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RESEARCH ARTICLE

Restoring frequent fire to dry conifer forests delays the decline of subalpine forests in the southwest United States under projected climate

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Abstract

1. In southwestern US forests, the combined impact of climate change and increased fuel loads due to more than a century of human-caused fire exclusion is leading to larger and more severe wildfires. Restoring frequent fire to dry conifer forests can mitigate high-severity fire risk, but the effects of these treatments on the vegetation composition and structure under projected climate change remain uncertain.
2. We used a forest landscape model to assess the impact of thinning and prescribed burns in dry conifer forests across an elevation gradient, encompassing low-elevation pinyon-juniper woodlands, mid-elevation ponderosa pine and high-elevation mixed-conifer forests.
3. Our results demonstrated that the treatments decreased the probability of high-severity fires by 42% in the study area. At low elevation, the treatments did not prevent loss in forest cover and biomass with decreases in *Pinus edulis* and *Juniperus monosperma* abundances. At mid-elevation, changes in fire effects maintained a greater diversity of tree species by favouring the maintenance of cohorts of old trees, in particular *Pinus ponderosa* which accumulated 5.41 $Mg\,ha^{-1}$ more above-ground biomass than without treatments by late-century. Treatments in dry conifer forests modified fire effects beyond the treated area, resulting in increased cover and biomass of old *Picea englemannii* and *Abies lasiocarpa* cohorts.
4. *Synthesis and applications*: Our findings indicate that thinning and prescribed burning can enhance tree species diversity in dry conifer forests by protecting old cohorts from stand-replacing fires. Moreover, our results suggest that treatments mainly implemented in dry pine forests with high risk of high-severity fires can be beneficial for subalpine species conservation by reducing the chance that high-severity fire at mid-elevation is transmitted into high-elevation forest.

KEYWORDS
elevation gradient, fire, forest management, modelling, ponderosa pine, prescribed burning, thinning

1 | INTRODUCTION

Global warming is intensifying wildfires in many parts of the world, impacting forest ecosystem structure and function (Running, 2006; Stevens-Rumann et al., 2018). In forests not adapted to high-severity or more frequent wildfire regimes, the provision of ecosystem services including carbon storage, wildlife habitat and water supply can be negatively affected by uncharacteristic wildfire (Jones et al., 2022; Lecina-Diaz et al., 2021; Liang et al., 2017; Seidl et al., 2014; Williams et al., 2022).

In forest types where human caused increases in biomass and tree density because of fire suppression or rural depopulation, climate change can make the system more flammable (Pausas & Fernández-Muñoz, 2012; Senande-Rivera et al., 2022; Singleton et al., 2019). To effectively reduce climate-driven increases in ecosystem flammability, management must be implemented at the scale at which wildfire is shaping the landscape and can result in immediate reductions in high-severity fire risk through changes in forest structure and in the distribution and quantity of fuels (Lydersen et al., 2017; North et al., 2021; Tubbesing et al., 2019). Although the immediate effect of this type of management intervention on fire behaviour has been widely studied, uncertainties persist regarding the effects on long-term forest structure and composition at the landscape scale under projected climate.

In the dry conifer and mixed-conifer forests of the southwestern United States, more than a century of human-caused fire exclusion has altered forest structure and increased fuel loads, leading to larger and more severe wildfires (Miller et al., 2009; Singleton et al., 2019). Simultaneously, increasing aridification is making forests more flammable as dead fuels become increasingly available to burn (Goodwin et al., 2020, 2021; Juang et al., 2022). High-severity fire combined with warmer and drier conditions is already decreasing conifer regeneration in the western United States (Stevens-Rumann et al., 2018) and projections under future climate show limited conifer regeneration following high-severity wildfire in southwestern US forests (Jung et al., 2023; Keyser et al., 2020). A greater increase in high-severity fires occurring at high elevation in mixed-conifer forests compared with lower elevations is also expected, leading to high mortality of the dominant species, Engelmann spruce and subalpine fire, which are not adapted to fire (Cassell et al., 2019; Flatley & Fulé, 2016; Remy et al., 2021).

In dry conifer forests that were historically maintained by frequent fire, current management objectives include restoring historical fire frequency to reduce the risk of high-severity fire. In the southwestern United States, these frequent-fire forests are commonly located at mid-elevation (ca. 2000–3000 m. a.s.l.), that is, ponderosa pine-dominated and white fir and Douglas-fir-dominated areas. Treatments include a combination of mechanically thinning younger trees that can carry surface fire into the crowns of mature trees and fire use, either through prescribed burning or managing lightening ignitions (Agee & Skinner, 2005; Hurteau et al., 2016; Krofcheck et al., 2017). In the short term, fuel reduction treatments can locally enhance vegetation diversity and tree growth by lowering forest density and resource competition (e.g. water, light and nutrients; Boisramé et al., 2017; Zald et al., 2022). However, these treatments could be less effective in preventing forest cover loss and biomass decline under a high emission scenario (RCP 8.5; Loehman et al., 2018; McCauley et al., 2019; O'Donnell et al., 2018; Stoddard et al., 2021). Reducing the risk of high-severity fire in mid-elevation forests may have effects on high-elevation forests, which are dominated by Englemann spruce and subalpine fir, because fires in mid-elevation dry forests can spread to historically less flammable higher elevation forests (O'Connor et al., 2014; Sibold et al., 2006). Assessing how dry conifer forest management affects vegetation composition and structure along the elevation gradient of the southwestern US forests is essential to addressing future challenges posed by increasing forest flammability.

Here, we used a forest landscape model to investigate how restoring frequent fire to dry conifer forests might influence vegetation structure and composition along an elevation gradient of southwestern US forests under projected climate. We hypothesized that thinning followed by burning treatments (1) would decrease the probability of high-severity fires along the elevation gradient relative to no management, (2) would delay the decline of subalpine species to high-severity wildfire relative to no management, but (3) would not prevent loss of forest cover and biomass decline by the end of the 21st century. Furthermore, we hypothesized that these outcomes would be more likely if management were applied across a larger proportion of dry conifer forests.

