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RESEARCH ARTICLE

Thinning and Managed Burning Enhance Forest Resilience in Northeastern California

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Understanding and quantifying the resilience of forests to disturbances are increasingly important for forest management. Historical fire suppression, logging, and other land uses have increased densities of shade tolerant trees and fuel buildup in the western United States, which has reduced the resilience of these forests to natural disturbances. One way to mitigate this problem is to use fuel treatments such as stand thinning and prescribed burning. In this study, we investigated changes in forest structure in the Lassen and Plumas National Forests of northern California following a large wildfire. We used long-term field data and aerial photos to examine what management techniques can be effectively used to restore a healthy forest structure and increase the resilience of forests to drought and wildfires. Forest resilience was quantitatively modeled using the forest vegetation simulator and analyzed under varied thinning practices and fuel management scenarios. Results showed that trees below 1,219 m in elevation had the least mortality and gained the most biomass. Trees taller than 45.7 m lost the most biomass. We found that thinning basal area to 16.1 $m^2 \cdot hm^{-2}$ resulted in the highest resilience score for California mixed conifer forest stands and thinning to 9.2 $m^2 \cdot hm^{-2}$ resulted in the highest resilience score for Jeffrey pine stands. Structural diversity had a negative relationship with resilience score. Understanding forest structure, forest resilience, and the factors that make trees vulnerable to mortality will allow managers to better plan fuel treatments for these forests.

Introduction

Historical fire suppression in the western United States has contributed to crowded forests that can result in large, difficult to control wildfires when conditions are favorable for fires to spread [1]. Fire suppression was historically used to prevent a direct loss of timber and to increase tree regeneration for future wood availability [2]. Foresters of the time also opposed prescribed burns, fearing that fire may escape and believing that trees damaged by fire would be vulnerable to fungi. Along with effects due to logging and grazing, fire suppression has greatly changed forest structure in California [3]. Tree densities have increased substantially, especially for shade-tolerant and fire-sensitive species [4,5]. These forests are now less resilient because of their vulnerability to large wildfires and to tree mortality during droughts [5]. Forest ecosystems have also become more structurally homogenous, making forests more vulnerable to higher intensity fire and bark beetle attacks [6,7].

To address these concerns, forest managers have utilized fuel treatments such as thinning and prescribed burning. Fuel treatments need to decrease surface fuel loads, which lowers fire intensity and raises the height to the base of the canopy to reduce the likelihood of crown fires [8,9]. Thinning is an effective tool to reduce tree density and increase stand diameter if thinning from below. Knapp et al. [5] found that it worked more quickly to restore forest structure than prescribed burning. Thinning also helps to address fire behavior issues, but it is more effective when combined with prescribed burning [10]. Prescribed burning is used to remove surface fuels and reduce small tree density without harming larger trees [11]. Because of the lack of stand density management and natural surface fires for long periods, these small saplings have grown large with thicker bark, which makes them more difficult to remove with a prescribed burn [5]. Removing these trees may require higher intensity burns or multiple burn treatments [12,13]. A single instance of prescribed fire is not likely to restore historic forest structure [14]. Therefore, thinning is necessary before a prescribed fire is conducted.

Although the effects of these treatments have been evaluated on stand-level attributes of forest resilience after posttreatments, a long-term effectiveness has not been fully explored. Some long-term studies established during the last century have shown that forest structure including stand density affects forest capacity to adapting fires and other environmental threats in ponderosa pine and true fir stands [15,16]. However, the long-term effects of structural and spatial configuration on residual stand recovery, carbon redistribution, forest floor decomposition, and their interaction with other treatments such as mechanical methods to treat the stands or prescribed fire were not yet been fully evaluated and understood. Understanding the effects of these treatments will help forest managers to find the best treatment combinations in their forest restoration projects [17,18].

This research aimed to determine the optimal treatments for forest resilience to natural disturbances by modeling stand structure and diversity based on data from long-term research plots in the region. Specific objectives were to understand how changes in forest structure and composition related to historic community dynamics and forest resilience and to determine the most effective management techniques (fire suppression, thinning, fuel reduction treatments, and prescribed burns) to improve forest resilience in these forests. We hypothesize that (a) optimal levels of thinning and prescribed burning restore the natural fire regime by reducing tree density and fuel, (b) thinning and prescribed burning increase resilience in forests, and (c) higher structural diversity in a forest increases adaptive capacity and resilience in that forest.

Materials and Methods

Study area

Our study area covers 2 national forests in northern California: Lassen National Forest and Plumas National Forest (Fig. 1). Both forests are characterized by geologic complexity, unique climate conditions, and diverse topographies and offer a rich variety of landscapes and forest types, making them important ecological areas. Climate is largely Mediterranean in the region, as the winters are cool and wet and the summers are dry and warm. The climate, topography, and geology have contributed to diverse soils across the area, with warmer, wetter westside areas yielding generally deeper more productive soils. Lassen National Forest features a range of elevations, from low foothills to high mountain peaks and consists of 3 ecoregions: the southern Cascade Mountains, the northern Sierra Nevada Mountains, and the Modoc Plateau. Elevation ranges from 152 to 3,048 m in Lassen Volcanic National Park, which is enclosed by Lassen National Forest [19]. Plumas National Forest is located in the northern Sierra Nevada Mountains and is known for its rugged terrain, encompassing mountainous areas with steep slopes, canyons, and meandering rivers [20]. Elevation ranges from 488 to 2,552 m. Annual precipitation ranges from 38 cm on the eastside to over 229 cm on the westside in the Plumas National Forest [20].

Common species in the national forests include white fir (*Abies concolor*), ponderosa pine (*Pinus ponderosa*), California red fir (*Abies magnifica*), Jeffrey pine (*Pinus jeffreyi*), incense cedar (*Calocedrus decurrens*), and Douglas fir (*Pseudotsuga menziesii*) (Table S1). The most common forest type in both national forests is California mixed conifer. In Lassen National Forest, the next most common forest types are white fir and ponderosa pine. In Plumas National Forest, the next most common forest types are Jeffrey pine and white fir.

In the historical fire regime, the fire return interval was between 8 and 22 years [20]. Fire suppression practices have resulted in higher tree densities and more surface litter than was present historically, leading to large fires [1,21]. The Storrie Fire burned in 2000 in both the Lassen and Plumas National Forests [22]. The Chips Fire started in 2012 within the area

