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Citation Details

Ecosphere

Widespread severe wildfires under climate change lead to increased forest homogeneity in dry mixed-conifer forests

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Abstract. Climate warming in the western United States is causing changes to the wildfire regime in mixed-conifer forests. Rising temperatures, longer fire seasons, increased drought, as well as fire suppression and changes in land use, have led to greater and more severe wildfire activity, all contributing to altered forest composition over the past century. To understand future interactions among climate, wildfire, and vegetation in a fire-prone landscape in the southern Blue Mountains of central Oregon, we used a spatially explicit forest landscape model, LANDIS-II, to simulate forest and fire dynamics under current management practices and two projected climate scenarios. The results suggest that wildfires will become more frequent, more extensive, and more severe under projected climate than contemporary climate. Furthermore, projected climate change generated a 20% increase in the number of extreme fire years (years with at least 40,000 ha burned). This caused large shifts in tree species composition, characterized by a decline in the sub-alpine species (*Abies lasiocarpa, Picea engelmannii, Pinus albicaulis)* and increases in lower-elevation species (*Pinus ponderosa, Abies grandis*), resulting in forest homogenization across the elevational gradient. This modeling study suggests that climate-driven increases in fire activity and severity will make high-elevation species vulnerable to decline and will reduce landscape heterogeneity. These results underscore the need for forest managers to actively consider climate change, altered fire regimes, and projected declines in sub-alpine species in their long-term management plans.

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Introduction

Climate change, land use, and land management policy have altered the way fire interacts with forests in the western United States. Ongoing warming has increased the frequency and size of wildfires (Westerling 2016, Keyser and Westerling 2019). In addition to lengthening the fire season, higher temperatures are responsible for extensive fuel drying, making western ecosystems more flammable during the fire season (Abatzoglou and Williams 2016). In dry forest types of the west, land use and fire suppression policy have altered forest structure and fuel loads, facilitating the spread of surface fires into the canopy (Hagmann et al. 2014).

Additional climate warming will likely lead to increasing occurrence and size of wildfires in western U.S. forests where adequate fuels exist (Abatzoglou and Williams 2016), but there is uncertainty around how climate-driven changes in forest dynamics and wildfire activity will affect future forest–wildfire relationships within individual landscapes.

The effects of climate on forest dynamics and wildfire have the potential to cause large shifts in tree species distribution (Coops et al. 2005, Liang et al. 2017, Mathys et al. 2017). Average temperatures in the northwestern United States have risen by about 1°C in the last century with expected additional increases of 1.8–5.4°C by late century (Mote et al. 2014). Projected changes in precipitation are variable, but climate models consistently project reduced summer precipitation in the Pacific Northwest and a greater proportion of winter precipitation falling as rain instead of snow, leading to lower snowpack, earlier snowmelt, and reduced summer streamflow (Hamlet et al. 2007, Mote and Salathé 2010, Mote et al. 2014). These climatic factors influence individual tree species growth, regeneration, competition, and mortality (Halofsky et al. 2013), which influences the fuel–fire feedbacks on long-term forest successional patterns (Hessburg et al. 2005).

Millions of hectares in the west were once covered by fire-adapted dry forests that experienced low-severity, frequent (<35-yr return intervals) fire regimes (Franklin and Johnson 2012). Because of fire suppression and land use (e.g., forest and meadow conversion for cattle grazing and agriculture, commercial timber harvest), many dry forests have shifted from large-diameter, widely spaced trees (interspersed with smaller groups of dense, small-diameter trees) to predominantly high-density forests composed of small-diameter trees (Franklin and Johnson 2012, Churchill et al. 2013, Merschel et al. 2014, Johnston et al. 2018). This has increased the continuity of horizontal and vertical fuels thereby causing higher overstory mortality when wildfires do occur (Agee 1998, Agee and Skinner 2005). Fire suppression has also altered forest composition by facilitating the establishment of fire-intolerant tree species such as grand fir (*Abies grandis*; Larson and Churchill 2012, Merschel et al. 2014, Johnston et al. 2018).

Forest managers often focus on improving forest resilience by increasing structural and compositional heterogeneity. This is done by managing for older/larger trees, reducing stand densities, favoring tree species that are fire- and drought-tolerant, and creating a patchy mosaic of forest stands across the landscape (Agee and Skinner 2005, Franklin and Johnson 2012, Churchill et al. 2013). Yet, ongoing climate change adds uncertainty to management decision making, which, if ignored, may lead to undesirable management outcomes. We sought to quantify the effects of climate-driven changes in fire regimes and tree species distributions under future climate–fire conditions in the Southern Blue Mountains of central Oregon. We hypothesized that projected climate would increase fire probability, annual area burned, and fire severity and that these changes would influence the distribution of tree species. Specifically, we hypothesized that species sensitive to both fire and hotter/drier climate conditions (e.g., Engelmann spruce, sub-alpine fir) would be replaced over time by more fire and climate-resilient species (e.g., ponderosa pine).

Methods

Study site

The study site is located in the southern part of the Blue Mountains in central Oregon, USA (Fig. 1), covering 938,786 ha, of which 71% is forested, 4% is recently burned forest, and 25% is grasslands and shrublands (LEMMA 2015). Elevation ranges from 719–2744 m above sea level.

Climate in the Blue Mountains is continental with cold, wet winters and hot, dry summers. Mean January and June temperatures are −3°C and 19.3°C, respectively (1981–2010; NOAA 2016, average of nine weather stations within the study area) with average annual precipitation of 364 mm (1979–2014; Abatzoglou 2013), most of which falls as snow (NOAA 2016). There is an increase in average summer precipitation (47–55 mm) and a corresponding decrease in average summer temperatures (27–25°C) from the southwest to the northeast of the study area (Fig. 2a).

Current forested communities (Fig. 2b) consist primarily of ponderosa pine (*Pinus ponderosa*) and dry mixed conifer, which is dominated by a mix of ponderosa pine, Rocky Mountain
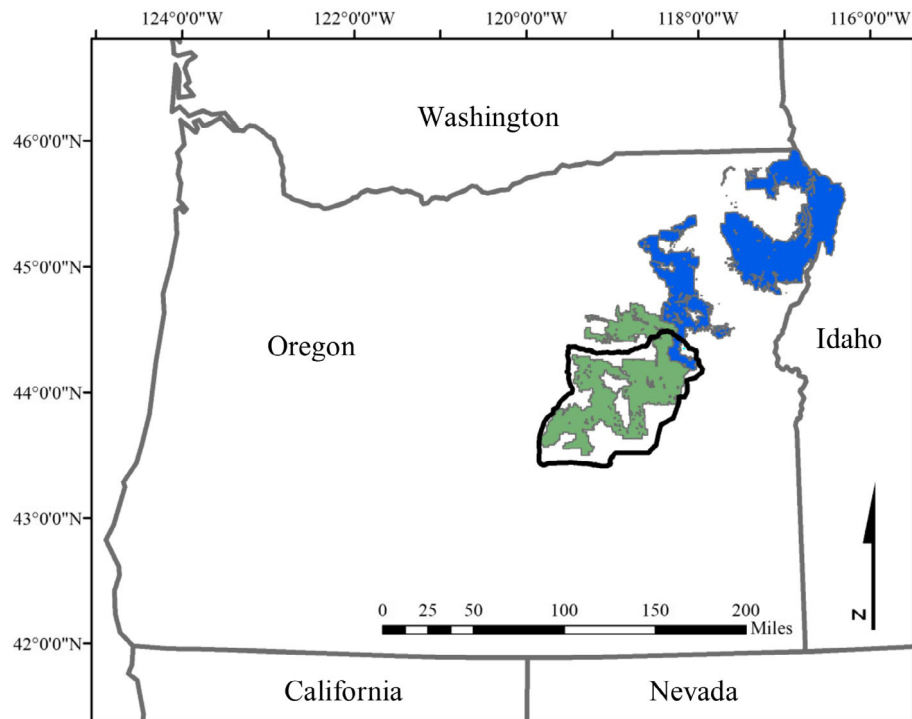
Fig. 1. The study site, indicated by a thick black line, is located in the region of the Malheur (green) and Wallowa-Whitman (blue) National Forests in the southern Blue Mountains in Oregon, USA.