2 | MATERIALS AND METHODS

2.1 | Study area description

Our study area comprised approximately 1.5×10^6 ha of forested land in the upper Rio Grande watershed in New Mexico and Colorado, USA (Figure 1). The climate is primarily continental, with cold, wet winters and warm summers; approximately 50% of the annual precipitation occurs from summer monsoonal storms. Mean annual temperature is 10°C between 1900 and 2200 m a.s.l. and 6.4°C at 3000 m a.s.l. (National Weather Service data available online at http://w2.weather.gov/climate). Mean annual precipitation varies from a low of 380 mm between 1900 and 2200 m a.s.l. to 650 mm at 3000 m a.s.l. The majority of soils are classified as clay loams with lesser areas of loam, sandy clay and silty clay (Miller & White, 1998).

Forest type varies by elevation; low-elevation woodlands and forests are more moisture limited while higher elevation forests are more temperature limited (see Figure S1 in Supporting Information). The low-elevation area (460,107 ha) is primarily dominated by pinyon-juniper woodlands (*Pinus edulis* Engelm. and *Juniperus monosperma* (Engelm.) Sarg.), two species susceptible to fire, with *Juniperus scopulorum* (Sarg.) and *Quercus gambelii* (Nutt.). The mid-elevation forests (725,364 ha) are dominated by a mix of fire-adapted species including *Pinus ponderosa* (C. Lawson), *Pseudotsuga menziesii* ((Mirb.) Franco) and *Abies concolor* ((Gordon) Lindley ex

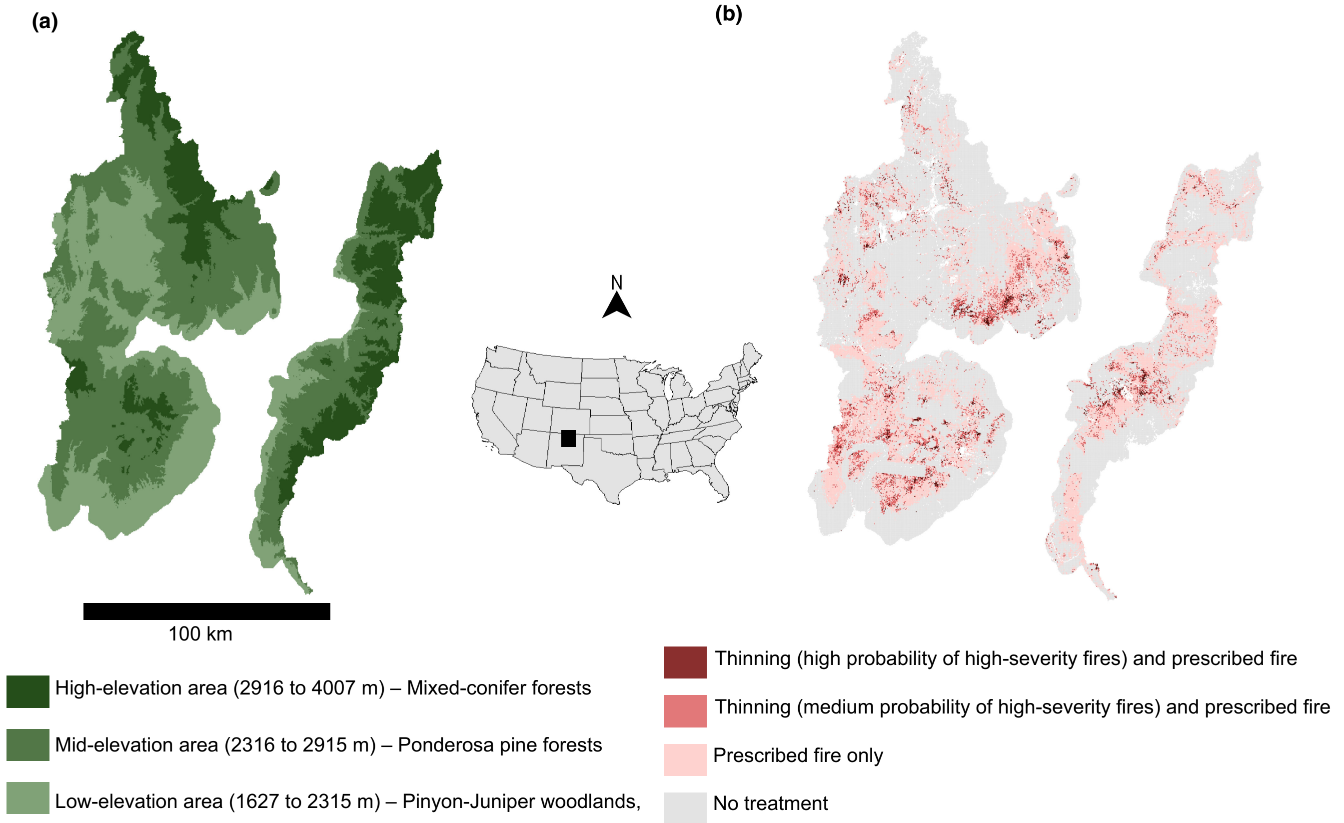


FIGURE 1 Study area with (a) dominant vegetation types by elevation bands and (b) areas with simulated treatments.

Hidebrand), with scattered junipers, *Q. gambelii* and *Populus tremuloides* (Michx.), an early-successional species. The high-elevation forests (316,962 ha) primarily consist of *Picea engelmannii* (Parry ex Englem.) and *Abies lasiocarpa* ((Hooker) Nuttall), two species highly vulnerable to fire, with the scattered presence of *P. menziesii*, *A. concolor* and *Q. gambelii*. The mean fire return intervals generally are <50 years in pinyon-juniper woodlands at low elevation, about 5–35 years in dry ponderosa pine and mixed-conifer forests at mid-elevation, and >100 years in spruce-fir forests at high-elevation (Wahlberg et al., 2013).