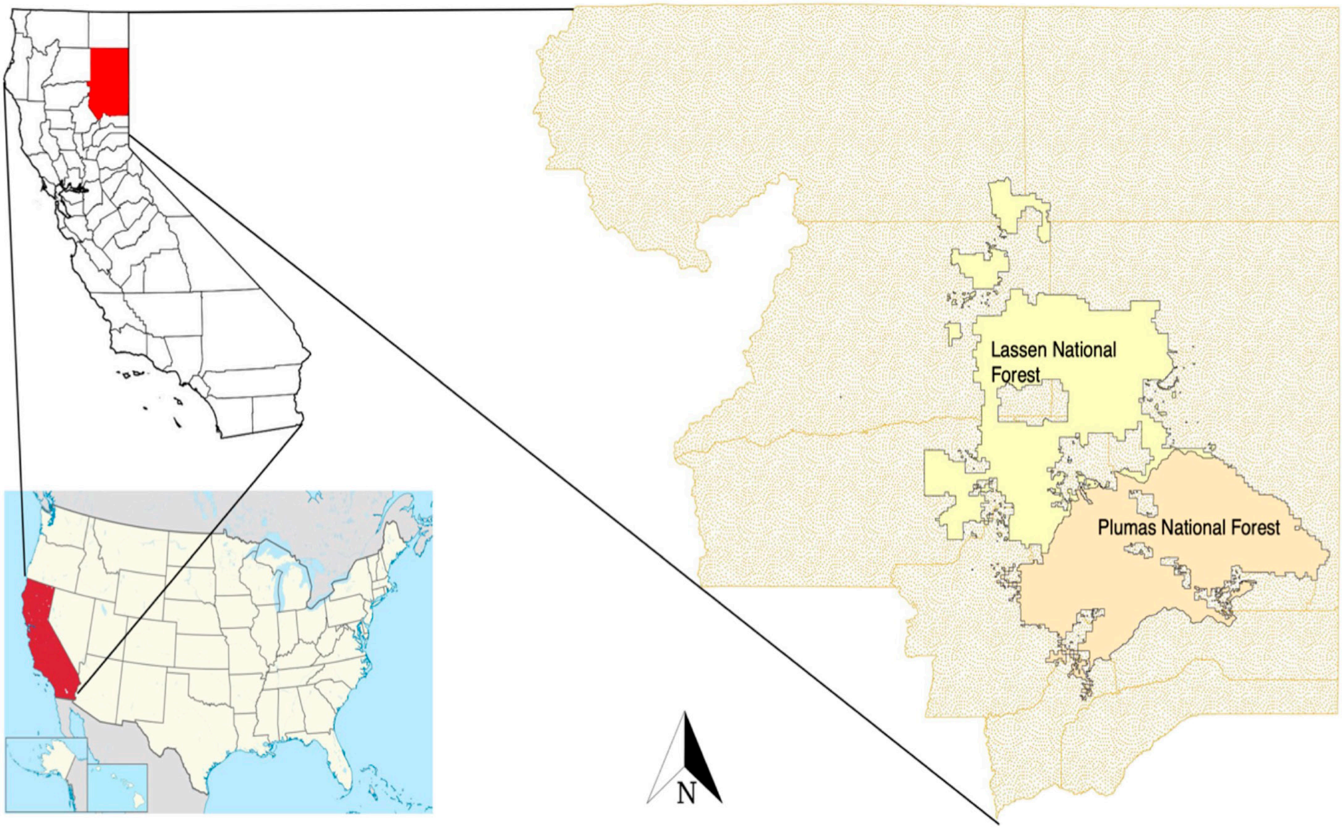

Fig. 1. Map of the study area (Lassen and Plumas National Forests in northern California).

burned by the Storrie Fire [23]. However, only 12% of the area where the Storrie Fire burned had experienced a fire in the previous century [24].

Data

Forest and tree data

Forest Inventory and Analysis (FIA) data record forest attributes for many field plots in each state, and these plots are revisited periodically. In California, one cycle of data collection lasts 10 years, which is also the time interval at which each plot is resampled. The first cycle of data collected at national standards in California was from 2001 to 2010 [25]. The second cycle is mostly finished but ongoing. California has 13 million forested hectares, and 5,575 forested plots were sampled between 2001 and 2010 [25]. FIA data contain a multitude of useful variables and allow for the estimation of forest type, volume, biomass, carbon storage, age, tree growth, and tree mortality, among other factors [25]. FIA data can be found on the FIA DataMart website (https://www.fs.usda.gov/research/products/dataandtools/datasets/fia-datamart) [26].

For this study, we used 414 FIA plots from the Lassen and Plumas national forests. In the first cycle, these plots contained 15,750 trees that had a total aboveground biomass of 14,214,848 kg (903 kg per tree). The dataset includes many variables that can help us define forest structure such as canopy cover, biomass of the bole, stand structure code, tree diameter, aboveground tree biomass, tree height, and tree volume [27].

In addition, we used data from permanent research plots in the Lassen and Plumas National Forests on the effects of management on forest stand dynamics [15,16,28]. Post-Storrie-Fire plots were established and measured [29] with data online (https://doi.org/10.2737/RDS-2015-0039, 18 August 2022).

Remote sensing

Aerial surveys are conducted annually by the US Forest Service's Pacific Southwest Region (https://www.fs.usda.gov/detail/r5/forest-grasslandhealth/?cid=fsbdev3_046696). Geodatabases containing the data are available from the website. They are used to calculate the number of trees and acres that have suffered damage [30]. Individual maps exist for the national forests in California.

Wildfire

Cal Fire in the State of California has historical fire data: https://www.fire.ca.gov/stats-events/. There are data on the number of fires and areas burned per year [31]. The US Forest Service has geospatial data for vegetation burn severity, including percent change in basal area (BA), percent change in canopy cover, and perimeters of mapped fires [32]. Fire regime interval data come from field studies by A. Taylor from Pennsylvania State University in Lassen National Forest and Lassen Volcanic National Park [33,34].

Analytical tool: Forest vegetation simulator

The forest vegetation simulator (FVS) is a forest growth simulation model. It is an individual-tree, distance-independent, growth, and yield model [35]. Each part of the United States has a variant that is specialized for that area. Lassen National Forest is split between the Inland California and Southern Cascades [35] and the South Central Oregon and Northeast California variants [32]. Plumas National Forest is located in the Western Sierra Nevada variant [36]. FVS also has several extensions that allow for the addition of more factors to the simulation. The Fire and Fuels Extension can estimate changes in carbon, while Climate-FVS allows users to predict the effects of management under climate change.

Four forest stands were chosen randomly on the basis of meeting criteria of having stand BA greater than 55.1 $m^2{\cdot}hm^{-2}$, being of California mixed conifer forest type, and being located in Lassen or Plumas National Forests. Square plots were used for the simulations. Stands needed to have at least 55.1 m^2 of BA per hectare in order for there to be a substantial difference between the smallest amount of thinning and the control in the FVS simulations. Five treatments were conducted for each stand: 4 levels of thinning and a control. The simulations lasted for 100 years: from 2021 to 2121. In 2031, the stands (except the control) were thinned from below to BAs of 16.1, 27.5, 39.0, and 50.5 $m^2{\cdot}hm^{-2}$. These values were chosen on the basis of the distribution of BAs within the California mixed conifer forest stands in the study area assuming that the BAs of the stands follow a normal distribution, and these values cover a range from about the 10th percentile of stands up to the 67th percentile of BAs.

We used 4 different fire regimes: no fires, presettlement, suppression, and future. We chose fire intervals of lengths ranging from 14 to 44 years [33,34]. There were no simulated fires in the no fires fire regime. In the presettlement fire regime, we simulated a fire every 14 years starting in 2028. Thirty percent of the area of the stand was burned in each fire, except in 2070 when 75% of the area was burned. For the suppression fire regime, we simulated a fire every 44 years starting in 2043. Seventy-five percent of the stand area was burned in each fire, except for 2087 when 100% was burned. For the future fire regime, we based the lengths on the ratio between the Douglas fir mean fire return intervals 2070–2099 projections and the 1971–2000 period [37]. We multiplied the suppression fire regime by this ratio to get the future fire regime. We simulated a fire every 29 years starting at 2035. Seventy-five percent of the area of the stand was burned in each fire, except for 2064 when 100% was burned.

