fire severity and we observed transitions in species composition, with resprouting species (*Quercus gambelii)* establishing post-fire more than any other new species. This study contributes to an emerging ecological understanding of forest vulnerability to changing 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. Our results point toward two key themes for land management: restoring low-severity fire regimes and retaining large trees to ensure the long-term persistence of ponderosa pine forests in the southwest US.

Keywords: *Pinus ponderosa*, type conversion, wildfire, composite burn index, transition, transformation, resistance, resilience

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INTRODUCTION

The ecology and evolution of 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. There is abundant evidence that historical fire regimes of ponderosa pine forests through the mid to late 18th century were generally dominated by frequent, low or occasionally moderate-severity surface fires (Swetnam and Baisan 1996, Brown and Sieg 1999, Hessburg et al. 2000, Stephens et al. 2015). These fires reduced understory vegetation, removed surface fuels, maintained open stand structures, and created fine-scale spatial heterogeneity across the landscape. Ponderosa pine exhibits many fire adapted traits that endowed survival and regeneration under these historical fire regimes (Fitzgerald 2005). Fire resistance is fostered by characteristically open crowns, thick bark, and tendency to self-prune limbs when mature, which reduces ladder fuels. Ponderosa pine is non-sprouting, non-serotinous, and relies on regeneration by nearby seed producing trees (Moir et al. 1997, Allen et al. 2002, Fitzgerald 2005).

Since the mid to late 19th century, Euro-American land 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, Battaglia et al. 2018). Without frequent surface fire, stands have become increasingly dense and homogeneous as shade tolerant species became established in the understory. High tree densities have provided ladder fuels to tree crowns and surface fuels increased (Hessburg et al. 2005). Increased fuel availability and continuity, combined with warmer and drier fire seasons associated with anthropogenic climate change, have led to 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). Across much of their range, historically-anomalous severe wildfire in ponderosa pine forests has raised concerns about the loss of ecological resilience in these forests (Mallek et al. 2013, Dennison et al. 2014, Johnstone et al. 2016, McKinney 2019)

Loss of forest resistance (ability of a community to remain essentially unchanged despite a disturbance occurring) can have diverse and interacting effects on these landscapes (Holling 1973). 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 (Chambers et al. 2016, Whitman et al. 2019). Large, high severity wildfires can alter soil properties with less nutrient availability and altered fungal communities, thereby effecting seed germination and seedling survival (Kurth et al. 2013, Owen et al. 2019). Further, in warm and dry climate settings, the direct effects of a warming climate reduce the capacity of many tree species, including ponderosa pine, to re-establish following fire (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, worsening the situation described here (Westerling 2016, Abatzoglou et al. 2019).

The ecological outcomes of the loss of forest resistance and resilience to wildfire include forest losses and conversions to alternate and non-forest vegetation types (e.g. shrublands and grasslands). 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). Emerging research across western North America demonstrates that contemporary wildfires are similarly poised to catalyze lasting ecological and environmental change under ongoing climate change (Davis et al. 2019, 2020, Stevens-Rumann and Morgan 2019, Williams et al. 2020, Coop et al. 2020, 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 2 degree C warming scenario, 16% of ponderosa pine forests are at a substantial risk of fire-catalyzed forest conversion under future conditions (Davis et al. 2020, Rodman et al. 2020).

Despite a rapidly growing understanding of forest vulnerability under increasing fire activity and climate change, landscape-scale quantification of the extent and direction of fire-induced forest changes are lacking. Here, we determine the extent of recent, fire-driven change in southwestern US ponderosa pine forests based on data from the national USDA Forest Service Forest Inventory and Analysis (FIA) program, collected across the range of ponderosa pine in Arizona and New Mexico. 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). We linked FIA vegetation data to satellite-derived burn severity, including the delta normalized burn ratio (dNBR) and modeled composite burn index (CBI). Briefly, dNBR is a commonly used burn severity metric computed with the normalized burn ratio (NBR) using near-infrared and short-wave infrared wavelengths from Landsat imagery. The 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, geographic, and climate variables using Google Earth Engine

(Parks et al. 2018, 2019b). Modeled CBI uses data from field collected CBI and incorporates spectral indices such as NBR, climatic indices including climatic water deficit and actual evapotranspiration, as well as latitude and longitude coordinates. 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). Both dNBR and modeled CBI severity metrics were used to assess the effectiveness of each in predicting tree mortality and to characterize fire effects.

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 patterns of wildfire in southwestern US ponderosa pine stands within the FIA plot network, (2) evaluate relationships between two metrics of satellite-derived burn severity (dNBR and predicted CBI) and tree mortality, (3) quantify temporal forest mortality and regeneration trends among ponderosa pines, with and without recent wildfire, and (4) characterize changes in vegetation composition associated with fire.

METHODS

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 about 1.6km, with most being within 800m 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 less than 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 follows 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 1 percent (Bechtold and Patterson 2005, Burrill et al. 2018).

Dataset Assembly and Extent

Given our objectives of assessing change in southwestern ponderosa pine forests, we required FIA plot data used in this study to meet the following criteria: 1) located in the southwestern US, 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. This led to the exclusion of plots from Colorado and Utah because none of the periodic data was completed under the annual inventory methodologies, yielding only two rounds of inventory rather than three. A total of 685 plots in Arizona and New Mexico were ultimately included in this study (Table 1; Fig. 1). These plots were re-measured approximately 5-12 years apart. Elevations ranged from 1490m to 2963m. Approximately 65% of plots fell on USFS land, with the remaining on private/Native American, other federal, and state/local government land.

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

Plots with any management treatment were included in the analysis. Approximately 5% of the selected plots experienced recent management treatments since 1996, labeled primarily by FIA field crews as “cutting”. These included 30 plots in the first annual inventory (from 1996-2010) and 34 plots in the second annual inventory (from 2006-2017). 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 determine which plots burned. To assess recent fire effects, we then examined 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 “recent burned”. In total, 26% (n=175) of plots burned at some time between the first and third inventory, 1996-2017 (Fig. 1). These 175 plots overlapped 88 distinct burns in the MTBS database. Based on the MTBS fire names and IDs of these burns, we developed raster grids of difference normalized burn ratio (dNBR) and modeled composite burn index (CBI) following the methods of Parks et al. (2018) and Parks et al. (2019). Briefly, dNBR is computed with the normalized burn ratio (NBR) using near-infrared and short-wave infrared wavelengths from Landsat imagery. The 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, a variable representing spatial variability in climate, and latitude (Parks et al. 2018, 2019b). Unfuzzed FIA plot coordinates were then used to extract both fire severity metrics for each burned FIA plot.