2.2 | Simulation model description

We used the LANDIS-II (v6.2, Scheller et al., 2007) forest landscape model with the PnET succession extension (v2.1, de Bruijn et al., 2014) to model vegetation development and dynamics at a 9-ha spatial resolution and annual time step. LANDIS-II simulates the dispersal, establishment, growth and mortality of forest species using species-specific age cohorts. The PnET succession extension includes elements of the PnET-II ecophysiology model (Aber et al., 1995), adding increased physiological control of tree growth, mortality and establishment, with competition for light and water affecting the growth and survival of individual cohorts. At each time step, a modified instance of PnET-II is run for each species cohort. Gross photosynthesis in the PnET succession extension can be reduced by multiple factors: water stress, radiation limits (e.g. lower canopy layers), vapour pressure deficit, temperature and age. Individual cohorts compete for available light and water to drive photosynthesis and carbon accumulation (de Bruijn et al., 2014). The PnET succession extension also calculates establishment probability at each time step based on water and light availability.

We used the Dynamic Fuels and Fire System extension (v2.1) to simulate landscape wildfire and fuel interactions (Sturtevant et al., 2009). At each time step, current species and stand age composition determine the assigned fuel type for each grid cell. Wildfire is simulated stochastically, drawing from fire size and fire weather distributions to simulate fire as influenced by the fuel type and topography. Fire severity is determined by the effects of fire on the individual cohorts. At each annual time step, each grid cell burned in a fire is assigned a severity class defined by the proportion of cohorts killed by the fire event. Severity classes range from low to high, with low-to-medium severity equivalent to surface fire with little or no cohort mortality and some overstorey tree torching that causes mortality. The high-severity class indicates crown fire activity that results in extensive cohort mortality.

2.3 | Climate data

LANDIS-II and the PnET succession extension require monthly climate data for maximum and minimum temperature, precipitation, incoming shortwave radiation and atmospheric CO_2 concentration. We used gridded downscaled climate simulations for 1950–2099 from four global climate models (Representative Concentration Pathway (RCP) 8.5) via the Coupled Model Intercomparison Project Phase 5 multi-model ensemble (CMIP5). See Supporting Information Text S1 for more details on the baseline and climate change scenarios.

2.4 | LANDIS-II parameterization and validation

LANDIS-II initial communities are defined by unique species-age cohorts and represent the vegetation condition at the start of the simulation. We used a gradient nearest neighbour approach to map existing vegetation using data from 836 unique Forest Inventory and Analysis (FIA) vegetation plots, topographic indices and recent Landsat 8 imagery following the method described by Remy et al. (2021). We used a random forest classification to produce the initial communities map with a 9-ha grid. We selected FIA plots that had been sampled since 2005, selecting the most recent measure year if multiple existed. We used species and region-specific allometric equations to assign ages to individual tree records and grouped them into 10-year cohorts to train the random forest algorithm.

The Dynamic Fuels and Fire System extension requires unique fire regions as an input, each with representative fire regimes (i.e. fire size distributions and weather that initiate fire ignition). Following the methods described in Krofcheck et al. (2017), we stratified the study area into three fire regions that correspond to the low-elevation woodlands, mid-elevation ponderosa pine forests and high-elevation mixed-conifer forests (Figure 1). These elevation bands correspond to the elevation distribution of major vegetation types on this landscape (Table S1).

Our model has been previously calibrated and validated against eddy covariance tower records and tree inventories in the three major vegetation types by comparing monthly net photosynthesis and total above-ground biomass (Remy et al., 2019). See Supporting Information Text S2 and Text S3 for more information on vegetation and fire parametrization and validation.

2.5 | Management treatment and scenario development

We developed two management treatments for the Biomass Harvest extension (Gustafson et al., 2000) to approximate common

