Climatic Change (2021) 166:46
https://doi.org/10.1007/s10584-021-03140-x

Future fire-driven landscape changes along a southwestern US elevation gradient

Cécile C. Remy, et al. *[full author details at the end of the article]*

Received: 28 September 2020 / Accepted: 8 June 2021/

Abstract

Over the twenty-first century, the combined effects of increased fire activity and climate change are expected to alter forest composition and structure in many ecosystems by changing postfire successional trajectories and recovery. Southwestern US mountain ecosystems contain a variety of vegetation communities organized along an elevation gradient that will respond uniquely to changes in climate and fire regime. Moreover, the twentieth-century fire exclusion has altered forest structure and fuel loads compared to their natural states (i.e., without fire suppression). Consequently, uncertainties persist about future vegetation shifts along the elevation gradient. In this study, we simulated future vegetation dynamics along an elevation gradient in the southwestern US comprising pinyon-juniper woodlands, ponderosa pine forests, and mixed-conifer forests for the period 2000–2099, to quantify the effects of future climate conditions and projected wildfires on species productivity and distribution. While we expected to find larger changes in aboveground biomass, species diversity and species-specific abundance at low elevation due to warmer and drier conditions, the largest changes occurred at high elevation in mixed-conifer forests and were caused by wildfire. The largest increase in high-severity and large fires were recorded in this vegetation type, leading to high mortality of the dominant species, *Picea engelmannii* and *Abies lasiocarpa*, which are not adapted to fire. The decline of these two species reduced biomass productivity at high elevation. In ponderosa pine forests and pinyon-juniper woodlands, fewer vegetation changes occurred due to higher abundance of well-adapted species to fire and the lower fuel loads mitigating projected fire activity, respectively. Thus, future research should prioritize understanding of the processes involved in future vegetation shifts in mixed-conifer forests in order to mitigate both loss of diversity specific to high-elevation forests and the decrease in biomass productivity, and thus carbon storage capacity, of these ecosystems due to wildfires.

Keywords Climate change · Wildfire · LANDIS-II · Forest diversity · Biomass · Fire severity · Fire size · Species richness

1 Introduction

Ongoing climate change is altering the geographic distributions of plant species worldwide (Chapin et al. 2008; Morin et al. 2008). In forest ecosystems, disturbance catalyzes distributional changes by disrupting the established equilibrium of species communities, leading to new successional dynamics which may be not be well adapted to future climate conditions (Franklin et al. 2016; Thom et al. 2017). Moreover, changes in forest community composition affect ecosystem structure and function, including the provisioning of ecosystem services (Ahlström et al. 2015; Pecl et al. 2017). Understanding how the interaction of changing climate and disturbance will impact the forest community composition, and the distribution of tree species is central to predicting ecosystem function (Millar and Stephenson 2015; Trumbore et al. 2015).

In a warming world, tree taxa shift predominantly toward currently colder and moister locations, at higher latitudes and higher elevations (Chen et al. 2011; Kelly and Goulden 2008). However, changes in the distribution of tree species in response to ecological and physiological processes are not linear. The ability of species to move geographically to track climate depends on species-specific ecophysiology and can involve ecological interactions such as competition for abiotic and biotic resources (Anderegg and HilleRisLambers 2015; Chen et al. 2011; Gratani 2014; Lenoir et al. 2008; Zhu et al. 2011). When disturbance processes interact with ongoing climate change, they can act as an additional constraint on the ability of species to move by impacting environmental variables (e.g., light, soil nutrients, water availability) and thus ecological interactions between species (Dale et al. 2000; Overpeck et al. 1990).