Douglas-fir (*Pseudotsuga menziesii* var. *glauca* hereafter referred to as Douglas-fir), grand fir (*Abies grandis*), and western larch (*Larix occidentalis*; LEMMA 2015). Western juniper (*Juniperus occidentalis*) is present in both forest types, although it is not dominant. At higher elevations, sub-alpine fir (*Abies lasiocarpa*), lodgepole pine (*Pinus contorta* var. *latifolia*), and Engelmann spruce (*Picea engelmannii*) are present, and both whitebark pine (*Pinus albicaulis*) and western white pine (*Pinus monticola*) are found in limited populations. Riparian areas contain trembling aspen (*Populus tremuloides*) as well as deciduous shrub species (e.g., *Vaccinium* spp., *Salix* spp.). Riparian areas also have encroaching young conifers resulting from fire suppression, ungulate browse, and a lowered water table (Dwire et al. 2017), as well as scattered relict conifers >120 yr of age. Shrublands at both high and low elevations are dominated by sagebrush (*Artemesia* spp.) and antelope bitterbrush (*Purshia tridentata*; LEMMA 2015).

The historical fire regime was characterized by mean fire return intervals ranging from 10.6 to 28.2 yr across both ponderosa pine-dominated and moister mixed-conifer sites (Heyerdahl 1997, Johnston et al. 2016) with fire years corresponding with hotter and drier than average years (Johnston et al. 2017). Dry summer lightning storms are frequent and provide the most common ignition source throughout the southern Blue Mountains (Díaz-Avalos et al. 2001). Forest structure and demographics have been shaped by a legacy of fire suppression and commercial timber harvest (Heyerdahl and Agee 1996) as well as current large-scale restoration efforts and large wildfires (USDA FS 2015). Active fire suppression continues on the landscape, limiting the number of wildfires. However, there continue to be an average of 1.6 fires per year within the study area boundary and an average of 9706 ha burned annually for the period 2000–2014 (MTBS 2016). To capture areas of forest and the surrounding grass and shrublands that provide continuous fuels for fire spread, we set the geographic boundaries of the study site to U.S. Highways 26 to the north and 20 to the south with a buffer to the east and
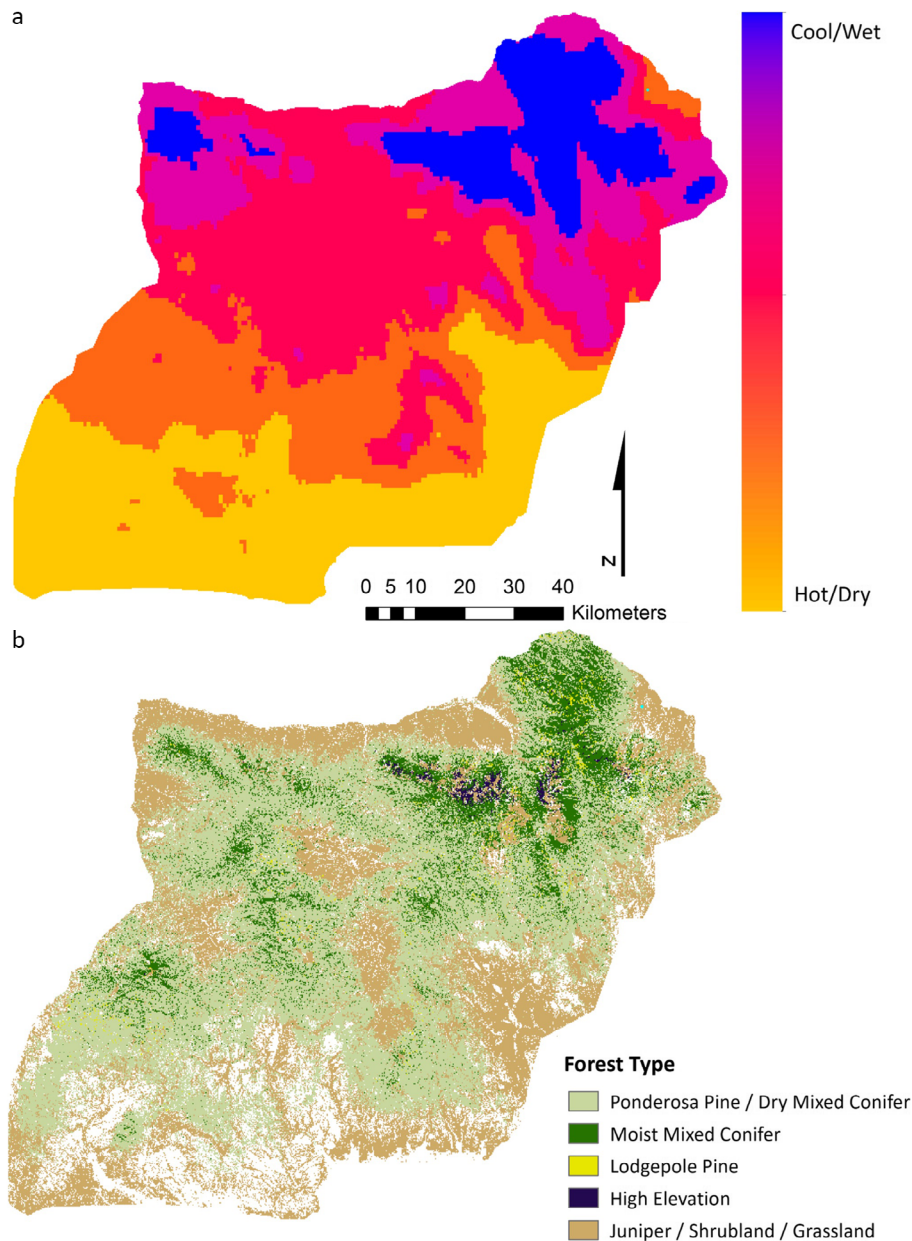
Fig. 2. Climate region (a) and forest type maps (b) of the study area. Five climate regions were determined by a combination of summer (June, July, August) mean maximum daily temperature and mean precipitation. Ponderosa pine/dry mixed-conifer forest is dominated by ponderosa pine, moist mixed-conifer forest is dominated by grand fir, and high-elevation forest is co-dominated by Engelmann spruce and sub-alpine fir.

west of the Malheur National Forest that ranges from ~2–30 km. The boundary also encompasses the southernmost portion of the Wallowa-Whitman National Forest that lies south of U.S. Highway 26.