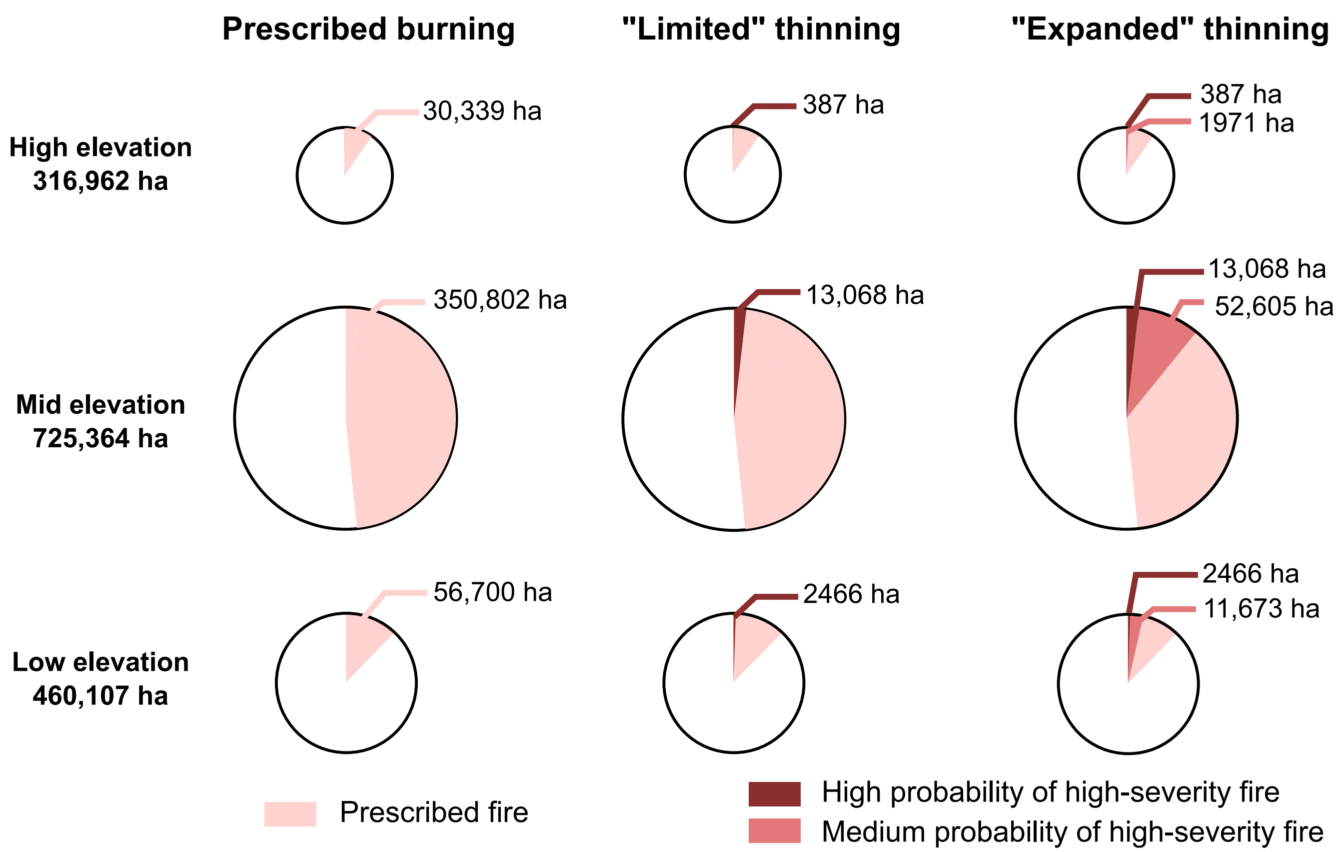


FIGURE 2 Area treated with prescribed burning and thinning along the elevation gradient for both treatment scenarios in hectares. The circles are scaled based on the total forest area in each elevation band. Prescribed burning (light pink) was simulated to reproduce the historical fire return intervals in stands dominated by ponderosa pine, Douglas-fir and white fir within each elevation band. The 'Limited' thinning scenario included thinning and burning locations with a high probability of high-severity fire (red), the 'Expanded' scenario included thinning and burning locations with high (red) and medium (salmon) probabilities of high-severity fire.

thinning and prescribed burning treatments implemented in the region (Figure 1; Table S2). These treatments targeted forest types with a historical high burn frequency, that is, ponderosa pine-dominated and white fir and Douglas-fir-dominated areas. In the 'Limited' scenario, thinning was limited to locations where more than 70% of the fire occurrences in the no-management scenario burned at high severity. In the 'Expanded' scenario, thinning was expanded to both the high-probability areas and locations where more than 50% of the fire occurrences in the no-management scenario burned at high severity. We used a procedure similar to Krofcheck et al. (2018) to calculate the probability of high-severity fire (i.e. the ratio of the number of fires within the high-severity class to the total number of fires for the 100-year simulation period) and determine the treatment priority (Figure S2). We implemented thinning treatments on 5% to 10% of the targeted areas per year until all areas identified for treatment were completed (Hurteau et al., 2016). Thinning treatments included preferential harvest of the youngest cohorts to reduce forest density, canopy continuity and increase height to live crown, which are common objectives for reducing high-severity wildfire risk (North et al., 2021). Areas with slope >30% were excluded from thinning due to operational constraints for thinning equipment. In both scenarios, the area treated by prescribed fire was the same as it was not constrained by the probability of high-severity fire. Prescribed fires were simulated such that initial-entry burns were implemented in the year following mechanical treatments and were simulated using a fire return interval consistent with the historical data, ranging from 10 to 33 years depending on whether the forest types were ponderosa pine or higher elevation stands co-dominated by ponderosa pine or Douglas-fir and white fir (Margolis & Balmat, 2009; Swetnam & Baisan, 1996). The resulting treatment areas and rates for mechanical thinning and prescribed burning are described in Figure 2 and in detail in Table S2.

2.6 | Simulations and analyses

To assess the impact of management treatments on fire regime and vegetation dynamics, we conducted simulations under projected climate conditions both with and without management interventions ('Limited' and 'Expanded' scenarios). For each of the four climate projections, we ran 10 replicates of 100-year simulations, aggregating the results for analysis. Data processing, statistical analysis and figure generation were performed using R-3.6.2.

We evaluated changes in projected fire severity resulting from treatments by comparing the probability of high-severity fires with and without management. The impact of treatments on above-ground biomass was assessed by comparing the results with the no-management scenario for each elevation band. Changes in above-ground biomass for various species were quantified by comparing mean above-ground biomass at the end of simulations (i.e. 2099) between scenarios (no management vs. with management) for each elevation band. The effect of treatments on vegetation composition and structure was quantified by comparing tree species richness (i.e. number of tree species), cohort age, and species abundance between scenarios with and without treatment for each elevation band. We categorized changes in tree species richness and abundances at the pixel level in terms of presence vs absence, assigning '−1' for species loss, '0' for no change, and '+1' for species gain. We then computed the percentage of areas with gains or losses by summing these scores for each species across the 10 replicates for each climate scenario at the end of the simulations (i.e. 2099).

Ethical approval, licences and permits were not required to conduct this study because it did not involve fieldwork or animals.