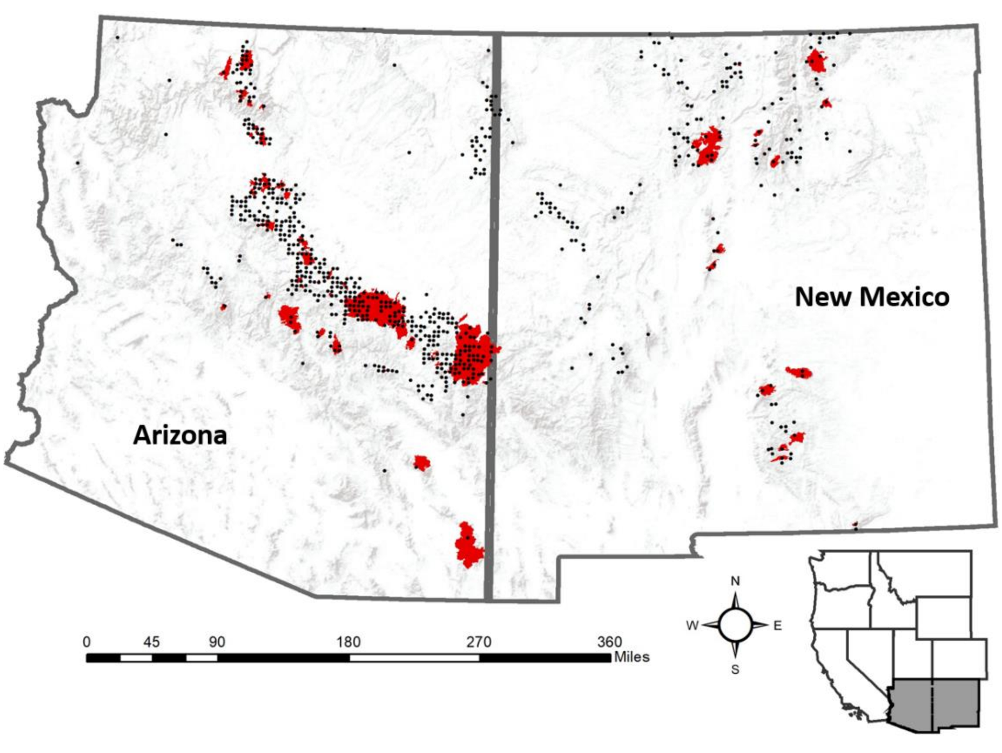

Figure 1. Study area showing FIA plot locations (points) and burn perimeters (red) in Arizona and New Mexico.

Data Analysis

Fire severity datasets of dNBR and CBI were categorized into discrete classes representing low, moderate, and high severity. CBI low severity corresponds to CBI values ranging from 0-1.24, moderate severity from 1.25-2.24, and high severity from 2.25-3.0 (Miller and Thode 2007, Parks et al. 2018). Fire severity classes for dNBR includes dNBR values ranging from 100-269 for low severity, moderate-low severity from 270-439, moderate-high severity 440-659, and high severity from 660-1300 (Key and Benson 2006). All ponderosa pine trees 12.7 cm or greater in diameter at breast height (DBH) were categorized into size classes as follows: small trees (12.7-24.5 cm), medium trees (25.4-38.1 cm), and large trees (> 38.1 cm). Saplings were classified as trees less than 12.7 cm. Seedlings were categorized the same as FIA size requirements (at least 15.24 cm tall). Basal area (m^2) 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 overarching categories: plots containing 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 pinon (*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 (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. Only 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 understory vegetation data, only two plots did not contain any tree or seedling vegetation; 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 (m^2) of live ponderosa pine trees by size class and numbers of saplings and seedlings within each plot and across all samples. Differences in basal area (m^2/ha) and number of trees/stems per hectare between each inventory period were tested using a one-way ANOVA. To test where the differences occurred, Tukey's post-hoc tests were applied if the ANOVA test was significant. To assess the relationships among tree mortality and fire severity, we 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 best fitting model was determined based on minimum Akaike information criterion (AIC) values. Negative binomial regression models were used to model the total number of ponderosa pine seedling and sapling stems as a function of fire severity. Significance among all statistics was determined if p-values were less than 0.05. To characterize changes in vegetation composition across the study area, we quantified changes among the assigned vegetation groups.

All data analysis was conducted in the program R (RStudio Team, 2021), and employed the following packages: tidyr (Wickham H., 2021), dplyr (Wickham et al., 2021), agricolae (de Mendiburu, 2020), ggplot2 (Wickham H., 2016), circlize (Gu, 2014), RColorBrewer (Neuwirth, 2014) and MASS (Venables and Ripley, 2002).

Table 2. Vegetation types classified from FIA species group code (SPGRPCD). The dominate species found within the study sample's listed SPGRPCD is listed. Vegetation types are grouped by those containing ponderosa pine and the associate SPGRPCD, plots containing no ponderosa pine but the dominate SPGRPCD, and non-forest (dominated by grass, forbs, or shrubs).

Vegetation Type	**FIA SPGRPCD**	**Dominant Species Found Within Selected Plots**
Ponderosa pine forests		
Pure ponderosa pine	Ponderosa and Jeffrey pines	*P. ponderosa*
Ponderosa pine-mixed oak	Ponderosa and Jeffrey pines, Woodland hardwoods	*P. ponderosa, Quercus gambelii, Acer grandidentatum, Quercus arizonica, Quercus emoryi*
Ponderosa pine-mixed conifer	Ponderosa and Jeffrey pines, Douglas-fir, true fir, Engelmann and other spruces, Other western softwoods	*P. ponderosa, Pseudotsuga menziesii, Abies concolor, Picea engelmannii, Picea pungens, Pinus strobiformis, Pinus flexilis, Cupressus arizonica, Pinus leiophylla*
Ponderosa pine-Pinyon juniper woodland	Ponderosa and Jeffrey pines, Woodland softwoods	*P. ponderosa, Juniperus deppeana, Juniperus osteosperma, Juniperus scopulorum, Juniperus monosperma, Pinus edulis*
Ponderosa pine-aspen	Ponderosa and Jeffrey pines, Cottonwood and aspen	*P. ponderosa, Populus tremuloides, Populus fremontii, Populus angustifolia*
Forests lacking ponderosa pine		
Forests lacking ponderosa pine- mixed conifer	Douglas-fir, true fir, Engelmann and other spruces, Other western softwoods	*P. menziesii, A. concolor, P. engelmannii, P. pungens, P. strobiformis, P. flexilis, C. arizonica, P. leiophylla*
Forests lacking ponderosa pine-Pinyon juniper woodland	Woodland softwoods	*J. deppeana, J. osteosperma, J. scopulorum, J. monosperma, P. edulis*
Non-forest		
Non-forest- oak	Woodland hardwoods	*Q. gambelii, A. grandidentatum, Q. arizonica, Q. emoryi*
Non-forest- shrub	NA	*R. neomexicana, A. pungens, R. woodsii*
Non-forest- herbaceous	NA	*P. fendleriana, M. straminea*

RESULTS

Recent fire frequency and severity in southwestern US ponderosa pine stands

A total of 88 recent fires ranging in fire severity overlapped with ponderosa pine plots across the AZ and NM study area. Many of the fires spanned large geographical distances and burned more than one plot. Approximately 26% of our sampled FIA plots burned between 1996 and 2017. Fire types included prescribed burns, wildland fire use, and wildfires. A total of 84 fires burned in selected ponderosa pine FIA plots between cycle 1 and 2 (68 in AZ and 16 in NM), and 98 fires burned between cycle 2 and 3 (87 in AZ and 11 in NM). A total of 13 plots burned in both sample intervals (12 in AZ and 1 in NM).