One such prevailing disturbance process in the western USA is wildfire. Increasing temperatures and earlier snow melt are lengthening the fire season and increasing fuel flammability, leading to larger area burned and higher fire severity (Abatzoglou and Williams 2016; Kitzberger et al. 2017; Singleton et al. 2019; van Mantgem et al. 2013; Westerling 2016). Moreover, since the early 1930s, fire exclusion has altered forest structure and increased fuel loads, leading to more area that is impacted by large and high-severity wildfire (Miller et al. 2009; Singleton et al. 2019). The combined effects of increasing aridification and fire are reshaping southwestern forest ecosystems (Cooper et al. 2018; Stevens-Rumann et al. 2017). Larger high-severity fire patches are causing dispersal limitations, and the combined effects of higher temperature and moisture deficit are reducing seedling recruitment (Anderson-Teixeira et al. 2013; Davis et al. 2019; Poulos et al. 2020a). Climate warming and resultant drying due to increased atmospheric water demand are also causing increased tree mortality (Allen et al. 2015; Breshears and Barnes 1999).

However, the elevation gradient in many western US landscapes is steep and covered by different vegetation types which may respond differently to changing climate conditions and fire regimes (Anderson-Teixeira et al. 2013; Liang et al. 2017a; Remy et al. 2019). Limited postfire tree regeneration is more common in low-elevation, dry forest types (i.e., pinyon-juniper woodlands and dry ponderosa pine forests) than in high-elevation forest types (i.e., mixed-conifer forests) in the western USA (Stevens-Rumann and Morgan 2019). However, altered fire regimes due to higher fuel continuity and fuel loads, combined with warming and drying, have the potential to further change postfire successional trajectories in mid- and high-elevation forest types. Several studies have shown regeneration failures in species commonly found in ponderosa pine and mixed-conifer forests in response to altered fire regimes and increased warming, leading to a decline in biomass and tree species richness (Flatley and Fulé 2016; Hansen et al. 2018; Liang et al. 2017a; Petrie et al. 2016).

Given uncertainties that persist about future vegetation shifts along elevation gradients in the western USA, we sought to disentangle the effects of projected climate from wildfire to improve our understanding of how species will move across the landscape. We used a species-specific, spatially explicit landscape modeling approach to simulate future vegetation dynamics under projected climate, with and without wildfire, across an elevation gradient in the southwestern USA that includes pinyon-juniper woodlands, ponderosa pine forests, and mixed-conifer forests. By comparing simulation outputs from scenarios with climate change only and climate change with wildfire, we quantified the effects of projected wildfires in the context of ongoing climate change on species distributions and productivity. We hypothesized (i) an increase in area burned by high-severity fire through the twenty-first century across the elevation gradient because of climate change, leading to (ii) decreases in biomass productivity and tree species richness due to projected fire regime and climate conditions, especially at low elevation (i.e., in pinyon-juniper woodlands), and (iii) higher recruitment of species adapted to fire over species sensitive to fire, especially at high-elevation where the current most abundant species are not adapted to fire.

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 (Fig. 1). The climate is primarily continental, with cold, wet winters, and warm summers; approximately 50% of the annual precipitation occurs in summer monsoonal storms (Sheppard et al. 2002). The 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). The 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 and White 1998).

Forest type varies by elevation; low-elevation woodlands and forests are more moisture limited while higher elevation forests are more temperature limited (Figs. S1). The low-elevation area (460,107 ha) is primarily dominated by pinyon-juniper woodlands (*Pinus edulis* Engelm. and *Juniperus monosperma* (Engelm.) Sarg.) with *Juniperus scopulorum* (Sarg.) and *Quercus gambelii* (Nutt.). Mid-elevation forests (725,364 ha) are dominated by a mix of species including *Pinus ponderosa* (C. Lawson), *Pseudotsuga menziesii* ((Mirb.) Franco), and *Abies concolor* ((Gordon) Lindley ex Hidebrand), with scattered junipers, *Q. gambelii*, and *Populus tremuloides* (Michx.). High-elevation forests (316,962 ha) primarily consist of *Picea engelmannii* (Parry ex Engelm.) and *Abies lasiocarpa* ((Hooker) Nuttall), with the scattered presence of *P. menziesii*, *A. concolor*, and *Q. gambelii*.