We then repeated this procedure, except using stands of Jeffrey pine forest type. For Jeffrey pine stands, we thinned the stands to BAs of 9.2, 18.4, 27.5, and 36.7 $m^2{\cdot}hm^{-2}$ plus a control. Assuming that the BAs follow a normal distribution, these values range from about the 10th percentile of stands to about the 77th percentile of stands. Jeffery pine forest stands needed to have at least 41.3 m^2 of BA per hectare at the start of the simulation to be selected. We chose fire intervals of lengths ranging from 5 to 89 years [33,34]. For the presettlement fire regime, we simulated a fire every 5 years starting in 2023, with a large fire in 2068. Each fire burned 30% of the stand area except for the large fire, which burned 75%. For the suppression fire regime, we simulated a fire every 89 years. There was only one fire within our study period—in 2065 (100% burn). For the future fire regime, we simulated a fire every 59 years starting in 2050. One hundred percent of the stand area burned during this fire, and 75% burned during the other fire that fell within the study period.

Resilience score calculation

The resilience score analysis is based on the methods described in Bryant et al. [38]. Resilience scores are calculated out of 5 points (Fig. 2). For California mixed conifer stands, one point

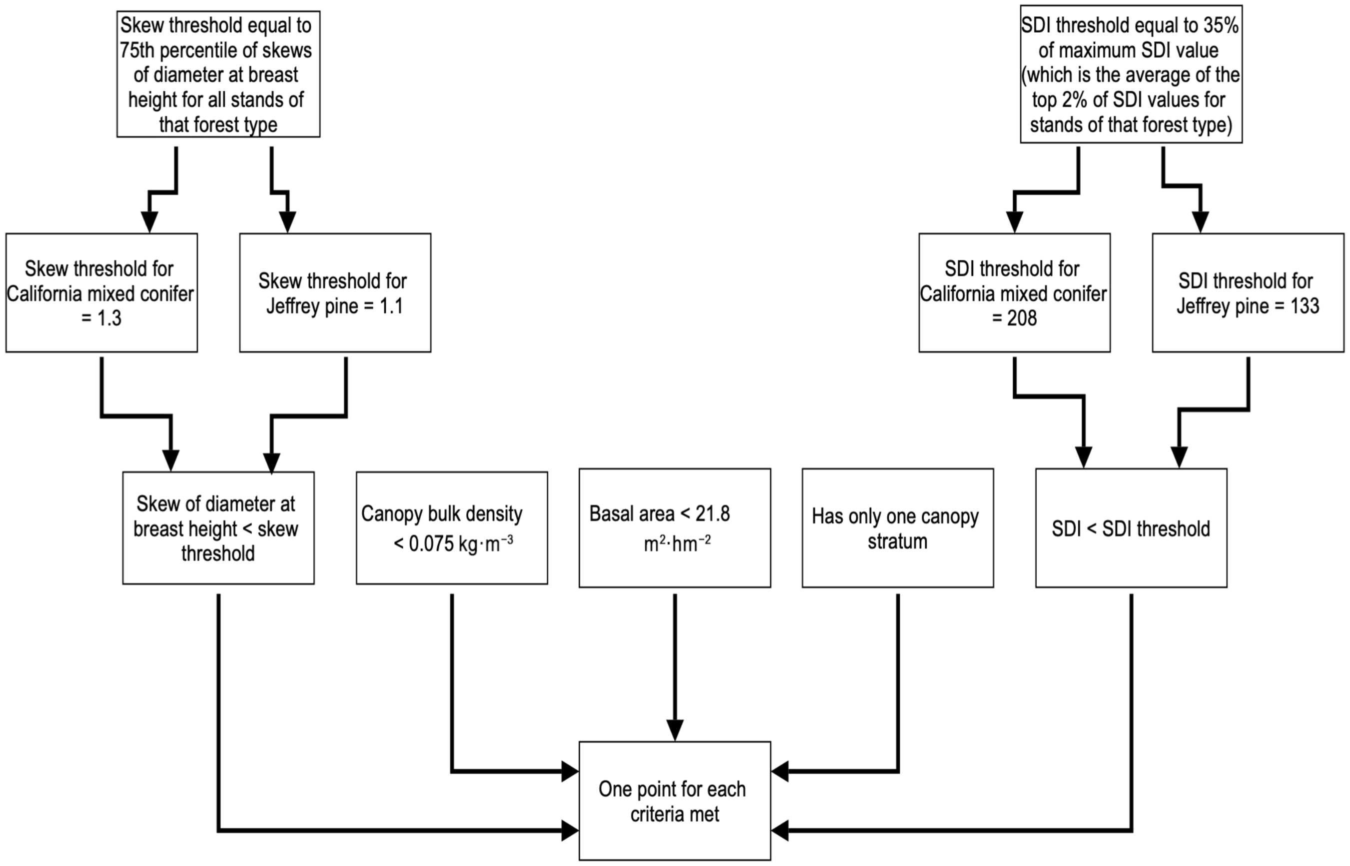

Fig. 2. The resilience scores are calculated out of 5 points, as shown in this flow chart.

is awarded for meeting each of the following conditions: the skew of the diameter at breast height of the trees in the stand being less than 1.3, the canopy bulk density being less than 0.075 kg·m^{-3}, the BA being less than 21.8 m^2·hm^{-2}, having only one canopy stratum, and having a stand density index (SDI) under 208. For Jeffrey pine stands, the thresholds were the same except the skew threshold was 1.1, and the SDI threshold was 133. The skew thresholds are equal to the 75th percentile of skews from all stands of that forest type [39]. The SDI thresholds are equal to 35% of the maximum SDI value, which was calculated to be the average of the highest 2% of SDI values in the stands of that forest type [40]. SDI measures competition between trees based on their diameters and the number of stems in the area [41]. Scores are calculated in 2021 (at the beginning of the run), 2041 (after thinning), 2071 (after the large fire in most runs), and in 2121 (at the end of the simulation).

Structural diversity

We calculated structural diversity for selected plots in the FIA dataset from 2001 to 2019 for Lassen and Plumas National Forests. All selected stands were of either California mixed conifer or Jeffrey pine forest type and occurred within the Western Sierra Nevada variant of FVS. For the California mixed conifer stands, 214 of the stands were in Plumas National Forest, and 7 stands were in Lassen National Forest. All 42 Jeffrey pine stands were in Plumas National Forest. We used a post hoc extended Shannon index as described by Staudhammer and LeMay [42]. We divided the trees into 10-cm DBH (diameter at breast height) classes, with one class for all DBHs over 150 cm. We also divided the trees into 5-m height classes, with one class for trees over 60 m. We then calculated a Shannon's index:

$$H' = -\sum_{i=1}^{S} p_i \ln p_i \qquad (1)$$

based on the diameter classes, height classes, and species where p_i is the proportion of BA of that class or species and S is the number of classes or species. We then averaged together the diameter, height, and species indices.

Statistical analysis and model validation

We calculated how tree mortality and biomass loss varied on the basis of factors such as height, diameter, species, elevation, and tree density. Tree mortality and biomass loss are both calculated as yearly rates: the percentage of trees that died each year or the percent change in biomass that year.

We used FVS to test how forest resilience is affected by disturbances, diversity, and management. We determined the optimal level of thinning and prescribed burning to maximize forest resilience by comparing different FVS simulation results. We use the method described by Bryant et al. [38] to calculate resilience scores for our study area under different management scenarios. Resilience score incorporates forest type change with no disturbance; diameter distribution, forest type change, and canopy bulk density in response to fire; BA, quadratic mean diameter, and vigor in response to bark beetles; amount of host species, canopy strata, and aspect in response to western spruce budworm; and stand density index, site index, and topographic moisture potential index in response to drought [38].