Overview of simulation model

We simulated changes in forest and fuel bed characteristics over time with the forest landscape change model LANDIS-II (Scheller et al. 2007), which has been widely used to simulate

forest succession and interactions with fire, harvest, wind, and insects (Scheller et al. 2008, Duveneck et al. 2014, Kretchun et al. 2016, Krofcheck et al. 2017, Loudermilk et al. 2017, Lucash et al. 2017). LANDIS-II uses the life-history traits of tree and shrub species, along with soil and climate data, to simulate succession and responses to disturbances over time. Trees are simulated as species-age cohorts, which represent all individual trees of each species as a single group within an age range (e.g., for this study, trees were grouped into 10-yr age cohorts). Each cell represents a 200 × 200 m (4 ha) site, in which all forested vegetation and topographical conditions are assumed to be homogeneous. Sites can be inactive, such as in the case of open water or rocky outcroppings. Some processes, such as competition, growth, and mortality, are simulated within a site, while others, like disturbance and seed dispersal, are simulated both within and between sites (Fig. 3). We used LANDIS-II v6.2 with the Net Ecosystem Carbon and Nitrogen (NECN) succession extension v4.2 (Scheller et al. 2011) to simulate forest growth and dynamics. Net Ecosystem Carbon and Nitrogen simulates aboveground and belowground C and N pools and fluxes based on air temperature, soil moisture, leaf area, and N availability at monthly timesteps. Net Ecosystem Carbon and Nitrogen derives daily weather from the Climate Library (Scheller et al. 2011), including temperature, precipitation, wind speed, and wind direction. We used the Biomass Output extension v.2.1 (Scheller and Mladenoff 2004) to obtain total aboveground biomass (AGB) and AGB of individual species.

We used the Dynamic Fire and Fuels System (DFFS) extension v4.0 (Sturtevant et al. 2009) to simulate wildfire and interactions with climate and fuels. This extension uses the same climate and vegetation as NECN, which allows it to dynamically change fuel beds based on vegetation (species and age cohorts) at the corresponding timestep to direct fire spread and severity. The Dynamic Fire and Fuels System integrates landscape topography into fire behavior algorithms via slope and aspect maps, and it outputs fuel type and fire severity for each cell on the landscape at each timestep. Fire ignitions are attempted in randomly selected cells, and fire occurrence is dependent on a probabilistic

function of the fuel categories present at ignition sites. Fire event size is determined by wind speed and direction on the day(s) of the fire event, which, along with the fuel types in neighboring cells, direct a fire's spread. Fuel moisture conditions, which are determined by fuel type, temperature, and precipitation (and lagged weather conditions for larger-than-fine fuels), affect the fire's rate of spread, which in turn affects fire severity. Fire severity is a function of rate of spread, the critical surface fire rate of spread (beyond which the fire travels to the crown), and the fraction of the crown that is burned. Fraction of crown burned is a function of crown base height (user-defined for each fuel type) and fuel moisture code (dependent on latitude/longitude, elevation, and Julian date). Fire severity is measured as an index from 1 (low-severity surface fire with 0% crown mortality) to 5 (high-severity crown fire with 95% or greater crown mortality). A fire event's mortality is a result of the fire severity, the user-defined species-specific fire tolerances, and the ages of the cohorts present at the site. In multi-species and multi-cohort stands, a greater proportion of less fire-tolerant species cohorts and younger age cohorts are killed. More information and equations for determining fire ignition, spread, and severity can be found in the extension's user guide (Sturtevant et al. 2018).

To simulate forest management, we used the Biomass Harvest extension v3.2 to harvest trees (Gustafson et al. 2000). This extension allows multiple prescriptions to be defined by tree species-age cohorts and carried out on stands allocated to management areas and prioritized by economic or other criteria (e.g., fire sensitivity of species present). Outputs include total and species-level biomass harvested for each prescription and in each management area at every timestep.

Model inputs.—All model inputs are publicly available at https://zenodo.org/badge/latestdoi/105837630, and many parameters are found in Appendix S1.

Landscape regions.—We used soil and weather data to classify the landscape into 25 regions that are assumed to each have homogeneous climate and moisture conditions. We assigned soil available water to each cell using SSURGO soil data (https://websoilsurvey.nrcs.usda.gov/) where they were available; where they were not, we used
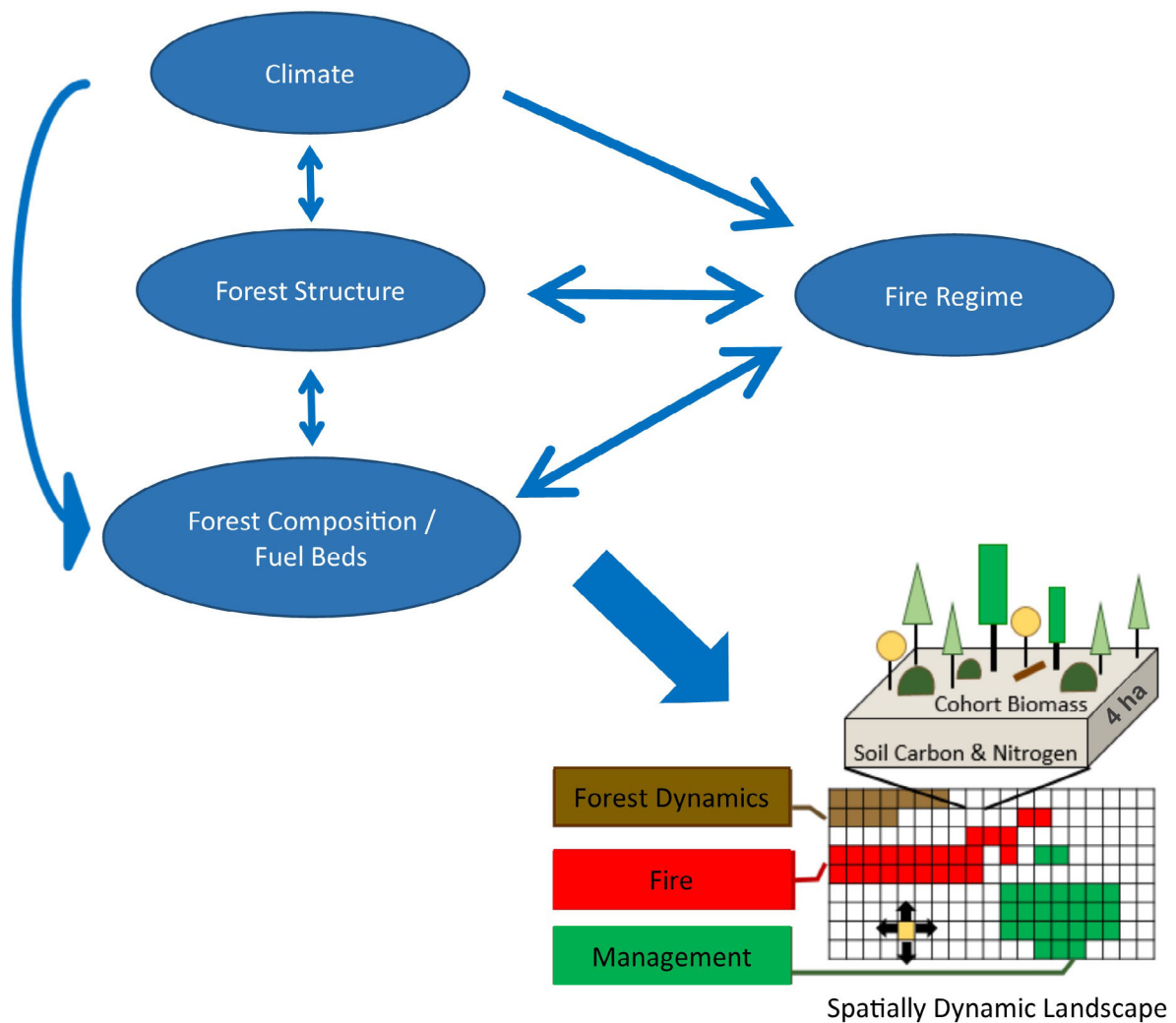
Fig. 3. Conceptual model and dynamic modeling design. Relationships among climate, forest structure, forest composition and fuel beds, and fire regimes are complex, operating at multiple temporal and spatial scales and with feedbacks. These inter-related factors are modeled in the LANDIS-II forest landscape model (FLM), which integrates forest successional dynamics with management and disturbance events across space and time. Processes occur within and across each 4-ha cell. The Net Ecosystem Carbon and Nitrogen Succession extension simulates complex biophysical above- and belowground processes.