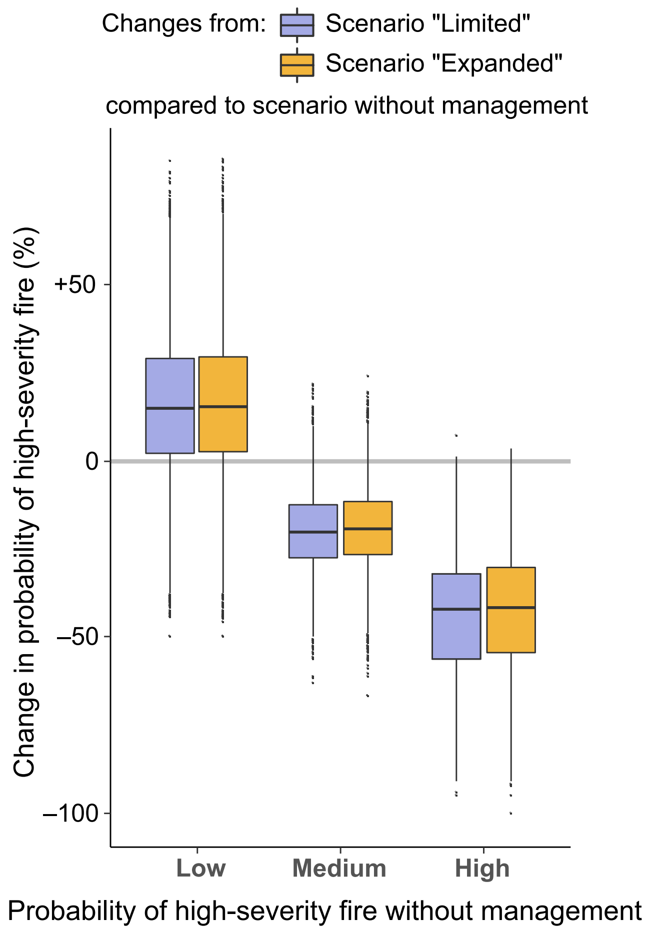


FIGURE 3 Changes in the probability of high-severity fire with limited and expanded management relative to no management for the period 2000–2099. The per cent change in probability relative to no-management is binned based on the probability of high-severity fire in the no-management scenario where the probability of high-severity fire was low (i.e. less than 50% of the total fire occurrences), medium (i.e. between 50% and 70% of the total fire occurrences) and high (i.e. more than 70% of the total fire occurrences). Values were calculated using annual fire occurrence and averaged from the 40 replicates.

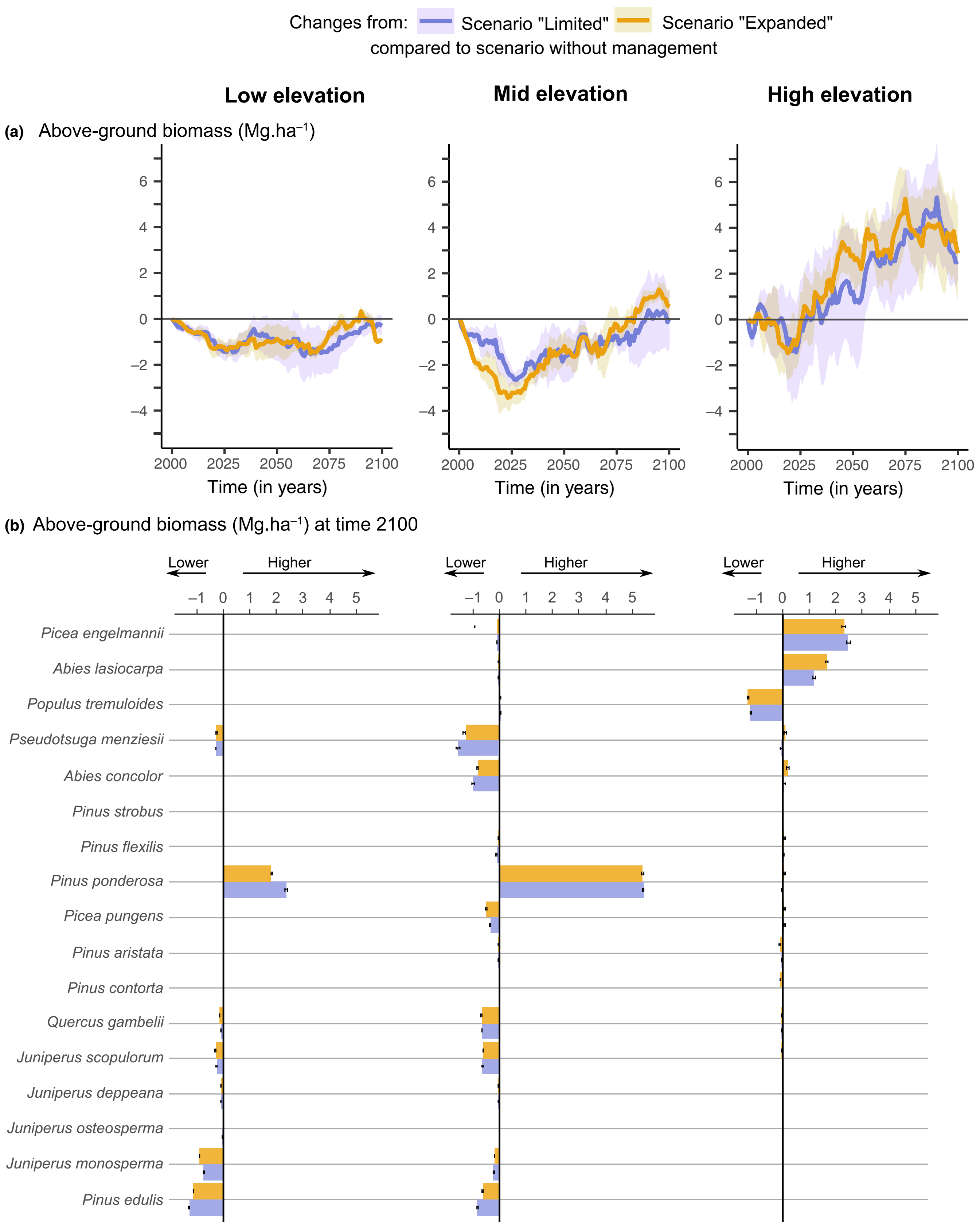


FIGURE 4 Changes in projected total above-ground biomass through time (a) and in species above-ground biomass at the end of the 21st century (b) from scenarios with management 'Limited' and 'Expanded' compared with the scenario without management. Values were calculated using the 40 replicates.