We also used FVS to generate data needed to calculate resilience scores for historical data (2001–2019). We then calculated resilience scores for each forest stand (separately for each time it was measured) and then observed the relationship between those resilience scores and the post hoc extended Shannon index. We analyzed this relationship using simple linear regression and used a *P* value of 0.05.

To evaluate the trends of where bias was observed at the stand level, we conducted model validation with a linear regression method by comparing the model predictions of FVS simulations with observed plot values of FIA-remeasured inventory tree data from in the Lassen National Forest and the Plumas National Forest. The dataset for regression analysis contains 2 entries for each of the 8 forest stands: One is a chronosequence developed from 8 FIA plots measured with FIA-observed BA as the dependent variable (FIA-observed) and one with FVS-modeled stand BA (FVS-modeled), with an explanatory variable identical.

Results

Changes in tree species composition

Among 5 common species (Table S1), the largest proportion of biomass in these forests are white fir, Douglas fir, and ponderosa pine (Table S1). California mixed conifer is the most common forest type in both national forests. White fir and ponderosa pine are the next most common forest types in Lassen National Forest, whereas Jeffrey pine and white fir are the most common forest types in Plumas National Forest.

Forest stand structure and age distribution

Most stands in the study area are under 160 years old. Many stands are under 10 years old, and the next peak occurs from around 70 to 110 years old. The oldest stand is over 350 years old.

Annual mortality and biomass loss

Annual percent tree mortality was similar for all heights, although trees under 15.2 m had slightly higher mortality rates (Fig. 3). Trees between 45.7 and 61.0 m lost about 0.0107 metric tons biomass per stem per year, whereas trees of other heights had little change in biomass. Trees below 1,219 m of elevation

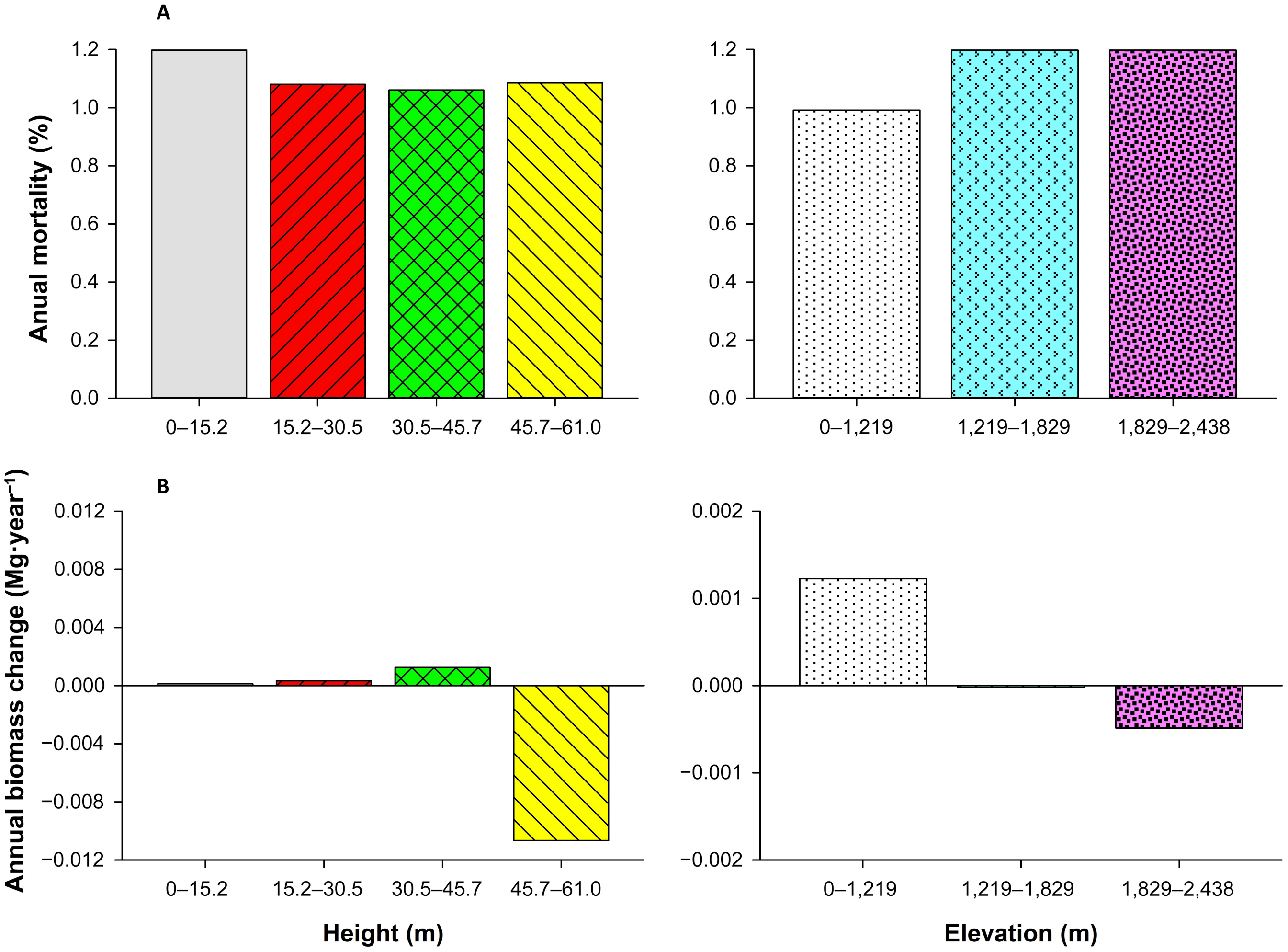

Fig. 3. (A) Annual percent mortality and (B) annual change in biomass of trees based on height and elevation for Lassen and Plumas National Forests.

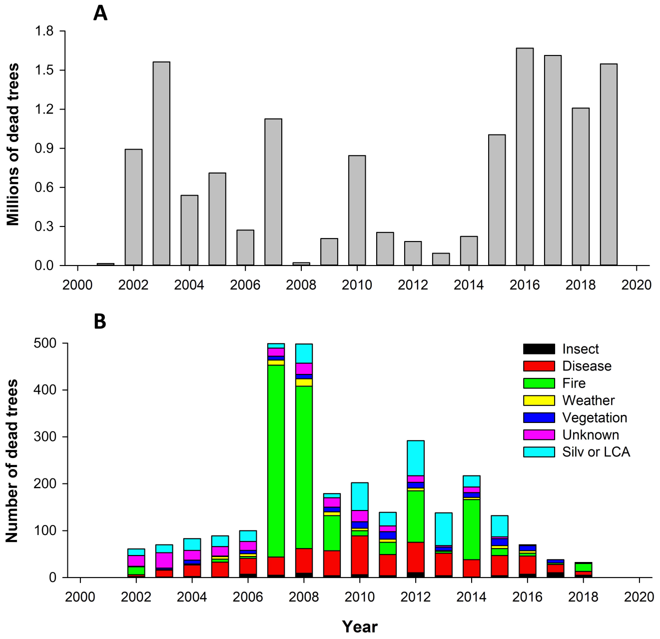

Fig. 4. (A) Number of dead trees per year in Lassen and Plumas National Forests based on aerial detection surveys by the US Forest Service's Pacific Southwest Region. (B) Annual tree mortality by cause of death based on FIA data. Not all trees in the data had a year of death recorded.

had the lowest annual mortality rate, and they also gained the most biomass per year. Trees between 1,219 and 1,829 m had little change in biomass, and trees between 1,829 and 2,438 m lost the most biomass.