SSURGO provisional data and Soil Resource Inventory (SRI) data (J. Noller, C. Ringo, K. Bennett, *unpublished data*) and reclassified cells into five soil moisture classes using Natural (Jenks) Breaks in ArcGIS 10.4.1. We obtained maximum temperature and average precipitation for growing season months (June, July, and August) as 30-yr normals (1980–2010; PRISM Climate Group 2015). We then classified five climate regions by using Isocluster Unsupervised Classification (ESRI 2018), within which we nested the soil moisture regions to create the final regions. Cells that share a region designation are not necessarily contiguous.

Weather data.—For contemporary climate, we used daily weather data retrieved from the USGS Data Portal (https://cida.usgs.gov/gdp/) including maximum and minimum temperatures (°C),

average precipitation (mm/d), daily average wind speed (m/s; Maurer et al. 2002), and wind direction (degrees clockwise from north; Abatzoglou 2013) for the period 1979–2010, using area-weighted grid statistics for each of the five climate regions.

For climate change scenarios, we used 1/8° downscaled bias-corrected constructed analogs V2 daily CMIP5 climate projections from ten climate models forced with representative concentration pathway (RCP) 4.5 and ten climate models forced with RCP 8.5 to represent the range of climate projections for both moderate and high emissions scenarios (USGS Geo Data Portal https://cida.usgs.gov/gdp/; Blodgett et al. 2011). We selected the four climate models that projected the least and most extreme change in precipitation and maximum temperature from 2010 to 2100 (See Appendix S1: Fig. S1) for each RCP and randomly selected an additional six climate models for each RCP to bracket the range of potential future climate. By late century, these projections include an increase in maximum summer temperature of 2.12°C (RCP 4.5) to 5.25°C (RCP 8.5) and average summer precipitation change ranging from −0.22 mm (RCP 4.5) to +0.08 mm (RCP 8.5).

Vegetation.—To develop the initial vegetation communities, we used vegetation data from the Gradient Nearest Neighbor (GNN) maps developed by the Landscape Ecology, Modeling, Mapping and Analysis (LEMMA) group (forested areas, Landsat imagery date 2012; https://lemma.forestry.oregonstate.edu/; Ohmann and Gregory 2002), and the GAP Analysis Program's Ecological Systems map (unforested areas, Landsat ETM+ imagery 1999–2001; https://gapanalysis.usgs.gov/gaplandcover/data/download/; USGS 2011). Of the 29 tree species in the GNN data, we selected 11 species that were present on at least 0.4% of the study area (see Appendix S1: Table S1). These tree species were grouped into species-age cohorts in 10-yr bins. There were 4631 unique communities on the landscape, each with up to 11 tree species in each 4-ha cell.

We assigned non-forest cells to 44 categories from the GAP Analysis Program's Ecological Systems map and grouped them into five unique non-forest categories based on similar vegetation and fuel characteristics (Disturbed and Invaded Grasslands; Perennial Grasslands; Sagebrush Shrublands; Deciduous Shrublands [Not Flammable]; and Deciduous Riparian Shrublands [Flammable]) and one inactive category that was not simulated (e.g., open water, bedrock, and scree). Using NatureServe Explorer (NatureServe 2015), 45 shrub species that occur in the GAP-identified ecosystem categories in the Blue Mountain region were identified and reclassified into functional groups based on whether they (1) are nitrogen fixing, (2) resprout after fire, and (3) are shade tolerant (see Appendix S1: Tables S2 and S3 for shrub types and shrub species). Non-forested cells were assigned cohorts of these shrub groups based on the combinations of individual shrub species that occur in each non-forest category. Shrubs were also included in forested cells according to the GNN Understory inventory data. Disturbed and Invaded Grasslands and Perennial Grasslands were assigned invasive and native grasses, respectively, in order to provide grass fuel types and allow fires to spread through cells that do not contain either trees or shrubs.

Model parameterization and validation

Forest succession.—We obtained model parameters from the literature and available datasets including the USDA Fire Effects Information System (Abrahamson; https://www.feis-crs.org/feis/), USGS Vegetation Atlas of North America (Thompson et al. 1999; https://pubs.usgs.gov/pp/p1650-a/), the Northeastern Ecosystem Research Cooperative's Foliar Chemistry Database (NERC 2015; http://www.nercscience.org/), the National Atmospheric Deposition Program (NADP 2015; http://nadp.slh.wisc.edu/data/ntn/), the Oak Ridge National Laboratory database (West 2014; https://daac.ornl.gov/SOILS/guides/West_Soil_Carbon.html), and from previous studies that utilized LANDIS-II species parameterization (Loudermilk et al. 2014, Lucash et al. 2014, Creutzburg et al. 2016).

Net Ecosystem Carbon and Nitrogen v4.2 spins up to the start year of the simulation by iterating succession at the number of timesteps equal to the oldest cohort in each site allowing comparison between simulated and observed biomass. We validated growth and biomass by comparing aboveground tree biomass after spin-up with Forest Inventory Analysis (FIA) data

(USDA FS 2013, Wilson et al. 2013). Simulated total AGB ranged from 0 to 106 Mg/ha (median of 60 Mg/ha, mean of 52 Mg/ha), while AGB estimates from FIA data ranged from 0 to 236 Mg/ha (median of 54 Mg/ha, mean of 53 Mg/ha) showing that while the model did not simulate the full range of variability in total biomass, it sufficiently captured average biomass and adequately reproduced tree growth. (See Appendix S1: Fig. S2 for a boxplot comparison of FIA and LANDIS-II total biomass.) We validated each of the 11 modeled tree species by comparing average species-level biomass, only in cells where that species occurs, with GNN data for that species. Out of the 11 tree species simulated, nine achieved average biomass within 30% of GNN (Fig. 4). Trembling aspen and mountain mahogany (*Cercocarpus ledifolius*), which were minor components of the landscape, were underestimated in our simulations.