Of the plots that burned recently, 47% burned at low severity (CBI values 0-1.24), 31% plots burned at moderate severity (CBI values 1.25-2.24) and 27% burned at high severity (CBI values 2.25-3.0) (Fig 2). A total of 12 plots burned twice and one plot burned three times from 1996-2017. In the plots that burned more than once, 77% burned at low severity the first interval and 85% burned at low severity the second interval. The plot that burned three times from 1996-2017 burned at low severity each time. Approximately 75% of plots (510) have not experienced any recent fire.

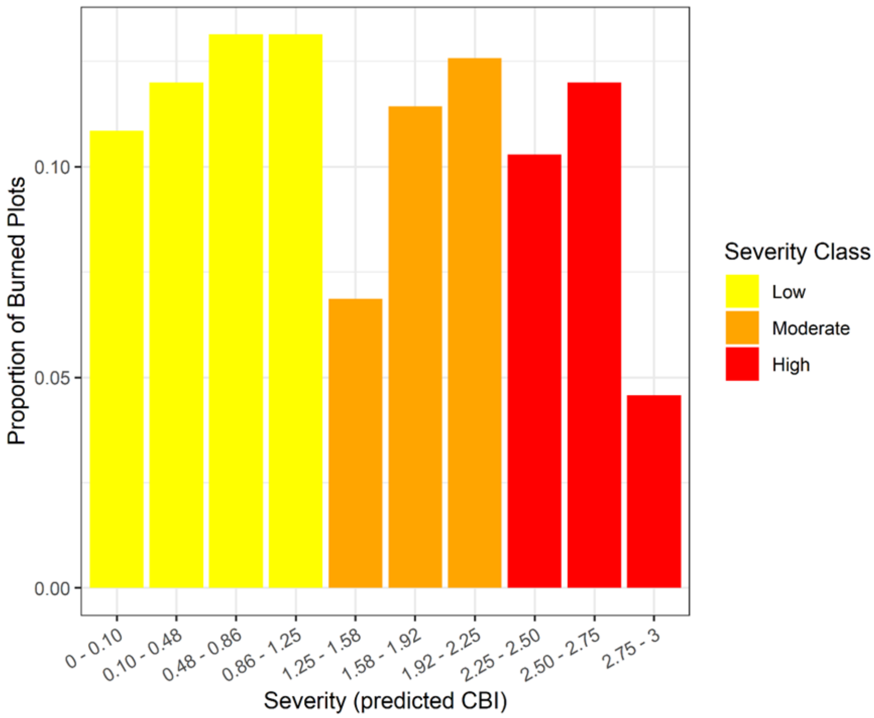

Figure 2. Among the sample of FIA plots, the proportion of burned plots (n = 175) that burned at predicted composite burn index (CBI) values: low, moderate, and high severity from 1996-2017. Predicted CBI low severity corresponds to values ranging from 0-1.24, moderate severity from 1.25-2.24, and high severity from 2.25-3.0

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 (p < 0.001, df= 2325, AIC= 2013.8 and p < 0.001, df= 2325, AIC= 2067.0, respectively). 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). Figure 3 illustrates the models predicting probability of mortality as a function of predicted CBI for each size class.

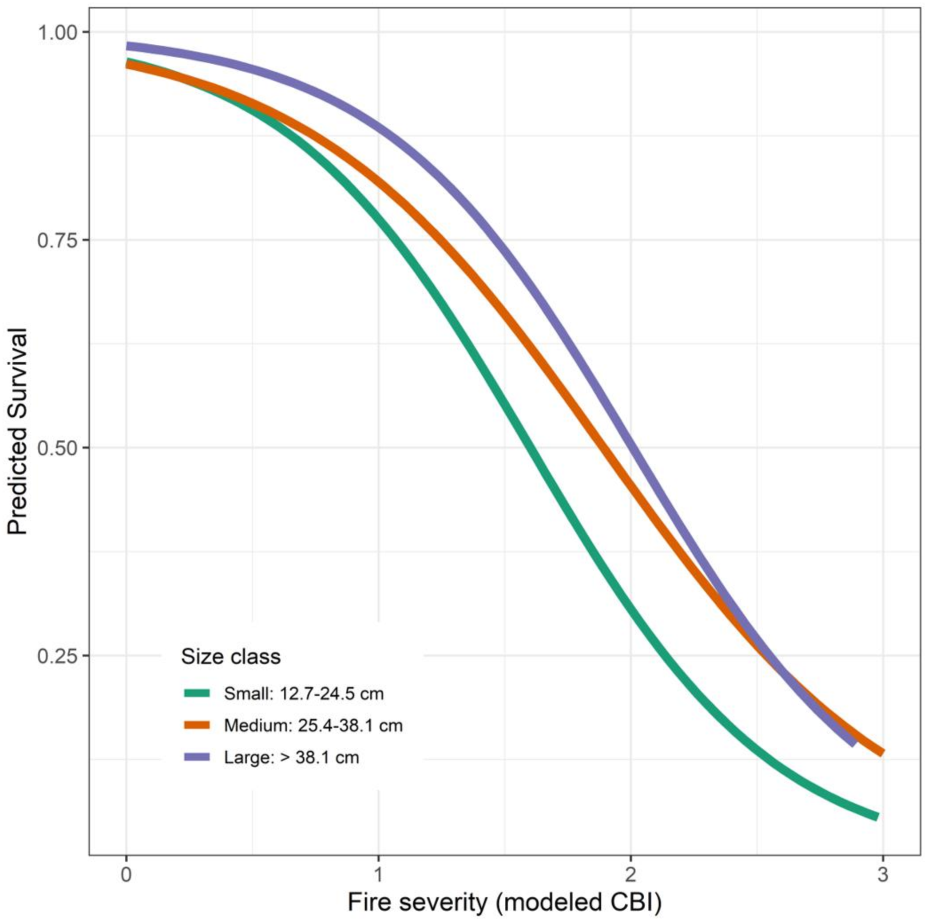

Figure 3. Predicted postfire survival for ponderosa pine trees as a function of fire severity expressed by CBI for small trees (12.7-24.5 cm), medium trees (25.4-38.1 cm), and large trees (> 38.1 cm). The predicted probability is expressed by the colored line among each size class. The confidence intervals 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.

Fire-induced losses of ponderosa pine trees (12.7 cm or greater in diameter)

There was a significant difference among the burned plots in mean basal area (m^2/ha) [$F(2,522)=4.176$, $p=0.0159$] and mean number of trees (per hectare) [$F(2,522)=11.36$, $p<0.001$] 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. Post hoc comparisons using the Tukey test were carried out for the burned plots. There was a significant difference between the basal area (m^2/ha) in cycle one and three ($p=0.0118620$) with the basal area in cycle three on average 5.52 m^2/ha less than cycle one. A Tukey post-hoc test also revealed there was a significant difference between the mean number of live trees (per hectare) in cycle one and two ($p=0.0101510$) and one and three ($p<0.001$) with the number of trees in cycle two on average 73 trees/ha less than cycle one and the number of trees in cycle three on average 118 trees/ha less than cycle one.