Tree mortality had substantial variation over the time period from 1999 to 2019. Tree mortality oscillates between years with high and low mortalities. According to data from aerial photos, mortality was lowest in the years 2001 and 2008 (16,455 and 21,732 dead trees, respectively) and highest in 2016 (1,669,000 dead trees; Fig. 4A). Recent years have featured high mortality, with the last 4 years all being in the top 5 in term of tree mortality. According to annual mortality estimates based on FIA data, 2007 had the most mortality (Fig. 4B). Year 2008 also had very high mortality. Fire was the most common cause of death, followed by disease and silvicultural or land clearing activity.

Fires in Lassen and Plumas National Forests

We looked at fire data for the years 1984–2017 to determine changes in fire frequency and size over time. There was substantial yearly variation in the number of fires and the amount of area burned each year in the Lassen and Plumas National Forests. In some years, such as 1998 and 2008, there were many fires; however, there was no overall trend present. Similarly, we found no trend in the total area burned by fires each year in the 2 national forests. The amount of forest burned was highest in the years 1990, 1999, and 2008 (Fig. 5). There were 8 years with no fires in the 2 national forests. An average of 2.94 fires burned per year. A total of 21.6% of the area of Lassen and Plumas National Forests experienced at least one fire between the years 1984 and 2017. While most of the national forest area had not burned during the study period, some areas burned multiple times. For example, the Chips Fire in 2012 burned most of the area that the Storrie Fire burned in 2000. The 1990 Campbell Fire, the 1994 Barkley Fire, and the 1999 Gun II Fire all overlapped in their burn areas as well.

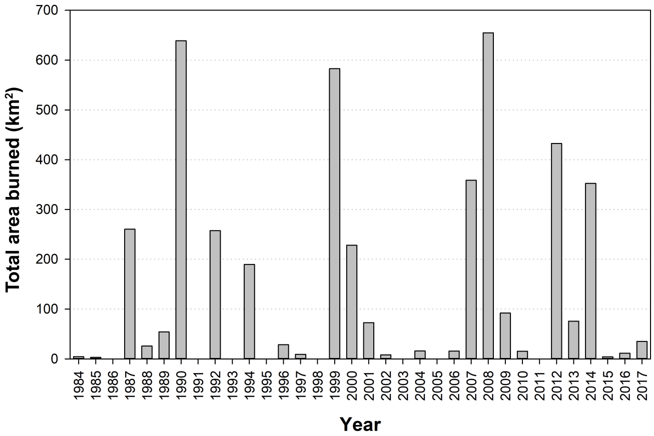

Fig. 5. Total area burned in kilometers squared by year in the Lassen and Plumas National Forests between 1984 and 2017. Data are based on perimeters of mapped fires from the US Forest Service.

Changes in resilience of California mixed conifer forest in Lassen National Forest

Total volume decreased with thinning, with greater levels of thinning losing more volume (Figs. 6 and 7). After the thinning, total volume increased slowly over time in most stands. In some cases, the total volume at the end of the simulation was higher than before the thinning occurred. In almost all cases, only stands that were thinned small amounts were able to recover their volume back to where it was before the thinning.

The FVS simulations show that the level of thinning affects forest resilience. Resilience scores are generally higher for runs that were thinned more (Fig. 8). When California mixed conifer stands were thinned to a BA of 16.1 $\mathrm{m}^2\cdot\mathrm{hm}^{-2}$, the average resilience score was the highest of any thinning level for all fire regimes. When Jeffrey pine stands were thinned to 9.2 $\mathrm{m}^2\cdot\mathrm{hm}^{-2}$, the average resilience score was also the highest of any of its thinning levels. The lowest average resilience score for California mixed conifer was at 39 $\mathrm{m}^2\cdot\mathrm{hm}^{-2}$ for one simulation, 50.5 $\mathrm{m}^2\cdot\mathrm{hm}^{-2}$ for one fire regime, a tie between 39 and 50.5 $\mathrm{m}^2\cdot\mathrm{hm}^{-2}$ for one fire regime, and a tie between 50.5 $\mathrm{m}^2\cdot\mathrm{hm}^{-2}$ and the control for the other regime. The lowest average resilience score for Jeffrey pine was at 27.5 $\mathrm{m}^2\cdot\mathrm{hm}^{-2}$ for one fire regime, 36.7 $\mathrm{m}^2\cdot\mathrm{hm}^{-2}$ for another fire regime, and a tie between 27.5 and 36.7 $\mathrm{m}^2\cdot\mathrm{hm}^{-2}$ and the control for the other 2 regimes. For California mixed conifer, resilience increased slightly after thinning but then decreased below its starting level by the end of the simulation for all fire regimes. For Jeffrey pine, resilience increased after thinning and then decreased by the end of the simulation for all regimes; however, it did not decrease below the starting resilience score. Changing the fire regime did not have much effect on resilience scores.

Structural diversity

We averaged 3 types of diversity using a post hoc extended Shannon index (Eq. 1): diameter, height, and species diversity. There were 221 different California mixed conifer stands and 42 different Jeffrey pine stands. Some were measured twice in different years, which resulted in 329 California mixed conifer