Wildfire.—We developed fuel types to represent 15 unique combinations of tree species and ages, as well as shrublands and grasslands, with individual ignition probabilities and fire behavior parameters. Fuel types and their type-specific equations for fire rates of spread were modified from the Canadian Fire Behavior and Prediction System (Sturtevant et al. 2009). At each timestep,
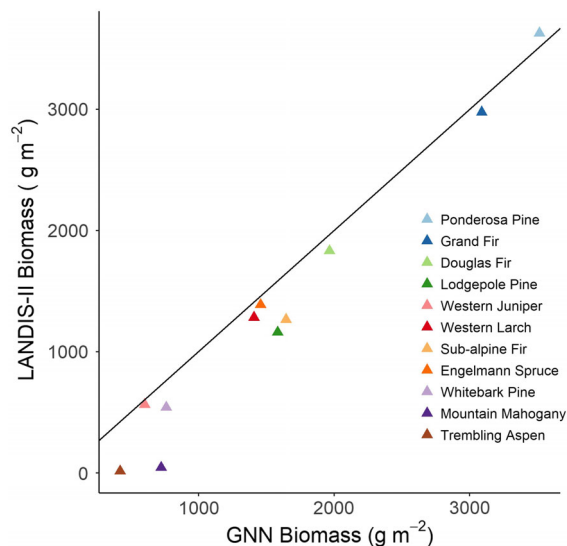

Fig. 4. Initial biomass (g/m^2) at time zero compared against Gradient Nearest Neighbor measures of biomass (r^2 = 0.97).

LANDIS-II updates fuels to reflect changes in forest composition and structure resulting from previous disturbance (e.g., wildfires, management) and from reproduction and age-related mortality. We calibrated fire to annual area burned (mean: 9706 ha, median: 615 ha, range: 0–81,010 ha, standard deviation: 24,481 ha) and fire size (mean: 6933 ha with a range of 434–56,484 ha) for the period 2000–2014 in the study area (MTBS 2016, USDA Forest Service Blue Mountains Fire History Polygons released 2016). Multiple small fires with the same wildfire designation were considered one fire. We first calibrated fire sizes by limiting the maximum fire size to achieve a distribution equivalent to the recent historical period. We also reconstructed fire duration, the time from ignition to the time when the fire is completely out, as measured in minutes. We then ran calibration simulations for fire as duration-limited to allow for the possibility of larger than historical fires and greater annual area burned, reflecting the influence of dynamic vegetation and weather over time (Sturtevant et al. 2009). The DFFS extension uses log-normalized duration data to generate the distribution of fire durations, and this derived duration distribution was then used to calibrate annual area burned, which also follows a log-normal distribution. Three replicates of 50 yr were run and averaged to validate the calibration, achieving a mean of 10,400 ha burned annually with a range of 0–134,700 ha. (See Appendix S1: Fig. S3 for fire duration-size calibration.)

Forest management

The forested landscape of the study area is currently managed according to ownership. Harvest on non-industrial private lands is focused on economic returns, while harvest on publicly managed lands, particularly those managed by the U.S. Forest Service, is generally designed to meet multiple objectives (e.g., to promote ecological integrity, social well-being, and economic well-being; USDA FS 2014). To reflect the current management practices with forest dynamics and fuel continuity on our landscape, we simulated management, including commercial harvest, precommercial thinning, and prescribed fire. (See Appendix S1: Table S4 for descriptions of prescriptions for each ownership and forest type.)

We developed our treatment prescriptions through a workshop with managers (USDA Forest Service, Malheur National Forest Supervisor's Office) and expert consultation (Bureau of Land Management, Oregon Department of Forestry) to ensure that simulated management reflected on-the-ground actions.

Scenarios

To isolate the effects of climate on vegetation and fire, we held management constant for all simulations. To quantify the effects of climate on vegetation and fire, we simulated a 90-yr period using contemporary and projected climate. For the contemporary climate scenario, we assigned each simulation year a random year of daily weather data drawn from 1979 to 2010 from the Gridded Observed Meteorological Data dataset (Maurer et al. 2002). We replicated this process ten times to create contemporary climate inputs for ten replicate simulations. We also ran ten replicate simulations using daily weather projections from the ten selected climate models for both RCP 4.5 and 8.5 for a total of 30 simulations.

Analysis

We compared annual area burned, fire severity, and AGB data among climate scenarios. Annual area burned data followed a log-normal distribution; therefore, we conducted analysis on log-transformed data. Following Bartlett's test for homoscedasticity, we ran analysis of variance (ANOVA) and Tukey's honestly significant difference tests to differentiate means. To compare changes in forest composition, we looked at biomass density (Mg/ha of live biomass) and species extent (proportion of the landscape) among scenarios. We calculated the change in biomass for total biomass (all species) and for each individual species between the start year and the end year of simulations. We completed all model calibration and data analyses in RStudio 1.0.153 (RStudio Team 2018) using R v3.4.1 (R Core Team 2016) and using the following packages: dplyr (Wickham et al. 2011), ggplot2 (Wickham 2009), plotrix (Lemon 2006), raster (Hijmans 2016), rgdal (Bivand et al. 2017), and sqldf (Grothendieck 2017). R scripts can be found on the online repository (https://zenodo.org/badge/latestdoi/105837630).

RESULTS

Wildfire

As expected, under current management practices, the probability of wildfire increased with climate change. The mean probability that a single cell would burn in any given year increased from 0.007 under contemporary climate to 0.011 for RCP 4.5 and 0.012 for RCP 8.5. Higher probability of burning occurred in the northeastern portion of the landscape in all scenarios, but under both climate change scenarios, there was a greater likelihood of fire across the landscape, including the central and western portions (Fig. 5).

Annual area burned also increased with increasing temperatures, and as a result, the fire rotation period decreased (contemporary = 150 yr, RCP 4.5 = 94 yr, RCP 8.5 = 86 yr). Annual area burned was significantly greater under the higher emissions scenario than under contemporary climate ($P = 0.049$; Fig. 6a), and although temperature increases were greater under RCP 8.5, the warming associated with RCP 4.5 was sufficient to cause a 59% increase in average annual area burned. On average, 6272 ha burned per year under contemporary conditions with a range from 0 to 245,016 ha. Under projected climate, annual area burned averaged 9970 ha with a range of 0 to 542,212 ha (RCP 4.5) and 10,873 ha with a range of 0 to 551,472 ha (RCP 8.5), more than double the most extreme extent of wildfire in a single year under contemporary climate. Additionally, 6% of simulated years under both climate change scenarios were extreme fire years, here defined as years with at least 40,000-ha (100,000 acres) burned compared with 3.9% of years under contemporary climate. When considering the entire 90-yr simulation period, cumulative area burned under climate change was 59.0–73.3% greater than under contemporary climate (Fig. 6b).