Across all plots, the total number of ponderosa pine trees (12.7 cm or greater in diameter) decreased 21% (from 10,154 to 8,010), and ponderosa pine basal area declined by 7% (from 620.81 m^2 to 578.23 m^2) over the 1995-2018 study period. The number of plots containing ponderosa pine trees decreased 10% (from 675 to 608). Approximately 11% of plots (77 of 685) that contained ponderosa pine at the beginning of the sample period experienced 100% tree mortality. In contrast, only 1% of plots (10 out of 685) did not contain ponderosa at the beginning of the sample 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 32%, the number of ponderosa pine trees decreased 46%, and the basal area decreased 34%. Across the plots that burned recently, these changes differed among size classes (Fig. 4). The number of small sized ponderosa pine trees (12.7-24.5 cm) decreased by 57% and the basal area decreased by 54%. The number of medium sized ponderosa pine trees (25.4-38.1 cm) decreased by 31% and the basal area decreased by 29%. The number of large sized ponderosa pine trees (> 38.1 cm) decreased by 25% and the basal area decreased by 27%. Among the 77 plots that suffered 100% tree mortality, 57 of the plots burned recently.

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%, and the

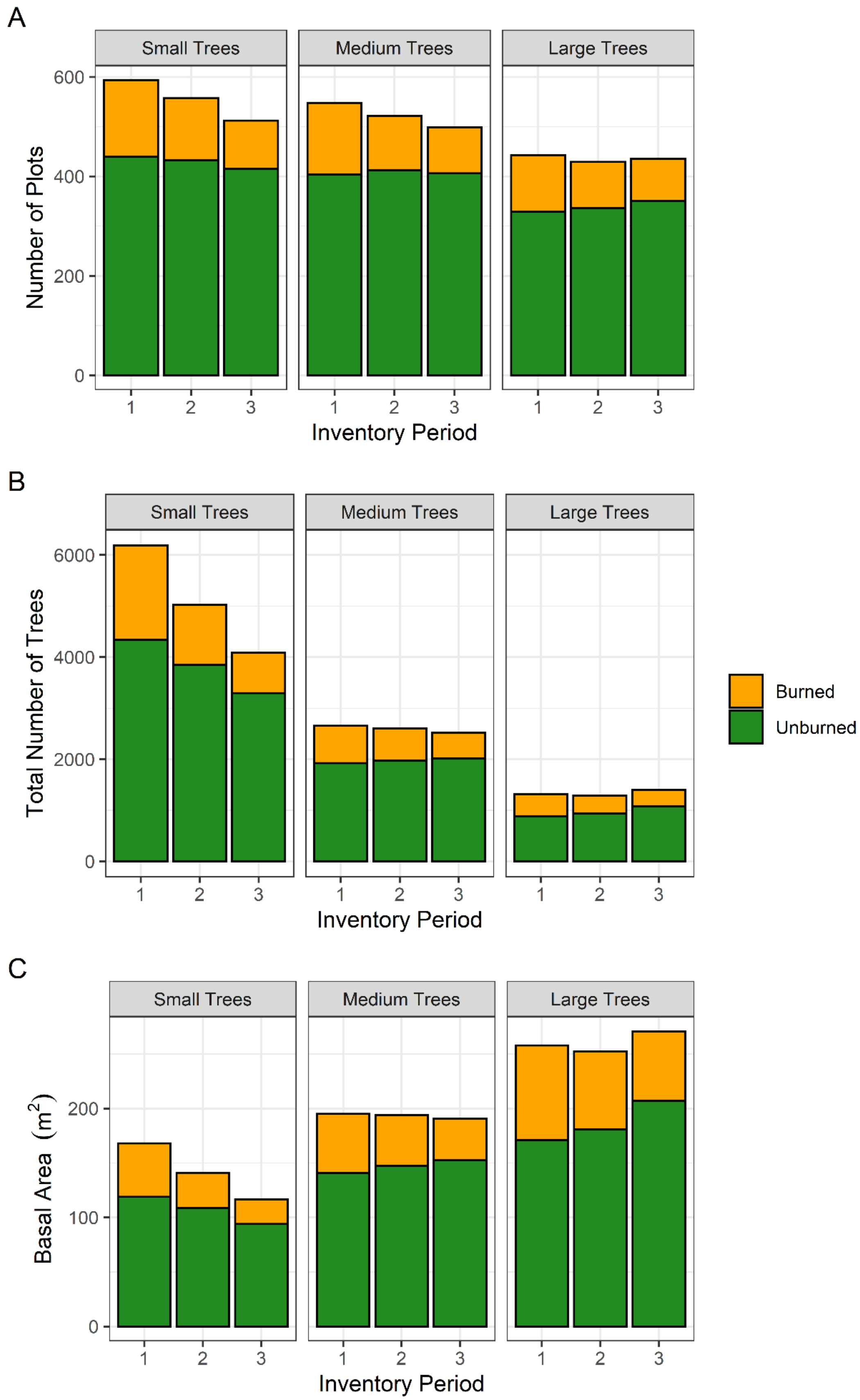
A
Small Trees
Medium Trees
Large Trees
Number of Plots
0
200
400
600
1
2
3
Inventory Period
B
Total Number of Trees
0
2000
4000
6000
C
Basal Area (m^2)
0
100
200
Burned
Unburned

Figure 4. Across the sample period (1995-2018), trends of **(a)** the number of plots containing live ponderosa pine greater than 12.6 cm diameter, **(b)** the number of live ponderosa pine greater than 12.6 cm diameter within each plot, and **(c)** the basal area (m^2) of live ponderosa pine greater than 12.6 cm diameter. Small trees are 12.7-24.5 cm DBH, medium trees are 25.4-38.1 cm DBH, and large trees are > 38.1 cm DBH. Inventory period 1 is from 1995-2000, 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.

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 (12.7-24.5 cm) decreased by 24% and the basal area decreased by 21%. The number of medium sized ponderosa pine trees (25.4-38.1 cm) increased by 5% and the basal area increased by 8%. The number of large sized ponderosa pine trees (> 38.1 cm) increased by 22% and the basal area increased by 22%.