3 | RESULTS

3.1 | Fire severity

We found a decrease in the probability of high-severity fire in response to both management scenarios in areas with medium (down 13%–14%) and high (down 42%) probability of high-severity fire prior to treatment (Figure 3). Interestingly, 10% of areas that had a low probability of high-severity fire in the no-management scenario had an increased probability of high-severity fire with management. Overall, the changes in the probability of high-severity fire were consistent across all vegetation types (Figure S3).

3.2 | Biomass changes

Relative to the no-management scenario, areas that were treated had immediate reductions in above-ground biomass, which resulted in landscape averaged above-ground biomass to drop below the no-management scenario (Figure 4a). Since the majority of treatment occurred in mid-elevation forests, the landscape averaged reduction was greater than at low elevation where less area was treated. At high elevation, most of which was untreated, above-ground biomass increased relative to the no-management scenario, with a maximum of +5.3 Mg ha^{-1} per year equivalent to ca. 1.7 million Mg per year at the elevation band scale (316,962 ha) by the end of the century and +3.2% of total biomass. Increasing *Pinus ponderosa* above-ground biomass was responsible for biomass recovery following management (Figure S4), with increases of 2.37 to 5.41 Mg ha^{-1} (equivalent to +0.9 to 2% of total biomass) for the 'Limited' scenario and 1.81 to 5.41 Mg ha^{-1} (equivalent to +0.7 to 2% of total biomass) for the 'Expanded' scenario at low- and mid-elevation by the end of the century (Figure 4b). At high elevation, the increase was caused by a greater accumulation of *Picea engelmannii* ('Limited' 2.48 Mg ha^{-1}; 'Expanded' 2.30 Mg ha^{-1}) and *Abies lasiocarpa*, ('Limited' 1.20 Mg ha^{-1}; 'Expanded' 1.65 Mg ha^{-1}) (Figure 4b and Figure S4).

3.3 | Vegetation dynamics

Treatments impacted the composition and mean cohort age of the vegetation (Figure 5) when compared to the no-management scenario. At low elevation, they caused a slight decrease in tree species richness ('Limited': −1 ± 1%; 'Expanded': −1 ± 1%, Figure 5a) and mean cohort age ('Limited' −3.14 ± 0.96 years; 'Expanded' −2.93 ± 1.47 years, Figure 5b) by late-century. Decreases in abundance occurred for *Pinus edulis* ('Limited' −8.403 ± 5.186 ha; 'Expanded' −8.253 ± 2.802) and *Juniperus monosperma* ('Limited' −7.094 ± 4.459 ha; 'Expanded' −7.713 ± 2.007) and, to a lesser extent, in *Juniperus scopulorum* and *Pinus ponderosa* cohorts (Figure 5c).

Over the simulation period, tree species richness in mid-elevation forests, where the majority of treated area was located, had the largest increase with +3 ± 1% for the 'Limited' scenario, and +2.5 ± 1% for the 'Expanded' scenario at the end of the century (Figure 5a). However, the mean late-century cohort age (i.e. 2090–2099) did not change relative to mean cohort age at the beginning of the simulation ('Limited' +0.70 ± 1.00 years; 'Expanded' −0.48 ± 1.82 years; Figure 5b) because of a large increase in *Populus tremuloides* cover (ca. 40,000 ha; Figure 5c).

In high-elevation forests, the simulated treatments tended to increase tree species richness in both the 'Limited' and 'Expanded' scenarios (Figure 5a). *Picea engelmannii* and *Abies lasiocarpa* abundances increased while *Populus tremuloides* abundance decreased (Figure 5c) and cohorts were older on average ('Limited': 3.18 ± 2.67 years; 'Expanded': 2.54 ± 2.64 years) by late century (Figure 5b).