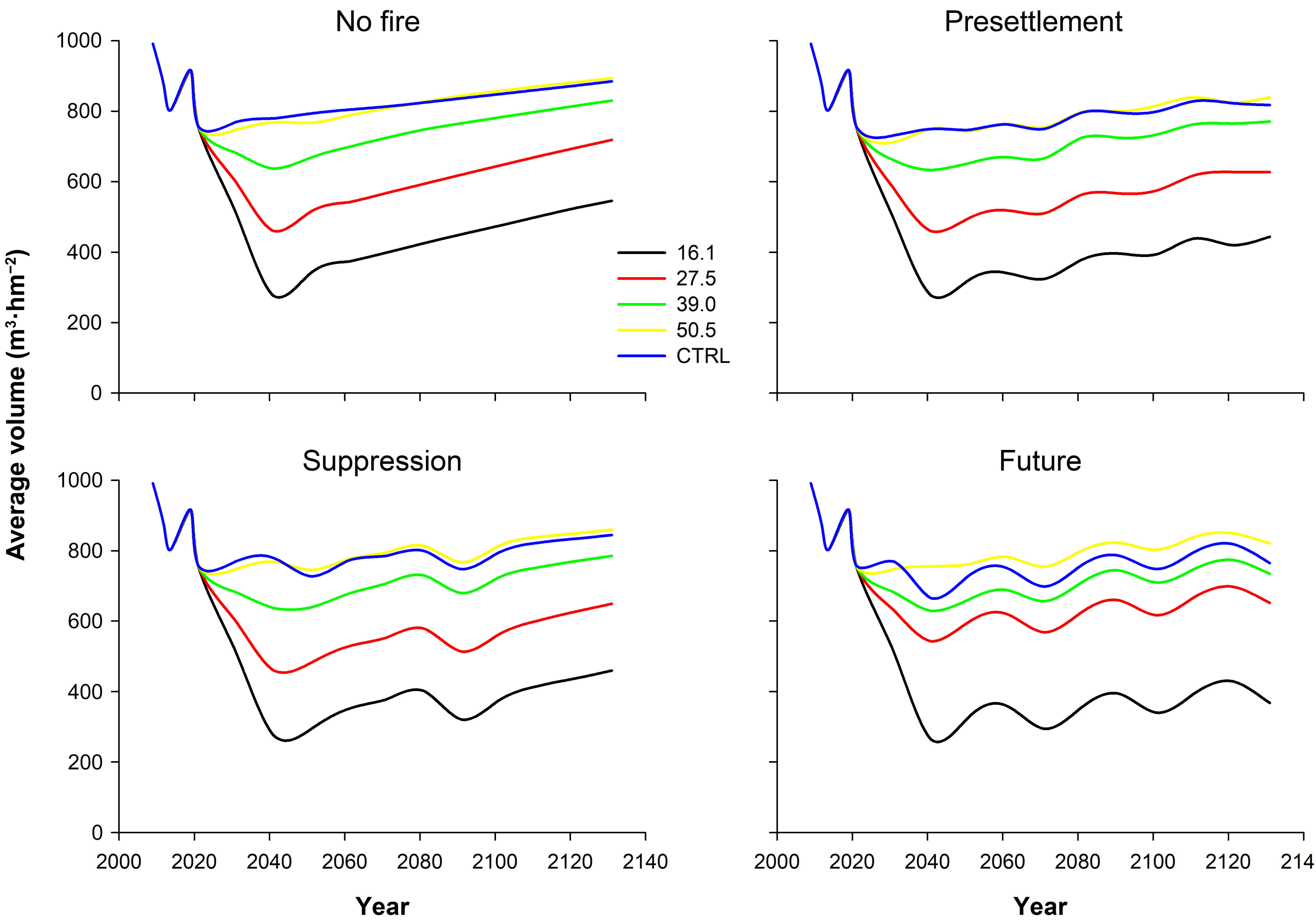

Fig. 6. Average total volume per hectare versus year of simulation for California mixed conifer stands. Each line is the mean volume of 4 stands. Four levels of thinning based on total volume per hectare (in cubic meters per square hectometer) and a control are shown.

stand measurements and 62 Jeffrey pine stand measurements. For California mixed conifer stands, overall post hoc Shannon index scores ranged from 0.49 to 1.99, with a standard deviation of 0.24. For Jeffrey pine stands, they ranged from 0.22 to 1.70, with a standard deviation of 0.32. We used a simple linear regression to analyze the relationship between resilience score and Shannon index. We found that there was a significant negative relationship between resilience score and structural diversity for both forest types ($P < 0.01$). More diverse stands had lower resilience scores. Stands with a resilience score of 5 had the lowest average Shannon index: 1.15 for California mixed conifer and 0.72 for Jeffrey pine (Fig. 9). Stands with a resilience score of 1 had the most diversity, with an average Shannon index of 1.58 for California mixed conifer stands and 1.23 for Jeffrey pine stands. For California mixed conifer, stands with resilience scores of 3 or less had similar Shannon indices (1.51 to 1.58). The negative trend in Shannon index is present among the top 2 resilience scores. For Jeffrey pine, there is a more consistent decline in structural diversity as resilience score increases.

Model validation of FVS simulations

Our graphical prediction analysis revealed that overall the FVS variants performed well in that the predicted values for BA (in square meters per square hectometer) from the Inland California and Southern Cascades and the South Central Oregon and Northeast California variants were similar to the observed values based on FIA plot measurements (Fig. 10, $R^2 = 0.69$).

Discussion

Tree mortality and biomass loss

Tree mortality and biomass loss varies on the basis of several environmental and temporal variables, including year, tree height, and tree elevation. Tree mortality was similar for trees of all heights. This differs from a study by Stovall et al. [43], who found that mortality rates increased as tree height increased. Tall trees lost the most biomass. We found that trees at low elevations had the lowest mortality rates, which is different from other research that has found that trees at lower elevation have greater mortality [39,44]. The small spatial scale and sample size of our study may have influenced our results. Tree mortality was greatest in 2007–2008 based on FIA data but was highest in 2016–2017 based on aerial detection surveys.

The mortality data derived from aerial photos showed very little mortality from fires—almost all the mortality was insects. The flight paths provided with the data also avoided the Chips Fire area after it burned. Therefore, we believe the aerial photography was mainly focused on surveying insect damage, which makes it incomplete for our purposes. Unfortunately, the FIA data are incomplete as well. Only about 9% of the trees

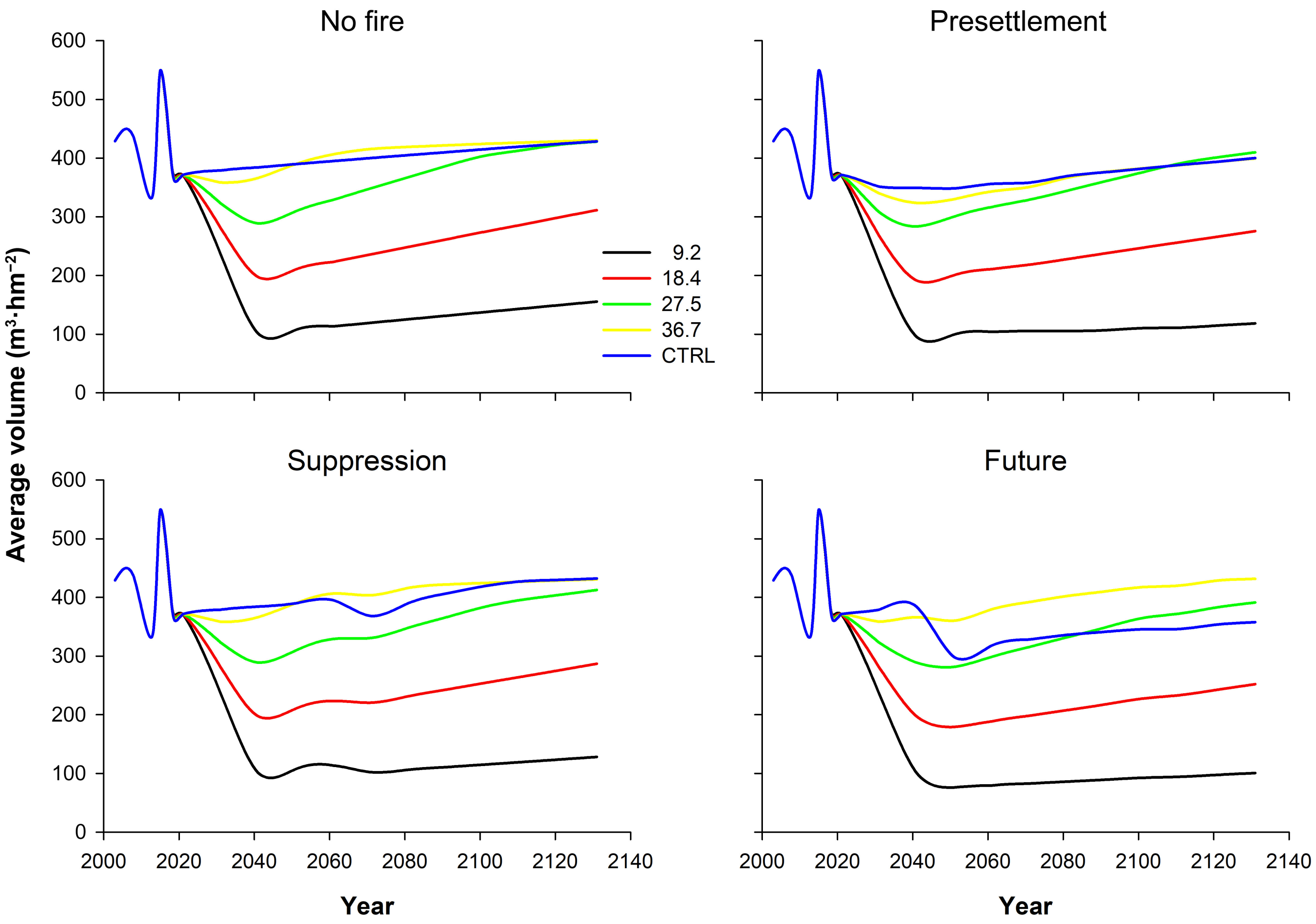

Fig. 7. Average total volume per hectare versus year of simulation for Jeffrey pine stands. Each line is the mean volume of 4 stands. Four levels of thinning based on total volume per hectare (in cubic meters per square hectometer) and a control are shown.