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 extension includes elements of the PnET-II ecophysiology model (Aber et al. 1995), adding increased physiological control of tree growth, mortality, and establishment, with

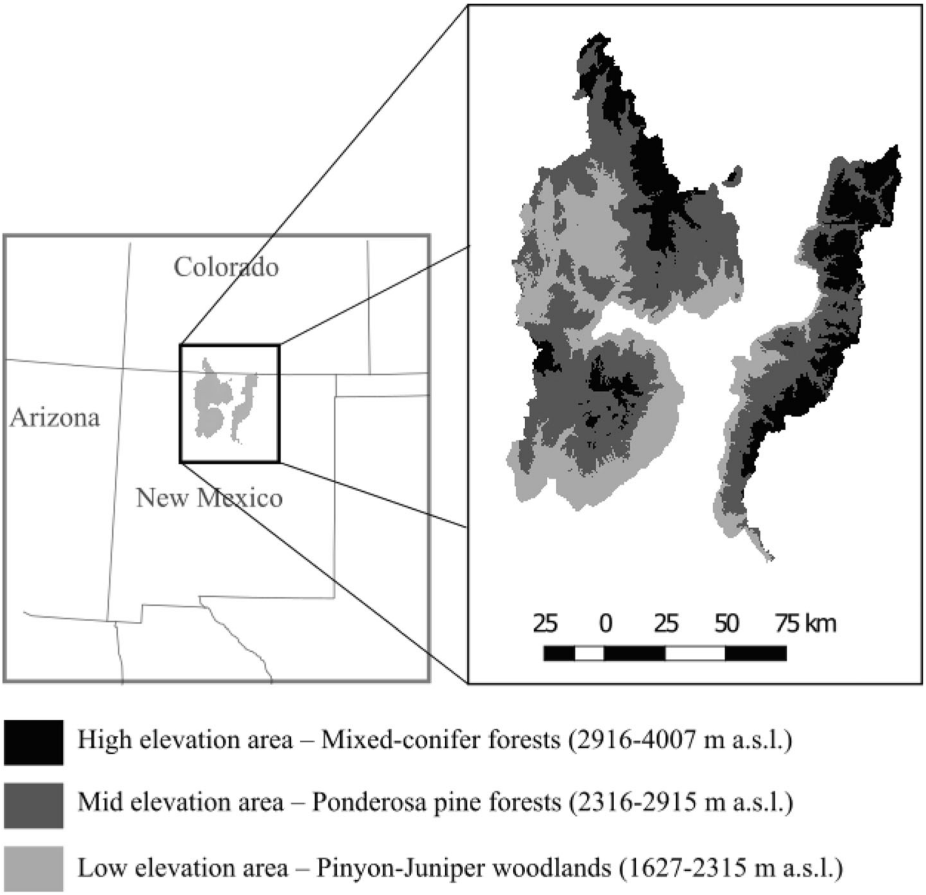

Figure 1: Location and characteristics of the study area

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 PnET-II can be reduced by multiple factors: water stress, radiation limits (e.g., lower canopy layers), vapor 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 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 fuels 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 age cohorts of biomass, and 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 resulting in surface fire with little or no tree mortality and some overstory tree torching that causes mortality. High severity coincides with crown fire activity that results in extensive tree mortality.