Changes in tree regeneration (less than 12.7 cm in diameter and 3.7 m in height)

No significant differences were found among the changes in the number of stems (per hectare) across inventory periods. Across all samples, the total number of plots containing ponderosa pine seedlings and saplings decreased 27% (from 364 to 265) and the number of ponderosa pine stems decreased 21% (10,154 to 8,010 stems; Fig. 5). In the plots that burned, the number of plots containing ponderosa pine seedlings decreased 41% and decreased 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

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. Fewer seedlings and saplings regenerated in plots that burned at values higher than 1.58 CBI (moderate to high severity). Among the burned plots, the total number of ponderosa pine stems were modeled as a function of fire severity and time since fire separately for seedlings and saplings. We found strong relationships between fire severity (predicted CBI) among sapling stem counts (β= 1.53, SE= 0.31, p-value < 0.001) and time since fire was a significant predictor of seedling stem counts (β= 0.26, SE= 0.09, p-value < 0.01). In burned plots, 82% of seedling counts appeared more than 12 years after a fire.

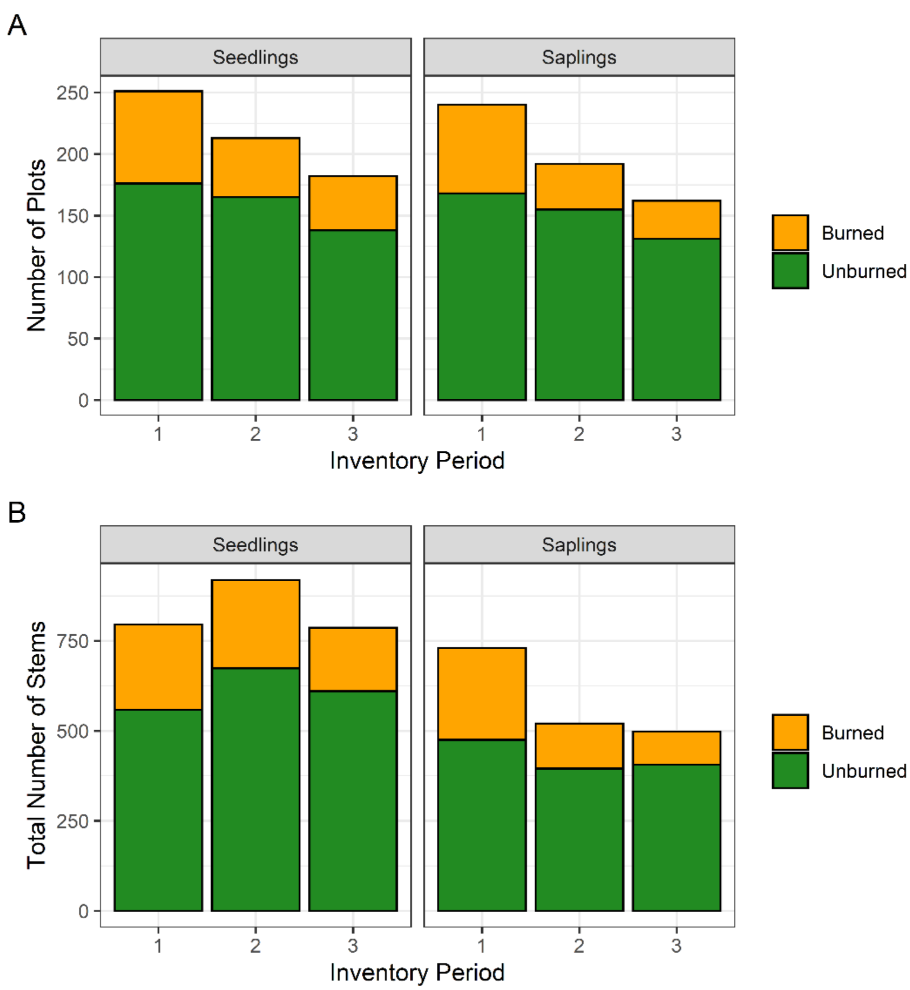

Figure 5. Regeneration (seedling and sapling) trends across the sample period (1995-2018) in the **(a)** number of plots containing live ponderosa pine stems and **(b)** the total number of stems. Seedlings are at least 30.48 cm tall and less than 2.54 cm diameter. Saplings are between 2.54 cm and 12.6 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.