Our hypothesis that fire severity would be higher under projected climate than contemporary climate was supported ($P = 0.02$), but severity did not differ between RCP 4.5 and 8.5. On average under climate change, 20.4 ($\pm$7.4%)–22.4% ($\pm$8.8%) of the forested landscape was burned by a high-severity fire (severity of 4–5) at least once over the simulation period, while under contemporary climate, only 12.2% ($\pm$3.4%)
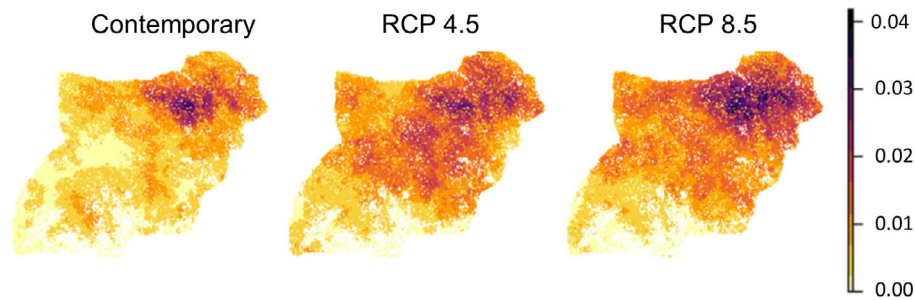
Fig. 5. Maps of probability that each individual site will burn during any given year under contemporary weather and climate change projections. Scale represents the probability of a grid cell burning over 90 yr and 10 replicates.
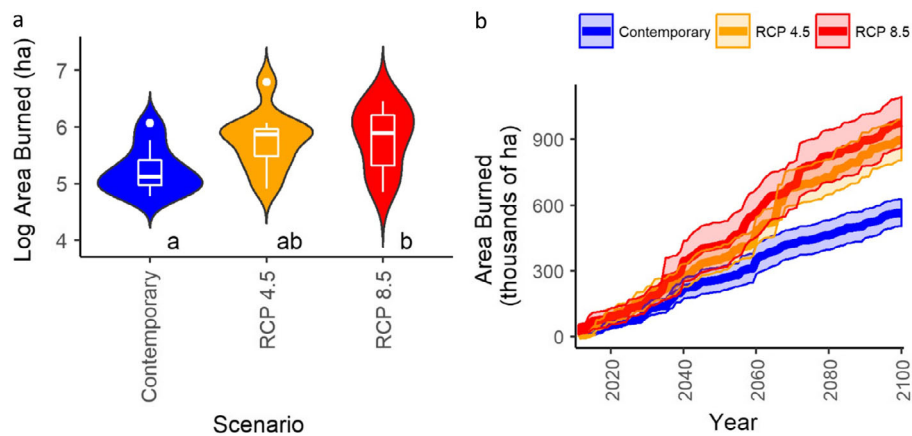

Fig. 6. Violin plot (a) shows annual area burned for the last 30 yr of simulations. Letters (a, b) indicate statistically significant groupings. Boxes encompass the 25th and 75th percentile, the horizontal line indicates the median, and whiskers extend to 1.5 times the interquartile range. Outliers are indicated by a circle. The width of the violin indicates the proportion of years with annual area burned with values on the y-axis transformed by the natural log. Annual area burned under the highest emissions scenarios was significantly higher than contemporary simulations ($P = 0.049$) and was more variable across replicates. Panel (b) shows cumulative area burned over time. The dark line indicates the mean across replicates, and the ribbon encompasses the 95% confidence interval.

was. Of the total area burned, the proportion that burned at high severity was also greater under climate change (Fig. 7). The highest severity fires occurred most often in the northeastern portion of the landscape in forests dominated by high-elevation species (sub-alpine fir, whitebark pine, Engelmann spruce).

Forest dynamics

Aboveground biomass increased over time under all scenarios (Contemporary +23.3%, RCP 4.5 + 23.7%, RCP 8.5 + 23.5%), and there was no difference in the change in total biomass among scenarios ($F = 0.016$, $P = 0.98$; Fig. 8). However, biomass and spatial distribution differed among individual species and among contemporary and projected climate scenarios. (See Appendix S1: Fig. S4 and Table S5 for species-specific data.) Species that tend to occupy warmer, drier sites (e.g., ponderosa pine and Douglas-fir) generally increased in overall biomass, while species that tend to occupy cooler, wetter sites (e.g., sub-alpine
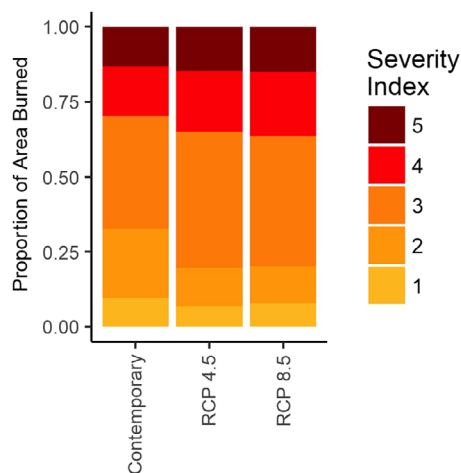
Fig. 7. Proportion of mean area burned under each fire severity class in forested areas under contemporary weather and climate change, averaged across 10 replicates for each scenario.
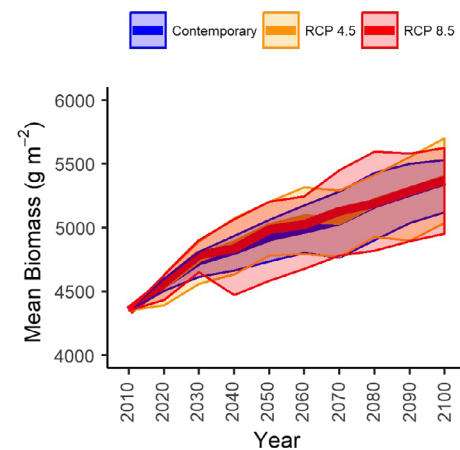

Fig. 8. Average total biomass through time for each climate scenario. Biomass is averaged across all vegetated 4-ha sites on the landscape. The dark line is the mean biomass and the ribbon encompasses the 5th to the 95th percentiles around the mean.

fir and Engelmann spruce) generally decreased in overall biomass. Landscape-level changes in biomass over time were a function of two species-specific responses to climate and wildfire: changes in biomass density (Mg ha^{-1}) in locations where each species occurred at the start of simulations (Fig. 9a) and changes in the spatial extent of a species' range across the landscape (Fig. 9b). Changes in site-level biomass density were driven by reproduction and wildfire mortality. Changes in extent were largely driven by species-specific establishment probabilities under projected climate. (See Appendix S1: Fig. S5 for species-specific establishment probabilities under each climate scenario.)

Ponderosa pine responded favorably to climate change and increased in both biomass density (Fig. 9a) and extent (Fig. 9b) with the greatest increases under projected climate. Grand fir biomass density increased under projected climate and extent under all scenarios, although its range increase was greater under contemporary climate. Douglas-fir's overall increase in biomass was due to an increase in extent, which was greatest under contemporary climate; however, site-level density declined under all scenarios. Conversely, western juniper's site-level density increased over time while experiencing range contraction under all scenarios, indicating that while some juniper

stands were removed by senescence and wildfire, growth and reproduction in the stands that remained outpaced mortality.

High-elevation species, including Engelmann spruce, sub-alpine fir, and whitebark pine, declined under all scenarios with the greatest declines under RCP 8.5 for both spruce and fir. Sub-alpine fir and Engelmann spruce density declined by more than 75%. Under contemporary climate and moderately hotter/drier conditions, however, their range expanded slightly, indicating that even though existing stands were being replaced by other species or converted to non-forest following senescence and disturbance, seed dispersal and reproduction were still occurring. Whitebark pine, which currently occupies only a small portion of the landscape (0.4%), declined in both site-level density and extent under all scenarios. Density in stands where it persisted decreased the least under projected climate's warmer conditions, but its range contracted to 0.03–0.07%, virtually disappearing from the landscape.