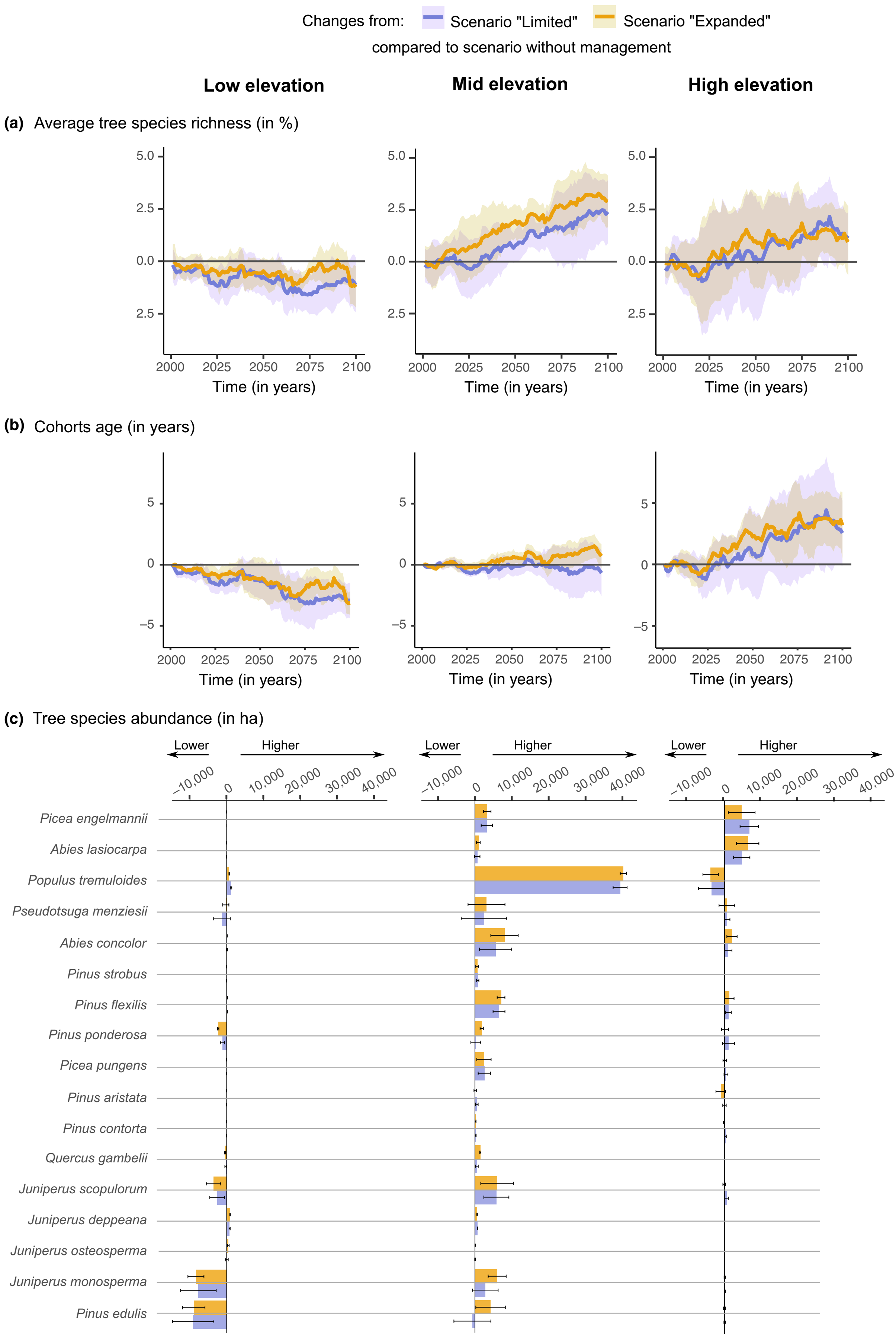
4 | DISCUSSION

Changing climate is affecting tree growth and mortality rates and, when combined with wildfire, can cause rapid shifts in vegetation type (Remy et al., 2021; Stevens-Rumann et al., 2018). While management treatments, including combinations of thinning and burning, can alter resource competition and may increase forest resilience to changing climate, it is not clear if the aridification of the southwest will allow for the same amount of treatment efficacy as has been found in other forest types (Cassell et al., 2019; Liang et al., 2018). Similar to other studies, treatments decreased the probability of high-severity fires in areas initially at high risk of high-severity fire under future climate conditions, but the structural and compositional response of the forests differed along the elevation gradient (Krofcheck et al., 2017; Liang et al., 2018; Loehman et al., 2018; McCauley et al., 2019). While we hypothesized that treatments would decrease the amount of forest cover and biomass relative to no management, unexpectedly we found that management increased biomass at high elevation by maintaining *Picea engelmanii* and *Abies lasiocarpa* cohorts, demonstrating a connection with management in mid-elevation forests.

4.1 | Impacts of management strategies on fire severity

In line with other simulations (McCauley et al., 2019; Tubbesing et al., 2019) and empirical observations (Fernandes, 2015; Lydersen

FIGURE 5 Changes in tree species richness (a), total cohort ages (b) and tree species abundance (c) for the 'Limited' and 'Expanded' management scenarios compared with no management. Species richness and total cohort ages were averaged by elevation band through time and changes in tree species abundances were based on the presence and absence of species at the end of the 21st century. Values were calculated using the 40 replicates.


Changes from: Scenario "Limited" Scenario "Expanded"
compared to scenario without management
Low elevation
Mid elevation
High elevation
(a) Average tree species richness (in %)
Time (in years)
(b) Cohorts age (in years)
Time (in years)
(c) Tree species abundance (in ha)
Lower
Higher
Picea engelmannii
Abies lasiocarpa
Populus tremuloides
Pseudotsuga menziesii
Abies concolor
Pinus strobus
Pinus flexilis
Pinus ponderosa
Picea pungens
Pinus aristata
Pinus contorta
Quercus gambelii
Juniperus scopulorum
Juniperus deppeana
Juniperus osteosperma
Juniperus monosperma
Pinus edulis

et al., 2017; Prichard et al., 2010), our results show that forest thinning followed by prescribed burning in areas with a high probability of high-severity fire can significantly reduce this risk, but that additional thinning in medium probability areas did not decrease risk further (Figure 3). Our finding that the probability of high-severity fire increased by 10% in areas that had a low probability in the no-management scenario was somewhat unexpected. This result is more likely an artefact of the model than a projected outcome. The rate of spread in the fire and fuels extension is determined based on conditions at the location of the ignition and is held constant throughout the burn period, that is, throughout the fire footprint (Sturtevant et al., 2009). If the fire starts in a treated area, a higher rate of spread is modelled throughout the fire footprint because thinning changes the fuel type to a more flammable class due to the dominance of old cohorts. While in an actual fire the rate of spread varies temporally and spatially as a function of weather, fuels and topography, surface wind speed can accelerate following thinning and cause torching in nearby denser stands (Banerjee, 2020).

4.2 | Impacts of management strategies on vegetation dynamics

Our hypothesis that treatments would delay the decline of subalpine species, the most threatened by projected climate and wildfires (Remy et al., 2021), was supported by our results because above-ground biomass and abundances of *Picea engelmanii* and *Abies lasiocarpa* increased after the period of thinning (i.e. after 2020; Figure 4). By decreasing the occurrences of high-severity fire, mid-elevation treatments favoured the maintenance of subalpine species populations, which became older and minimized their replacement by *Populus tremuloides*, an early-successional species (Figure 5; Campbell & Shinneman, 2017). This aligns with prior research suggesting that the combination of thinning and prescribed fire may reduce the occurrence of high-severity fires that spread from mid-elevation dry pine forests to historically less flammable high-elevation mixed-conifer forests (O'Donnell et al., 2018).