2.3 Climate data

LANDIS-II and the PnET 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) 4.5 and 8.5; see IPCC AR5 WGI 2013) via the Coupled Model Intercomparison Project Phase 5 multi-model ensemble (CMIP5; Bureau of Reclamation 2013). These included global models from Commonwealth Scientific and Industrial Research Organization and Bureau of Meteorology (ACCESS1-0, The Commonwealth Scientific and Industrial Research Organisation 2017), the Canadian Centre for Climate Modeling and Analysis (CanESM2; Christian et al. 2010), the United Kingdom Met Office Hadley Centre (HadGEM2-ES, Collins et al. 2008), and the Community Earth System Model Contributors (CESM1-BGC, Long et al. 2013). The climate scenarios were downscaled to a 1/16 degree latitude-longitude grid using the localized constructed analogs statistical downscaling methodology to produce temperature and precipitation data (Pierce et al. 2014; Pierce et al. 2015). We downloaded incoming shortwave radiation data from TerraClimate for years 1958–2017 (http://www.climatologylab.org/terraclimate.html, Abatzoglou et al. 2018); for years 2018–2099, we sampled from the distribution of monthly values. We converted the shortwave radiation from TerraClimate to photosynthetically active radiation following Britton and Dodd (1976). We downloaded CO_2 data for the CMIP5 RCP 4.5 and 8.5 from http://tntcat.iiasa.ac.at/RcpDb/dsd?Action=htmlpage&page=download (Riahi et al. 2007). The projections include data from 1950 to 2099, and we used data from 1958 to 2000 for model spin-up.

2.4 Landis-II parameterization and validation

The LANDIS-II core and PnET extension require the landscape to be divided into "ecoregions" that represent unique climatic and soil conditions. The scale of our projected climate data (~ 6 km) defined our ecoregions, resulting in 493 unique ecoregions across our study area. We assigned soil class and depth to each ecoregion with the type that covered the majority of the ecoregion from CONUS-SOIL spatial data (Miller and White 1998).

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 neighbor approach to map existing vegetation using data from 836 unique Forest Inventory and Analysis (FIA, https://www.fia.fs.fed.us/) vegetation plots, topographic indices, and recent Landsat imagery 8 (available at https://landsat.usgs.gov/landsat-8) (Crookston et al. 2007; Ohmann and Gregory 2002). We used the yaImpute package (v1.0-31, Crookston and Finley 2008) with a random forest classification in R to produce the initial communities map with a 9-ha grid (R Core Team). 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.

We obtained species-specific physiological parameter values for the PnET extension using a literature search and the TRY database (https://www.try-db.org/TryWeb/Home.php, Kattge et al. 2011). The majority of the parameters for the species included in our simulations were previously tested and validated using eddy covariance tower data (Remy et al. 2019). We conducted additional validation by comparing the distribution of model spin-up aboveground biomass with the distribution of biomass calculated from the FIA plots using genus-specific allometric equations (Jenkins et al. 2003).

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 (1627–2315 m), mid-elevation ponderosa pine forests (2316–2915 m), and high-elevation mixed-conifer forests (2916–4007 m) (Fig. 1). These elevation bands correspond to the elevation distribution of major vegetation types on this landscape (Table S1). The fuels and fire extension are based on the Canadian Fire Behavior and Prediction System (Sturtevant et al. 2009) and assigns a fuel type to each grid cell at every time step based on the species-age combinations present, incorporating prior successional and disturbance processes on the vegetation structure and composition. We used published fuels parameters to represent the fuel-type characteristics and stand-age dynamics for northern New Mexico forest types (Keyser et al. 2020; Krofcheck et al. 2019; Krofcheck et al. 2017).

We used existing model parameterizations for the fire size distribution developed for a subset of our study area by Krofcheck et al. (2019), and we estimated the number of ignitions per year using fire perimeter data for the period 2000–2019 from northern New Mexico (https://data-nifc.opendata.arcgis.com/search?tags=HistoricWildfires_OpenData). Consequently, the maximum number of ignitions and the fire size distributions did not vary for the period 2000–2099 in our simulations. In order to calculate fuel moisture as a function of future climate, we needed relative humidity projections which were not present in the CMIP5-downscaled projections. We used climate projections from the MACA dataset (https://climate.northwestknowledge.net/MACA/) to drive fire weather, taking air temperature, relative humidity, and precipitation outputs from the relative concentration pathway (RCP) 8.5 to produce a distribution of fire weather every 10 years in the simulation. We chose three models that represent the range of projected outcomes for the region as well as contained the outputs required by the model (CNRM, GFDL, and MIROC5-ESM2) and produced an ensemble mean of fire weather from the three projections. Consequently, every 10 years in the model progression, the fire weather distribution matched local projections for the region. However, wind speed and direction draws were appended to each decadal distribution using local nearby remote access weather station (Pecos, NM at 2620 m [35.57°N; 105.66°W], Coyote, NM at 2680m [36.1°N; 106.67°W], Mountainair, NM, at 1981m [34.52°N; 106.24°W]) data and a statistical approach described by Krofcheck et al. (2018).