Discussion

This study illustrated the southern Blue Mountain region's vulnerability to projected changes in climate and wildfire. Our forecasts of increased
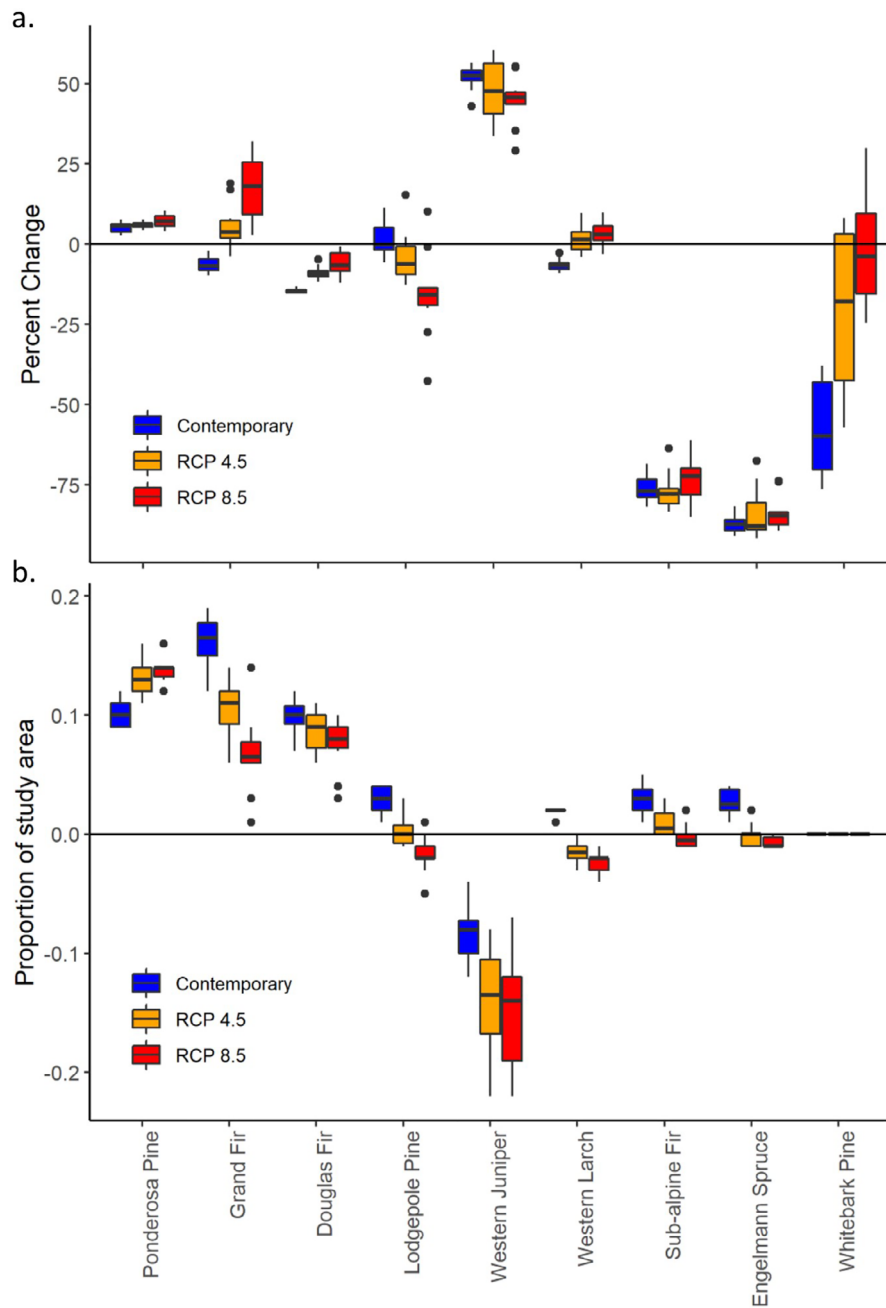
Fig. 9. Mean percent change in biomass density averaged across sites where each species occurred (a) and change in the proportion of the landscape where the species was present. (b) Boxplots show change from 2010 to 2100 for all modeled conifer species. Horizontal line indicates no change over the 90-yr simulation period. Boxes represent the percent change within a species. The lower and upper hinges correspond to the 25th and 75th percentiles, whiskers extend to the largest value up to 1.5 times the interquartile range, and the horizontal line indicates the median.

wildfire frequency, extent, and severity indicate a continuation of observed trends of increasing wildfire activity in the western United States (Littell et al. 2009, Abatzoglou and Williams 2016, Westerling 2016). Our results are also consistent with previous studies that have predicted future increased fire activity and severity (Spracklen et al. 2009, Kitzberger et al. 2017) and increased likelihood of large fires (Stavros et al. 2014) in this region, notwithstanding the potential for long-term fuel limitations (McKenzie and Littell 2017, Hurteau et al. 2019). Simulated vegetation dynamics underscore the complexity of climate–wildfire–forest relationships that will drive fuel composition and structure as well as future forest resilience to wildfires.

Fire can act as a catalyst for vegetation change, especially when accompanied by changing climate (Liang et al. 2017). In our simulations, area burned increased under projected climate for both emission scenarios, and more so than simulations under contemporary climate (Fig. 6). Our fire simulations do not explicitly include suppression efforts and, as a result, show increasing area burned for the first four decades of the simulation under contemporary climate. This result is also in part influenced by the fire deficit on this landscape (Heyerdahl et al. 2001, Parks et al. 2015, Johnston et al. 2017), which has increased fuel buildup and continuity and allows fires to readily spread.

The increased area burned in our simulations created an opportunity for species movement across the landscape, which favored species that are more fire and drought tolerant, particularly under climate change (Fig. 9b). Of the species that experienced range expansion, the change in biomass density was variable (Fig. 9a). Ponderosa pine's fire-adapted characteristics and legacy of dominance on the study landscape gave it a competitive advantage both in persistence and in regeneration in the model. Expansion of ponderosa pine at high elevations was facilitated by fire-related mortality of sub-alpine species, which provided additional light for establishment. Higher temperatures favored ponderosa pine regeneration over the sub-alpine species, a result in line with previous research based on physiological modeling (Coops et al. 2005). Rocky Mountain Douglas-fir is less fire tolerant than ponderosa pine (Kalabokidis and

Wakimoto 1992), which our simulations reflect through a small loss in site-level biomass density. However, its ability to establish remained high over time, even under the hottest/driest climate scenario, which allowed it to expand its range. These results are consistent with previous research that has shown an increase in more fire- and drought-tolerant forest types in central Oregon under projected climate (Halofsky et al. 2013); however, pre-defined potential vegetation types do not allow for the interaction between disturbance, climate, and life-history characteristics to govern species movement across the landscape.

Grand fir biomass increased under all scenarios, with regeneration making up 3–25% of total simulated grand fir biomass under the highest emissions scenario. Grand fir expansion is explained in part by its plentiful seed supply, as grand fir is the second-most common species in the study landscape after ponderosa pine. Furthermore, grand fir is also the most drought-tolerant fir in the Pacific Northwest (Howard and Aleksoff 2000), and it can establish and survive on a range of sites from moist to warm and moderately dry (Lillybridge et al. 1995). In the Blue Mountains, as well as in the neighboring Ochoco and Cascade Mountains to the west, infilling of late-seral species (grand fir and, to a lesser extent, Douglas-fir) in formerly ponderosa pine-dominated sites has been demonstrated beginning around the 1880s, likely as a result of widespread fire suppression (Merschel et al. 2014, Johnston et al. 2018). Grand fir is moderately fire resistant once it reaches maturity (Howard and Aleksoff 2000) and generally only dominates in areas where fire has been excluded (Habeck and Mutch 1973). Unexpectedly, at higher elevations where simulated wildfires became more frequent, larger, and of higher severity over time, grand fir persisted. This occurred because there was a shift from primarily fire-susceptible (sub-alpine fir, whitebark pine, Engelmann spruce) to primarily fire-resistant (ponderosa pine) species, which facilitated grand fir establishment in the understory and survival in fire-free and low-severity fire patches. However, grand fir was less successful at establishing under higher emissions scenarios, especially after 2060, when temperature and moisture conditions were less favorable and wildfires were larger, more severe, and more

frequent. In the lower-elevation grasslands and shrublands, our simulations also showed grand fir establishment over time, although to a lesser extent than at mid- and high elevation. High establishment rates in the understory following ponderosa pine migration into grasslands and shrublands may facilitate encroachment of grand fir in these areas, although frequent fires in these low-lying areas would suppress grand fir survival.