in the data have a date for which year they died. Because the trees are only surveyed once every 10 years, without this information, we cannot know which year the trees actually died. In addition, the first few years and last few years of the data are also likely unreliable—for the first few years, tree year of mortality was less likely to be recorded because there were no previous FIA measurements at those locations. For the most recent years, the plots have not been revisited, so we do not know how many trees died at those plots. Because it does include fire-related deaths, it may be more useful than the aerial photography data for viewing the year-to-year change in tree mortality.

Fires

There were no trends over time in the frequency or size of fires burning in Lassen and Plumas National Forests. There was large year-to-year variation in mortality, signifying disturbances as fires being responsible for large amounts of mortality in some years. However, beyond several large wildfires (e.g., the Storrie and Chips Fires), most forest stands within these 2 national forests experienced only minor surface fires to no burns at all from 1984 to 2017. In the natural fire regime of the area, fires burned at least once every 9 years [22]. Therefore, fire suppression, along with other factors, has had an effect on the number of fires burning within the national forests and has altered the fire regime, as we hypothesized [45].

Forest resilience

From FVS simulations of future conditions, we found total volume decreased after thinning but recovered slowly over time. As we hypothesized, we found that stands that were thinned more tended to be more resilient. Therefore, thinning and tree density affects the growth and health of forest stands, as well as aspects of forest structure. We found that thinning to a BA of 16.1 $m^2 \cdot hm^{-2}$ resulted in the highest average resilience score for California mixed conifer and a BA of 9.2 $m^2 \cdot hm^{-2}$ resulted in the highest resilience score for Jeffrey pine. Thinning to only 39.0 or 50.5 $m^2 \cdot hm^{-2}$ was not effective for California mixed conifer stands, as the average resilience score for those stands was equal or only slightly greater than the control. However, resilience scores for stands that were thinned to 27.5 $m^2 \cdot hm^{-2}$ or less were greater than the control, supporting our hypothesis that thinning and prescribed burning increase resilience in forests. For Jeffrey pine, the pattern was similar. Thinning to 27.5 or 36.7 $m^2 \cdot hm^{-2}$ resulted in worse resilience than in the control, but thinning to 18.4 $m^2 \cdot hm^{-2}$ or less was much better than the control, also supporting our hypothesis. Changing the frequency of fires had little effect on resilience scores.

Stands with greater structural diversity had lower resilience scores. This does not support our hypothesis that forests with more structural diversity would be more resilient. When looking at only the indices for diameter diversity or height diversity,

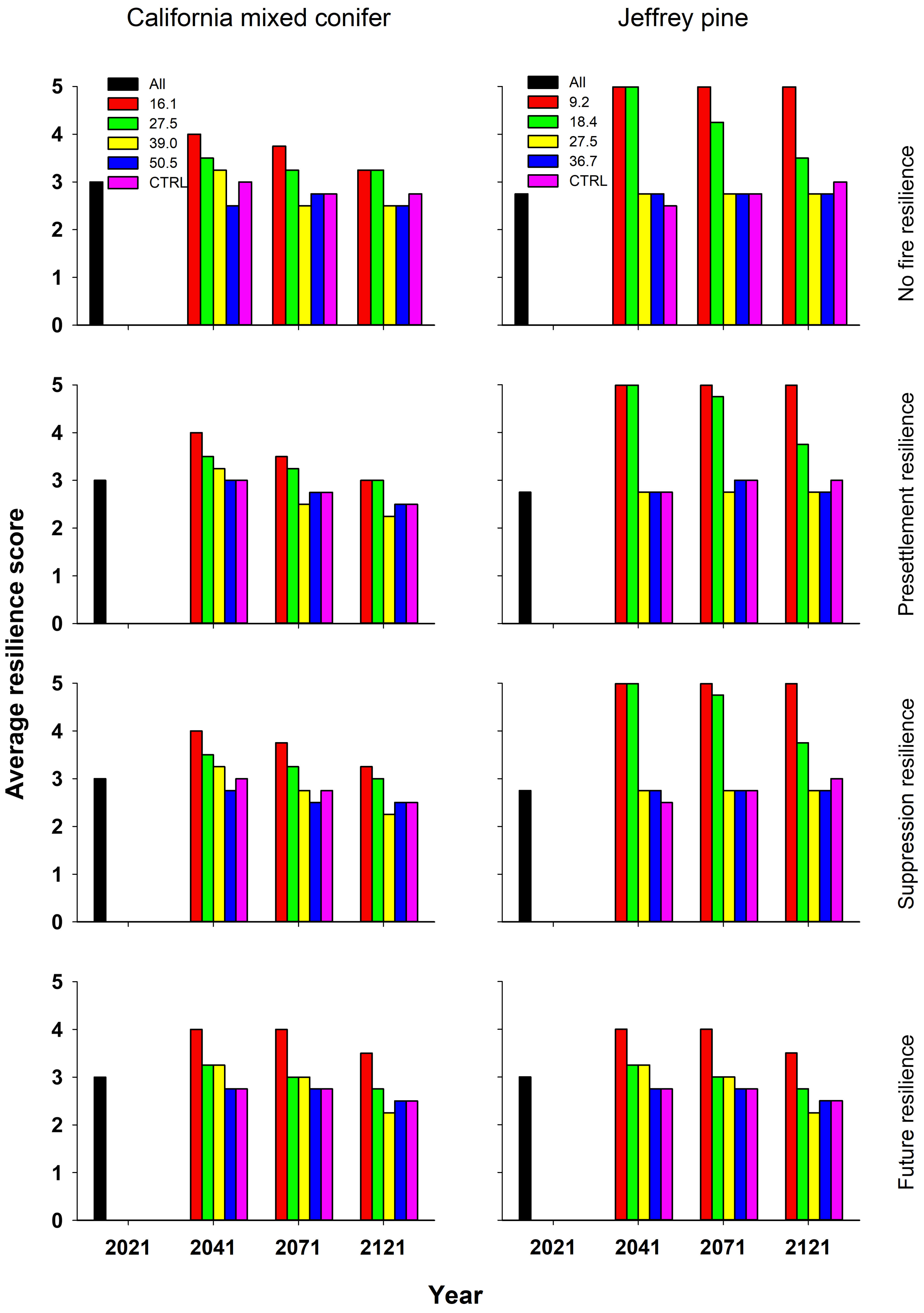

Fig. 8. Average resilience score based on year and level of thinning for the simulations. The graphs on the left show California mixed conifer stands; the graphs on the right show Jeffrey pine stands. The fire regime is shown on the right side of the figure. Stands are thinned from below, and the thinning is measured in square meters of BA per hectare. The ALL level is before thinning occurs, when all runs at each stand are the same. CTRL refers to the control run. All stands are in Lassen or Plumas National Forest.