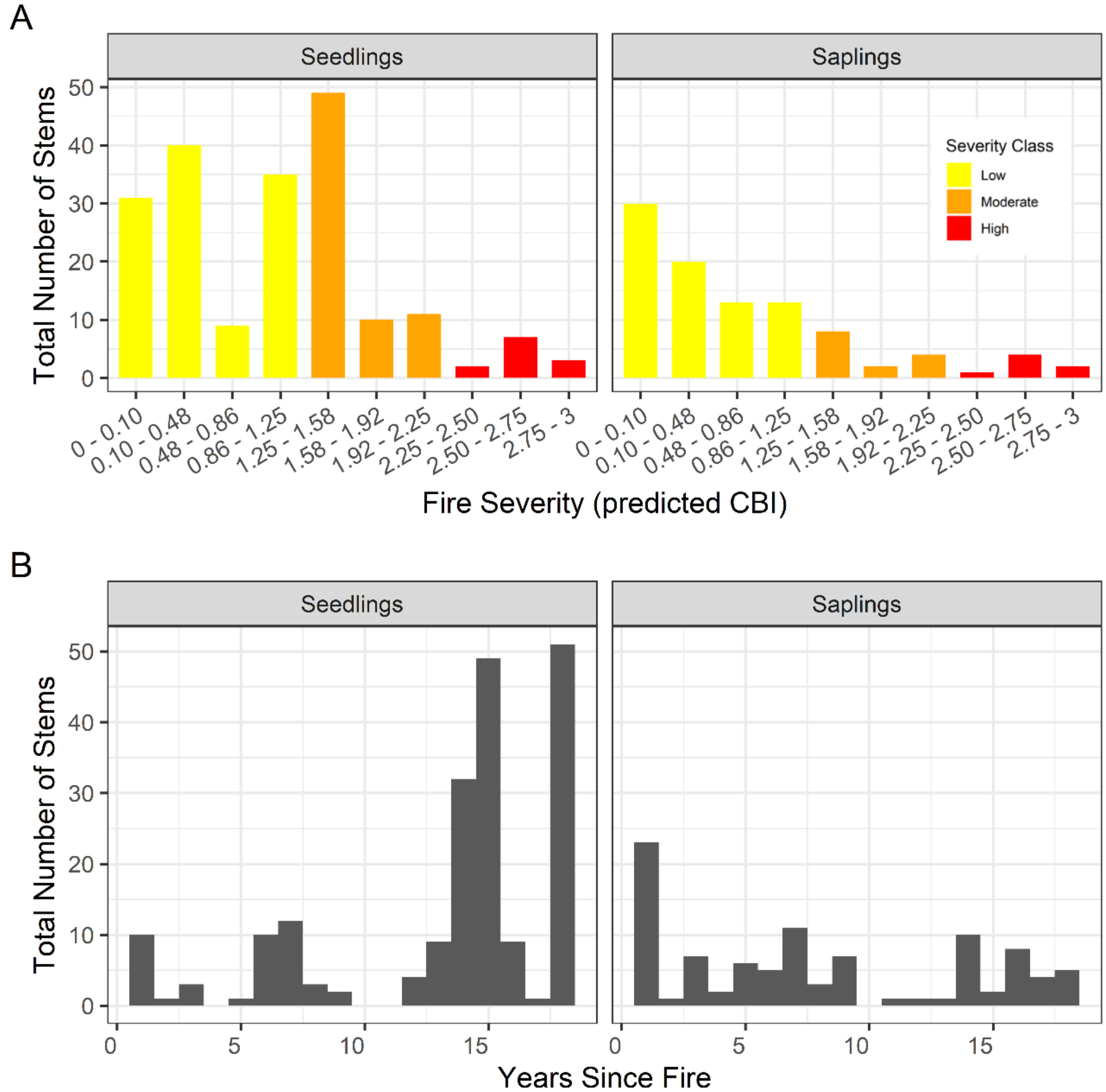

Figure 6. Differences in total number of ponderosa pine seedlings and saplings in recently burned plots by **(a)** fire severity (predicted CBI) and **(b)** time since fire (years). Seedlings are at least 30.48 cm tall and less than 2.54 cm diameter. Saplings are between 2.54 cm and 12.6 cm diameter. Predicted CBI low severity corresponds to values ranging from 0-1.24, moderate severity from 1.25-2.24, and high severity from 2.25-3.0

Shifts in vegetation

Among the plots that did not burn within the study period (510 plots), approximately 82% of plots (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-mixed oak group to ponderosa pine-PJ woodland group (26 plots) and ponderosa pine-woodland to ponderosa pine-mixed oak (16 plots). A total of 16 plots transitioned from forest type groups containing ponderosa pine in the first inventory, to not containing any ponderosa pine in the last inventory. Among those, nine plots shifted to the non-forest: mixed oak group, one plot transitioned to mixed conifer without ponderosa pine, and four plots transitioned to PJ woodland without ponderosa pine.

Of the 175 plots that burned, 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- mixed oak, 9% remained as ponderosa pine- mixed conifer, 8% remained as ponderosa pine- PJ woodland, 6% remained as pure ponderosa pine, and 1% remained as ponderosa pine- aspen. Approximately 52% (91 plots) 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- mixed oak, 3% ponderosa pine- PJ 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 types lacking ponderosa pine, consisting of 4% mixed conifer and 1% PJ woodland. The remaining 23% (41 plots) of plots transitioned to non-forest vegetation consisting of 17% mixed oak, 5% herbaceous vegetation, and 1% mixed shrubs.

Our results show fire severity varies by vegetation type and influences vegetation change. Plots that were pure ponderosa and ponderosa pine- aspen pre-fire (in the first inventory cycle) burned at low severity and all other pre-fire vegetation types burned at moderate-high severity (Table 3). The probability of post-fire transitions to other vegetation types are also influenced by fire severity (Fig. 8). The average predicted CBI of plots that contained ponderosa pine post-fire was 1.18 CBI (low severity). The average predicted CBI of plots that transitioned to forests lacking ponderosa pine increased to 1.93 CBI (moderate severity) and the predicted CBI of plots that transitioned to non-forest increased further, to 2.34 CBI (high severity). Plots that remained or transitioned to pure ponderosa pine stand post-fire burned at the lowest predicted CBI (0.93) while plots that transitioned to shrubs (2.95 CBI) and herbaceous vegetation (2.41 CBI) burned at the highest predicted CBI.

Table 3. Average fire severity (predicted CBI) corresponding to each post-fire vegetation type.

Vegetation type	Fire Severity (predicted CBI)
Ponderosa pine forests	
Pure ponderosa	0.93 ± 0.82
Ponderosa pine-oak	1.29 ± 0.91
Ponderosa pine-mixed conifer	1.33 ± 0.74
Ponderosa pine-PJ woodland	1.01 ± 0.76
Ponderosa pine- aspen	1.40 ± 0.59
Forest lacking ponderosa pine	
Mixed conifer	1.88 ± 0.68
PJ woodland	2.09 ± 1.02
Non-forest	
Oak	2.29 ± 0.63
Mixed shrub	2.95 ± 0.08
Herbaceous	2.41 ± 0.24

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

Table 4. Average fire severity (predicted CBI) of classified vegetation types pre-fire.

Vegetation type	Fire Severity (predicted CBI)
Ponderosa pine forests	
Pure ponderosa	0.98 ± 0.82
Ponderosa pine-oak	1.52 ± 0.95
Ponderosa pine-mixed conifer	1.72 ± 0.81
Ponderosa pine-PJ woodland	1.34 ± 0.98
Ponderosa pine- aspen	0.79 ± 0.66

Notes: Predicted CBI low severity corresponds to values ranging from 0-1.24, moderate severity from 1.25-2.24, and high severity from 2.25-3.0. Values of predicted CBI are mean ± 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.

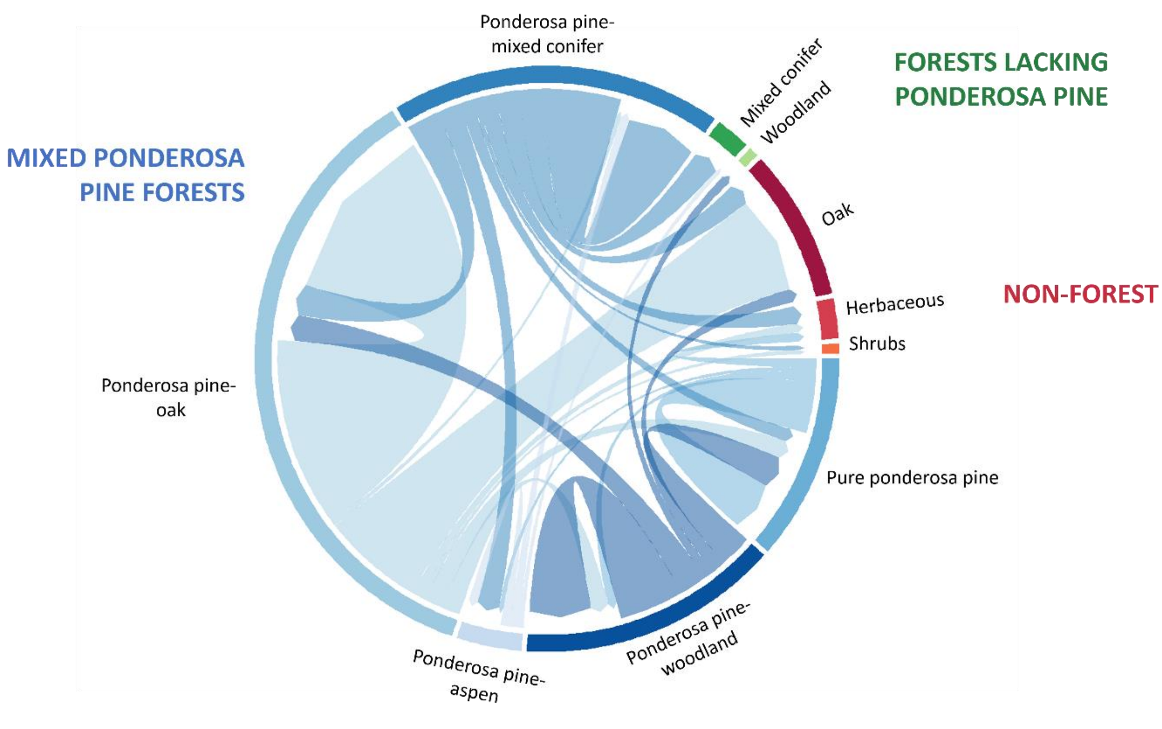

Figure 7. Postfire patterns by vegetation classification group. Groups containing ponderosa pine are in blue, groups lacking ponderosa pine are in green, and non-forest groups are in orange. The arrows are directional, linking prefire vegetation groups (flat ends) to postfire replacing vegetation groups (arrow ends). The link widths are proportional to the number of plots showing such change. There were no burned plots within our study that were non-forest or forests lacking ponderosa pine in the first inventory.