Our study projected a decline in high-elevation tree species concurrent with expansion of more drought-tolerant species. These projections are consistent with other modeling studies that projected losses in sub-alpine forests in eastern Oregon under a range of climate change models (Halofsky et al. 2013). Species distribution research (Mathys et al. 2017) has also found range constriction and increased water and temperature stress under climate change for whitebark pine, sub-alpine fir, and lodgepole pine. While the latter study did not account for wildfire, they found that lodgepole pine distribution is limited by both high summer temperatures and soil water deficit from insufficient snowmelt. This is consistent with our simulated reduction of lodgepole pine biomass density and extent under the higher temperatures and lower annual precipitation of the high emission scenario (RCP 8.5). In some ecosystems, the increase in high-severity wildfire under projected climate could lead to successful post-fire lodgepole pine regeneration from seed stored in serotinous cones (Anderson 2003). However, most lodgepole pines in the study area produce non-serotinous cones (Crowe and Clausnitzer 1997; thus, we simulated non-serotinous lodgepole pine) and do not gain a competitive advantage from the increased wildfire activity.

Whitebark pine establishment was historically supported by stand-replacement patches within mixed-severity fires and low-to-moderate-severity fires that reduced competition from co-occurring species (Perkins et al. 2016). However, whitebark pine has already been largely replaced by later-successional species following widespread mortality from white pine blister rust (USDA FS 2014) as well as decades of fire suppression. Our simulations found whitebark pine had a smaller reduction in site-level biomass density relative to the other sub-alpine species

(Fig. 9a), reflecting its higher drought tolerance and regeneration advantage as a pioneer species following wildfire (Lillybridge et al. 1995). We found little change in the proportion of the study area occupied by whitebark pine due to its limited distribution at the start of the simulations (Fig. 9b). In contrast, sub-alpine fir and Engelmann spruce had difficulty establishing under the hottest/driest conditions of the RCP 8.5 scenario, leading to decreased extent. Both species lost site-level biomass density due to high mortality during fire events and an inability to re-establish following fire.

Forest homogenization

The decline of sub-alpine species, coupled with encroachment of more climate-resilient species at both high and low elevation, characterizes an increase in forest homogenization. This loss of heterogeneity can have detrimental effects. Landscapes containing multiple species and forest types are more resilient to disturbance through functional redundancy (Oliver 2015, van der Plas 2016), variable response to a disturbance among forest patches (Hessburg et al. 2019), and variable responses to different disturbances (e.g., windthrow, insect infestations, disease; Folke et al. 2004). They also provide a variety of wildlife habitats, natural resources, and recreation environments that produce a broad range of ecosystem services. In terms of wildfire, homogenization through infilling of small-diameter trees of a single species (e.g., grand fir) leads to continuous fuels that propagate larger, higher-severity fires than in forests with diverse composition and structure (Stine 2014). In our study, the areas most affected by forest homogenization were the high-elevation forests and low-elevation grasslands, which provide critical and unique habitats and increase patch diversity on the landscape. While forest homogenization toward ponderosa pine-dominated forest may lead to increased landscape-level resilience, or ability to remain in the same state following wildfire (Carpenter et al. 2001), this reduction in heterogeneity on the landscape is a tradeoff that may have other far-reaching ecological and social effects.

Management implications

Our results may be useful for land managers and local communities as they plan long-term

forest management activities. Feedbacks between climate change-driven losses in sub-alpine tree species, infilling of young cohorts of ponderosa pine, Douglas-fir, and grand fir, and increasing wildfire activity on forested landscapes illustrate the need to proactively consider priorities around restoration and fuel management. Our simulations held current management practices constant through time, and management did not keep pace with biomass accumulation at the landscape scale in both dry pine and mixed-conifer sites. Historical (pre-1900) wildfires on this landscape burned at similar frequency in grand fir-dominated sites as in drier ponderosa pine-dominated sites (Johnston et al. 2017). In light of the projected grand fir expansion, we suggest that reducing fuel continuity through accelerated rates of thinning and prescribed burning, especially in sites with young fire-prone grand fir cohorts, is likely needed to reduce the extent and severity of future fires. Reducing density of young cohorts has been found to provide the added benefit of making remaining trees more resilient to drought (Voelker et al. 2019).

In addition to reducing landscape-level wildfire spread and severity, management actions may be designed to allow fire in areas where it is ecologically desirable such as areas where fuel loads are low enough to facilitate low-severity fire or in high-elevation locations where mixed-severity fires may create patch diversity. Management actions may also be taken to prolong the survival of species of interest. For instance, managers could prioritize the survival of white-bark pine by removing other competing species, using controlled wildfires to create open patches, and planting white pine blister rust-resistant seedlings in burned (or cleared) areas as proposed by Keane et al. (2012). In grasslands and shrublands, young cohorts of ponderosa pine, Douglas-fir, western juniper, and grand fir could be harvested to restore historical composition and structure.

Limitations

In this study, we simulated forest succession (seed dispersal, reproduction, growth, competition, age-related mortality), current harvest practices (mechanical tree removal and prescribed fire), and wildfire. We did not include wind disturbance or insect damage. However, these omissions would not likely influence our results under contemporary climate because the model was calibrated to include typical mortality rates, inclusive of these disturbances, using empirical data and expert consultation (M. Jennings, *personal communication*). If there was an increased susceptibility to insects or other pathogens under warmer conditions (Kurz et al. 2008, Sturrock et al. 2011), biomass projections would likely be lower and more variable than projected in this study (Scheller et al. 2018). We also did not project future CO_2 concentration or the effects of CO_2 fertilization on tree growth. The increasing CO_2 concentration associated with the different emission scenarios may increase water use efficiency (Keenan et al. 2013), which could facilitate improved drought tolerance. This has potential implications for short-term growth stimulation, though it could be curtailed over the long-term by nitrogen availability (Johnson et al. 2006, Thornton et al. 2009, Norby et al. 2010).

Conclusions

General circulation models consistently project hotter temperatures, a greater proportion of precipitation falling as rain rather than snow, earlier snowmelt, and longer fire seasons in the western United States (Scholze et al. 2006, Littell et al. 2009). This study, which looked at the effects of those changes on wildfire activity and forest dynamics in the intermountain west, found that even with uncertainty about the magnitude of future climatic trends, wildfire frequency, extent, and severity will be more extreme than what this landscape has experienced in the recent past. We found that changes in forest composition will be driven by changes in the fire regime, which are driven by fuel loads and composition as well as fuel moisture conditions. The greatest impacts of climate change on this landscape occurred at the higher elevations where fire- and high-temperature-sensitive species were replaced by the migration of tree species typically found at lower elevations. These findings underscore the critical need for forest managers to actively consider climate change, shifting fire regimes, and social and ecological priorities around managing for high-elevation species in their long-term management plans.

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DATA AVAILABILITY

Data and code are available from Zenodo at https://zenodo.org/badge/latestdoi/105837630.

SUPPORTING INFORMATION

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.2934/full