At mid-elevation, treatments may protect old cohorts of *Pinus ponderosa* (i.e. youngest cohorts were preferentially thinned) from stand-replacing fires, as shown by the increase in its above-ground biomass, which is not accompanied by an increase in its abundance in the landscape (Figures 4 and 5). The higher frequency of burning and resulting decrease in high-severity fire increased the area occupied by *Abies concolor*, *Pinus flexilis*, *Juniperus* sp. and *Picea engelmanii*, causing an increase in species richness (Figure 5). Fewer stand-replacing fires increased recruitment probability by increasing seed supply (Davis et al., 2023). The treatments also favoured the regeneration of *Populus tremuloides* that can benefit from less resource competition in treated areas (Krasnow et al., 2012). Greater tree diversity and the maintenance of old cohorts were higher in the 'Expanded' relative to the 'Limited' scenario, which resulted from the additional thinning rearranging the spatial occurrence of high-severity fires on the landscape (Figure 5).

At lower elevations, pinyon-juniper woodland did not show the same beneficial response as the spruce-fir forest did at higher elevations. The spatial extent and above-ground biomass decreased relative to no management for both *Pinus edulis* and *Juniperus monosperma* (Figures 4 and 5). This result could be partially due to the competition and canopy closure where *Pinus ponderosa* was protected from stand-replacing fires by treatments, mostly in the ecotonal transition between woodlands dominated by *Pinus edulis* and *Juniperus monosperma* and the dry pine forests (Minott & Kolb, 2020). Most of the pinyon-juniper woodland was not treated because their probability of high-severity fires was low (Tables S1 and S2). Moreover, our results show that the probability of high-severity fire increased where it was low without management (Figure 3). The decrease in *Pinus edulis* and *Juniperus monosperma* would therefore also be due to the increase in stand-replacing fires.

Several sources of uncertainty may have influenced our results. Firstly, the spatial resolution of the climate data used (~6-km grid) does not capture fine-scale variability in a complex topography, potentially masking temperature and precipitation changes in steep elevation gradients and during the summer monsoon (Franklin et al., 2013; Petrie et al., 2014). The spatial resolution of the simulations (9-ha grid) also limits the consideration of intra- and inter-specific interactions dependent on the abundance and age of species, as well as soil types. Despite our efforts to stratify by elevation bands, some species movement lags may persist. Secondly, we did not account for insect outbreaks and browse pressure, which interact with extreme drought events to cause widespread mortality (Anderegg et al., 2015; Kane et al., 2017). Furthermore, the simulated number of ignitions and fire size distribution are constrained by empirical data (2000–2019), likely underestimating area burned associated with future climate conditions (Westerling, 2016). These limitations could have led to optimistic results, with the possibility of more significant ecosystem changes under future conditions. However, our simulations were unable to consider adaptative strategies adjusted through time to reintroduce fire in response to changing fire regimes, with the goal of developing fire-adapted communities which could be less vulnerable to wildfire under future conditions (Schoennagel et al., 2017). Lastly, our treatment scenarios used accelerated rates of implementation, 1592 ha/year of thinning for the 'Limited' scenario and 16,434 ha/year for the 'Expanded' scenario for the first 20 years of the simulations and 34,109 ha/year of prescribed burning over the century. Current rates of treatment are below these rates (North et al., 2012), but treatment rates are increasing with recent US government investment in hazardous fuels reduction in the Bipartisan Infrastructure Law of 2021.

Our findings indicate that thinning and burning treatments implemented in areas with a high risk of high-severity fire under projected climate can prevent the loss of forest cover and biomass decline that occur by late-century in a no-management scenario in mid- and high-elevation forests. Reducing high-severity fire also helped maintain older cohorts of tree species, which could have benefits for old-forest obligate wildlife species. Treatments, primarily implemented in dry pine forests, can reduce the transmission of high-severity fire into higher elevation forests and extending treatments to forest stands at lower risk of high-severity fire can be beneficial for the maintenance of species vulnerable to fire on a local scale but does not have a significant impact on a regional scale. Overall, restoring frequent fire to dry conifer forests in this southwestern US landscape has the potential to reduce forest cover loss and tree species range contraction at mid- and high elevations under projected climate.

AUTHOR CONTRIBUTIONS

Cécile C. Remy and Matthew D. Hurteau conceptualized the study. Dan J. Krofcheck processed and parametrized fire data and the related model extensions. Alisa R. Keyser curated climate data and performed the initialization of the vegetation, soils and ecoregions. Cécile C. Remy curated all other data, conducted the analysis, visualized the results and wrote the first draft of the manuscript. All authors commented, edited and approved the manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest associated with this study. Cécile Remy is an Associate Editor of the *Journal of Applied Ecology*, but took no part in the peer review and decision-making processes for this paper.

DATA AVAILABILITY STATEMENT

Data are available from Zenodo: https://doi.org/10.5281/zenodo.10805139 (Remy et al., 2024).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Text S1. Climate data.

Text S2. Vegetation parametrization and validation.

Text S3. Fire parametrization.

Table S1. Species coverage in percentage of each elevation bands.

Table S2. Management treatments simulated in each vegetation type.

Figure S1. Averages annual temperature (°C) and precipitation (mm) in each elevation area during the 21st century under RCP 8.5.

Figure S2. Maps of all fire occurrences (A), occurrences of high-severity fires (B) and probability of high-severity fires (C) in the study area for the period 2000–2050 from the no-management scenario.

Figure S3. Changes in probability of high-severity fire with management (combined "Limited" and "Expanded" scenarios) for the period 2000–2099 in areas where the probability of high-severity fire was low, medium, and high without management by vegetation type.

Figure S4. Changes in projected species aboveground biomass through time from the scenarios with management compared to those with no management for each species. Values were calculated on average from the 40 replicates.

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