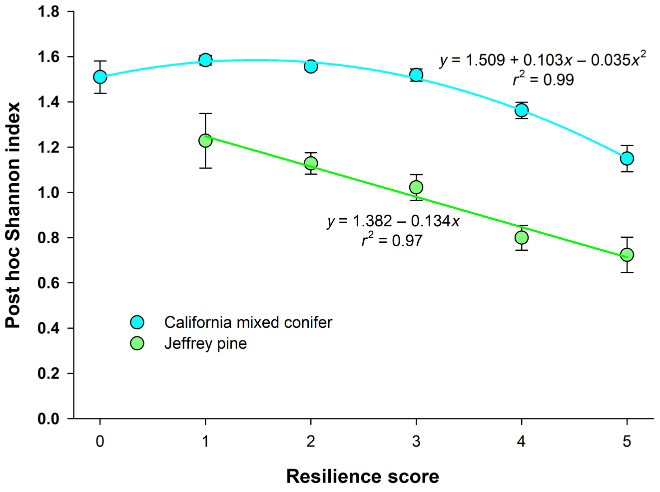

Fig. 9. Average post hoc extended Shannon index of 329 California mixed conifer and 62 Jeffrey pine stand measurements in the Lassen and Plumas National Forests. All stands occurred with the Western Sierra FVS variant. Stands with higher resilience scores had less structural diversity.

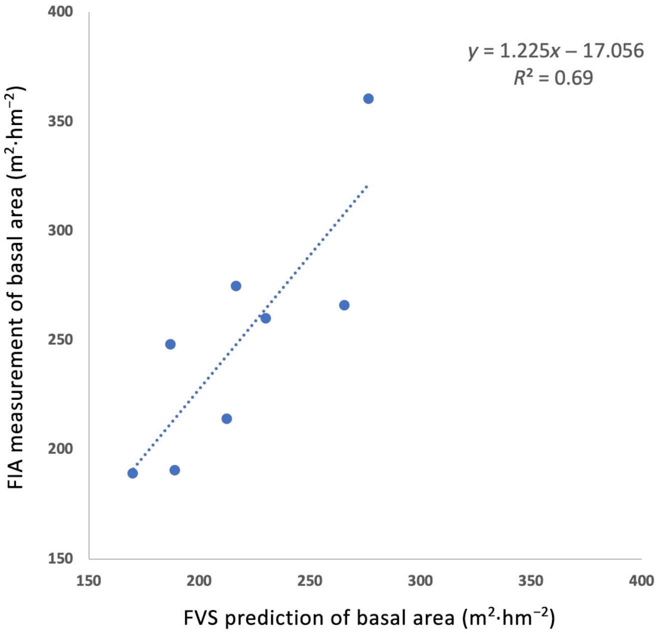

Fig. 10. The graphical prediction analysis showed comparison between FVS predicted vs. FIA observed values. $R^2 = 0.69$.

a significant negative trend still exists ($P < 0.001$). Looking at only the species diversity, no significant trend exists for California mixed conifer ($P = 0.15$) or Jeffrey pine ($P = 0.37$). The resilience score conditions that are met much more frequently by stands with low diversity than stands with high diversity are low BA and low SDI. For California mixed conifer, stands with a resilience score of 5 had an average BA of 12.1 $\text{m}^2{\cdot}\text{hm}^{-2}$, whereas stands with a resilience score of 1 had an average BA of 51.7 $\text{m}^2{\cdot}\text{hm}^{-2}$. For Jeffrey pine, stands with a resilience score of 5 had an average BA of 11.8 $\text{m}^2{\cdot}\text{hm}^{-2}$, whereas stands with a resilience score of 1 had an average BA of 30.1 $\text{m}^2{\cdot}\text{hm}^{-2}$. California mixed conifer stands with a resilience score of 5 had an average SDI of 79, whereas stands with a resilience score of 1 had an average SDI of 361. Jeffrey pine stands with a resilience score of 5 had an average SDI of 77, whereas stands with a resilience score of 1 had an average SDI of 209.

Our finding that stands with greater structural diversity had lower resilience score appears to be relevant to how the resilience score is calculated from the combination of multiple indices. The methodology of Bryant et al. [38] is designed to test for resilience to fire, insects, and droughts and could be used for other natural disturbances. Therefore, having low structural diversity may not be an impediment to resilience to all disturbances. Structural diversity may not be conducive to resilience to these events. However, lowering tree densities does help provide resilience to fire, bark beetles, and droughts [46]. We believe that stands that have fewer trees may not only be less diverse but also be able to score highly on resilience metrics by having low BA density and low SDI. Those results may imply that at stand-level forest, manager should assess the possibility of individual stands demonstrating resilience using multiple routinely measured forest attributes and should consider to manage structural diversity as a long-term management practice.

Model validation and limitations

FVS is the USDA (US Department of Agriculture) Forest Service's nationally supported growth and yield modeling system. Over the past 4 decades, FVS has proven to have a well-designed, modular architecture for simulating forest growth, and FVS has been widely used with the capability of including silvicultural, fire, insect, and disease impacts on forest stands. Each of the geographically based variants, including variants used in this study, has been calibrated to most forest types in the region as part of model building. A qualitative verification evaluation procedure to qualitatively verify model behaviors of the structure and logic of the FVS by comparing the model predictions with well-observed relationships about stand dynamics has been conducted by the USDA Forest Service.

While our model validation indicated overall the FVS variants in the region performed well, some potential limitations of the FVS simulations may exist, for example, FVS was not directly sensitive to environmental changes that influence tree growth. In this study, we did not include future climate projection data and did not include any specific climate change scenarios in the simulations. In addition, only limited forest stands were simulated. In future efforts, it is recommended to use more sample stands for FVS simulations and include both stand-level and landscape forest resilience simulations in the context of a warmer and drier climate in the region [47].

Conclusion

Historical fire suppression, logging, and other land uses have increased densities of shade tolerant trees and fuel buildup in the Lassen and Plumas National Forests of northern California, which has reduced the resilience of these forests to natural disturbances. Our study underscores the importance of thinning and prescribed burning on the resilience of forests to wildfire and drought disturbances. On the basis of FVS modeling effects under varied thinning practices and fuel treatment scenarios on the changes in forest structure and forest resilience following a large wildfire, we conclude that stand thinning and prescribed burning can be effectively used to restore a healthy forest structure and increase the resilience of forests to future wildfires and drought. We found that structural diversity had a negative relationship with resilience score and thinning BA to 16.1 $m^2 \cdot hm^{-2}$ resulted in the highest resilience score for California mixed conifer forest stands while thinning to 9.2 $m^2 \cdot hm^{-2}$ resulted in the highest resilience score for Jeffrey pine stands. Our simulations support an increased level of forest stand thinning and more fuel treatments in the region to increase forest health and resiliency to wildfires and drought. Understanding forest structure, forest resilience, and the factors that make trees vulnerable to mortality will allow managers to better plan stand thinning and fuel treatments for these forests toward sustainable uses.

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Author contributions: J.Z. and W.X. helped in project administration and funding acquisition. J.Z., W.X., and H.S. conceived the ideas and designed the project. J.K.L. obtained and analyzed the data. J.K.L. and W.X. drafted the original manuscript with input from all coauthors. All authors conducted result interpretation, review, and editing.
Competing interests: The authors declare that they have no competing interests.

Data Availability

The data that support the findings of this research are available on request from the corresponding author.

Supplementary Materials

Figs. S1 to S5
Table S1

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