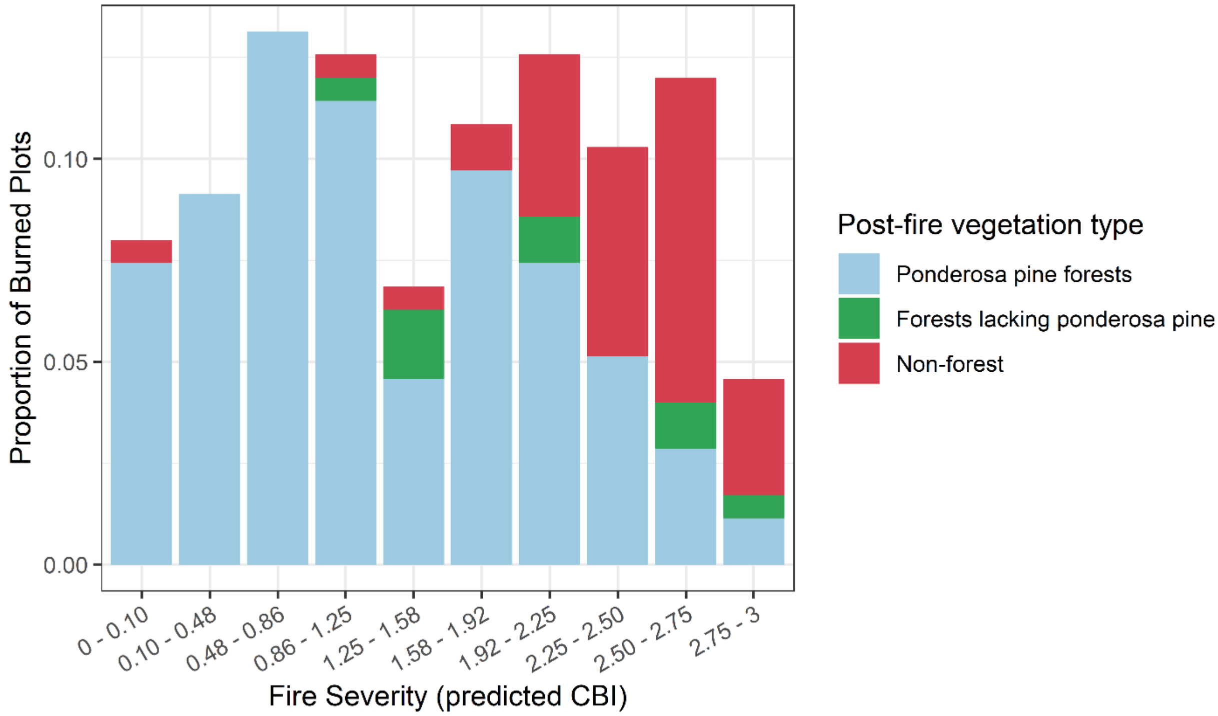

Figure 8. Among the sample of burned FIA plots (n=175), the proportion of plots that burned at predicted composite burn index (CBI) values and the corresponding post-fire vegetation type. All burned plots were classified as ponderosa pine forests pre-fire. Post-fire ponderosa pine forests contain pure ponderosa pine, ponderosa pine with mixed conifer, ponderosa pine with pinyon-juniper woodland, and ponderosa pine with aspen forests. Forests lacking ponderosa pine contain mixed conifer and pinyon-juniper woodland; non-forest contains oak, shrub, and herbaceous vegetation. Low severity CBI corresponds to values ranging from 0-1.24, moderate severity from 1.25-2.24, and high severity from 2.25-3.0

DISCUSSION

Over the past three decades, wildfires drove major reductions of southwestern US ponderosa pine forests. In Arizona and New Mexico, approximately 4.1 million hectares have burned in all vegetation types in the past three decades and the largest fires historically documented have occurred since 2000 (Singleton et al. 2019). Prior to 1900, fire regimes in ponderosa pine forests specific to this region were characterized by high-frequency, low severity surface fires (Falk et al. 2011). Conversely, low-frequency, high severity fires were rare or nonexistent (Swetnam and Baisan 1996). While fire has shaped ponderosa pine forests for millennia, increases in the size, frequency, and severity of recent fires have altered these landscapes. Our findings are consistent with several studies demonstrating that forests are vulnerable to fire-driven conversion to a different forest type or non-forest vegetation. Building on these localized and broad geographic studies, the results of our field vegetation data and remote sensing-based analysis demonstrate the widespread extent of fire-induced ponderosa pine forest loss distinctly in Arizona and New Mexico since 1995.

Within our study, 24% of plots burned once between 1996 and 2017 and 2% of plots burned more than once. More than half of the burned plots burned at moderate to high severity levels, showing considerable departure from historical conditions. Only 7% of plots (13 plots) experienced fire return intervals likely within the historic range of variation (approximately 2-20 years). 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. These are not the same trees that would have been removed historically by low-moderate severity wildfires. 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 did by the end.

The structure and function of vegetative communities that develop following wildfires is highly contingent on regeneration (Korb et al. 2019). Across the southwestern US, we found ponderosa pine regeneration rates among seedlings and saplings decreased over time both in plots that burned recently and did not. In plots that burned within the past three decades, seedling counts decreased by 25% and sapling counts decreased by 64%. Because ponderosa pines are non-sprouting and non-serotinous, they rely on regeneration by nearby seed producing trees (Korb et al. 2019). Ponderosa pine seedlings are found to be most abundant at distances less than 50 meters from a seed source. 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). Widespread losses among any size class raises concern, but 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 offer wildlife habitat (Kaufman et al. 1992, Mast et al. 1999).

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). Our results show fire severity varied as a function of pre-fire vegetation type. Pure ponderosa pine plots burned at low severity, while ponderosa pine-mixed oak and ponderosa pine- mixed conifer groups burned at moderate-high severity (Table 3). Moreover, the composition 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). Similarly, we found that fire severity shaped post-fire vegetation type, allowing species persistence, or driving transitions toward alternate vegetation types. Plots that burned at the highest fire severity transitioned to non-forest while plots that transitioned to a different forest type that still contains ponderosa pine burned at low-moderate severity (Table 3; Fig. 8). Approximately 28% of burned plots no longer contain ponderosa pine and shifted to vegetation types dominated by resprouting shrubs (*Quercus gambelii)* alternate tree species (*Pseudotsuga menziesii*), or non-forest vegetation (*Poa fendleriana, Muhlenbergia straminea, Robinea neomexicana, Arctostaphylos pungens, Rosa woodsii).* Our results show that ponderosa pine forests exhibit a fire severity threshold near 1.92 CBI before the likelihood of a conversion to non-forest increases.

Major shifts in species composition coupled with barriers to recovery by pre-fire forest species can result in a conversion of the prefire forest to a persistent alternate state (Johnstone et al. 2016, Coop et al. 2020, Davis et al. 2020). Here, we documented shifts from ponderosa pine-dominated forests to a range of vegetation types lacking ponderosa pine, instead composed of other forest and woodland trees, and resprouting shrubs and herbaceous vegetation (Fig. 7). These findings are aligned with a growing body of research that ponderosa pine forests are not resilient to contemporary fire regimes, and resprouting species, shade-tolerant species, and less fire-tolerant species are encroaching 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 stems. Fires can result in sharp increases in densities of small-diameter oak stems as well as abundant dead and down woody debris (Abella 2008). Plots shifted to woodland hardwoods more than any other group containing no ponderosa pine postfire. One might conclude that the vegetation changes present in the latter portion of this study are more resilient and will be better suited to new fire regimes and changing climate factors (Savage and Mast 2005).

In plots that did not burn within our study period, the number of small diameter trees and basal area exhibited declines over time, while the number and basal area of medium and large diameter trees area increased. Large diameter trees may continue to grow without severe disturbances, resembling a critical piece of historical conditions (Kaufman et al. 1992, Allen et al. 2002). Yet, the associated species present in the plots that burned are the same in those that haven't burned within our study period. The longer these stands go without a disturbance, shade-tolerant and less fire-tolerant species are likely to increase the density of these forests, thereby making the tree canopies more connected and increasing ladder fuels (Covington and Moore 1994, Agee and Skinner 2005). When a wildfire inevitably occurs, these stands will be maladapted to fire and the probability of a surface fire transitioning to a crown fire increases. The changes observed among the plots that burned foreshadow the conditions that are likely to occur when the unburned plots burn.

As the area burned increases each year, so too does the probability of fires burning at high severity and that a fire burns over a recently burned area. Although our results show shifts to vegetation containing no ponderosa pine in both plots that burned and did not burn, recent fires catalyzed these changes over large geographical areas. This begs the question: how long will the current post-fire states persist – do fire-induced conversions away from ponderosa pine forest represent semi-permanent changes or successional stages? New small-diameter regenerating vegetation and down woody debris from previous fires can fuel a second fire. Increasing research shows short interval fires or early seral reburning can eliminate any remaining seed sources, further expanding resilient resprouting species and reinforcing a vegetation conversion (Coop et al. 2016).

Forest losses and conversion associated with increasing disturbance activity such as those we describe here, are not unique to ponderosa pine forests in western North America. Increases in conifer mortality across multiple biomes around the world from boreal forests in Siberia to moist tropic forests in the Amazon are attributed to disturbances and moisture stress (Batllori et al. 2020, Kharuk et al. 2021). And yet conversions from forests to an alternate state have larger implications that exist past the direct ecosystem. The potential for changes in ecosystem carbon sequestration, biological diversity, and reduced opportunities for timber harvest and recreation is of growing concern. Wildfires are inevitable; fire and climate models for the southwestern US suggest an increase in the severity and extent of future wildfires and drought events. 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 nonforest by 2090 (Flatley and Fulé 2016, Parks et al. 2019a). In a time of complex environmental change, land management decisions are more important than ever before.

Management implications

The long-term undesirable consequences that appear to result from altered fire regimes within our study area bring attention to an increasingly urgent question: how can science and management best support and enhance the resiliency of southwestern US ponderosa pine forests? In the past decade, three land management strategies to ecosystem transformations have emerged: resisting, accepting, or directing change (the RAD framework). Specifically, managers can *resist* change and strive to maintain existing ecosystem composition, structure and function; *accept* transformation when it is not feasible or socially acceptable to resist change; or *direct* change to a future ecosystem configuration that would yield desirable outcomes (Aplet and Cole 2010, Schuurman et al. 2020). Contemporary forest management generally take on the resist framework in the form of restoration ecology. The fundamental premise of restoration ecology is that ecosystems function best under the conditions in which they adapted over evolutionary time. However, in a time of rapid change, the assumption that future management should reflect historical conditions is questionable.

The directing and accepting paradigms lack the framework and 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 mangers can proactively plan for future conditions under shifting fire and climate regimes. Yet, if we wish to resist fire-induced conversions in ponderosa pine ecosystems, we can assume that restoring the composition, structure, and characteristic processes in these forests will at least increase ecosystem survival probabilities in the face of current disturbances as well as uncertain changes in disturbance types and intensities due to climate change. It may not always be feasible or desirable to restore exact reference compositions and structures, but restoration of key compositional and structural elements on a site-by-site basis can enhance the resiliency of these forests (Reynolds et al. 2013).

Where retaining ponderosa pine forests is prioritized, our findings point toward two key themes for management: restoring low-severity fire regimes that are less likely to drive conversion and retaining large trees that are less susceptible to burning severely. Both principles are already widely incorporated in forest restoration efforts in the southwestern US (Allen et al. 2002). Undoubtedly, management will require type and location specific approaches, in which reducing tree density and ladder fuels through thinning and prescribed burns may be needed before low-severity fire regimes can occur (Allen et al. 2002, Agee and Skinner 2005, Walker et al. 2018). Equally important is management that retains and promotes large trees to foster regeneration and species persistence in the future. Though treatment costs, public support, and topographic constraints can limit the pace and scale of these projects (Hessburg et al. 2019).

Study limitations and directions for further research

The FIA program provides the most comprehensive forest database currently available in the US, and 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. Recent applications of FIA data include informing the forest plan revision process and supplying managers with timely information on important forest attributes at the 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 many limitations to the database. Though periodic data ran for approximately 70 years (beginning in 1930) much of this data 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 1995-2018), many plots were not included that contain ponderosa pine. For example, 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. We found challenges to using the understory species percent cover data, including considerable increases in percent cover by many species that did not seem plausible.Such variations across the database present limitations to broad-scale analyses.

Nevertheless, there are endless research opportunities within the FIA database to continually study forest structure and composition, woody fuels, understory vegetation, and wildlife habitat at large spatial scales (Burrill et al. 2018, Tinkham et al. 2018). Successful conservation in an era of rapid and widespread ecological change requires land managers to collaborate at large scales across jurisdictions. There are many opportunities to link FIA data to other publicly available large regional databases. For example, MTBS or other remotely sensed databases can link dNBR, CBI, or other satellite-derived measures of disturbance to exact FIA plot locations (Shaw et al. 2017).

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