2.5 Simulation experiment description

To quantify the effects of projected climate and wildfire on vegetation dynamics, we ran projected climate-only simulations and simulations that included both projected climate and wildfire. We ran 10 replicate, 100-year simulations for each climate projection (10 replicates for each of the 8 projected climate scenarios), with and without wildfire. We aggregated the simulations from the four climate projections under each RCP for analysis of the climate-only and climate and wildfire scenarios. We conducted data processing, statistical analysis, and figure generation in R-3.6.2 (R Core Team 2019).

We quantified the projected wildfires based on three characteristics: area burned by high-severity fire, area burned by low- to moderate-severity fire (see part. *Simulation model description*), and total area burned. We averaged each of these metrics by year between 2000 and 2099 for the 40 replicate simulations and used linear regression to identify any trends during the twenty-first century.

We evaluated the degree of landscape composition similarity at the start and end of the simulations under both scenarios by computing Pearson's correlations between presence and absence of species at 2000 and 2099 with the *cor.test* function (package *stats v3.6.2*).

Aboveground biomass (further referred to as biomass), tree species diversity, and species-specific abundance were computed at the beginning (i.e., 2000) and the end (i.e., 2099) of the simulations to quantify the effects of climate change and the combined effects of climate change and wildfire within each elevation band. Biomass data were extracted from the simulation outputs and summed for each elevation area. Tree species diversity index was computed using the tree species richness in each pixel (9-ha grid scale) averaged by the percentage of pixels within each elevation area occupied (i.e., presence or absence) by each species for the 40 simulation replicates. We calculated the change in species abundances between scenarios by differencing the 2099 results.

We extracted burned pixel data from the 40 simulations and quantified changes in species presence to evaluate the sensitivity of the vegetation to different wildfire characteristics along the elevation gradient. In order to categorize changes in species presence on a per pixel basis for each burned pixel, we compared species composition at the start (2000) and end (2099) of the simulation and assigned "−1" for a loss of species presence, "0" for no change, and "+1" for a gain of species presence. For each of these burned pixels, we also extracted the total number of fire occurrences (hereafter frequency), the average severity, and the average distance from the closest unburned pixels (hereafter size) from the period 2000 to 2099. We used this approach to computing fire size to mitigate the risk that overlapping fires that occur in the same year would be treated as one large fire. We used Pearson's correlations to evaluate relationships between species-specific abundances and the fire variables (i.e., frequency, severity, and size) along the elevation gradient with the *cor.test* function (package *stats v3.6.2*).

All the code used to perform data analysis and data are available at https://datadryad.org/stash/share/Oc4lWABDBprodPJAx0_m3tZenq4Rj0Nc-TDGQwkhahw.

3 Results

3.1 Fire activity

At the beginning of the century, the majority of the area was burned by low- to moderate-severity fire. However, increased warming and drying caused an increase in the proportion of area that burned at high severity for all three elevation bands throughout the twenty-first century, but the rate of increase in area burned by high severity did not differ between elevation bands (Fig. 2A, C, Table S2). Total area burned is higher on average at high elevation than at lower elevations throughout the twenty-first century, but did not increase through time along the elevation gradient (Fig. 2A,C and Table S2). Finally, we found that high-elevation forests also exhibited the highest variability per year in area burned, especially under RCP 8.5 (Fig. 2B,D).

3.2 Landscape dynamics

The degree of similarity in landscape composition between the beginning and end of the simulations was significantly higher for the climate change only simulations (Table S3).

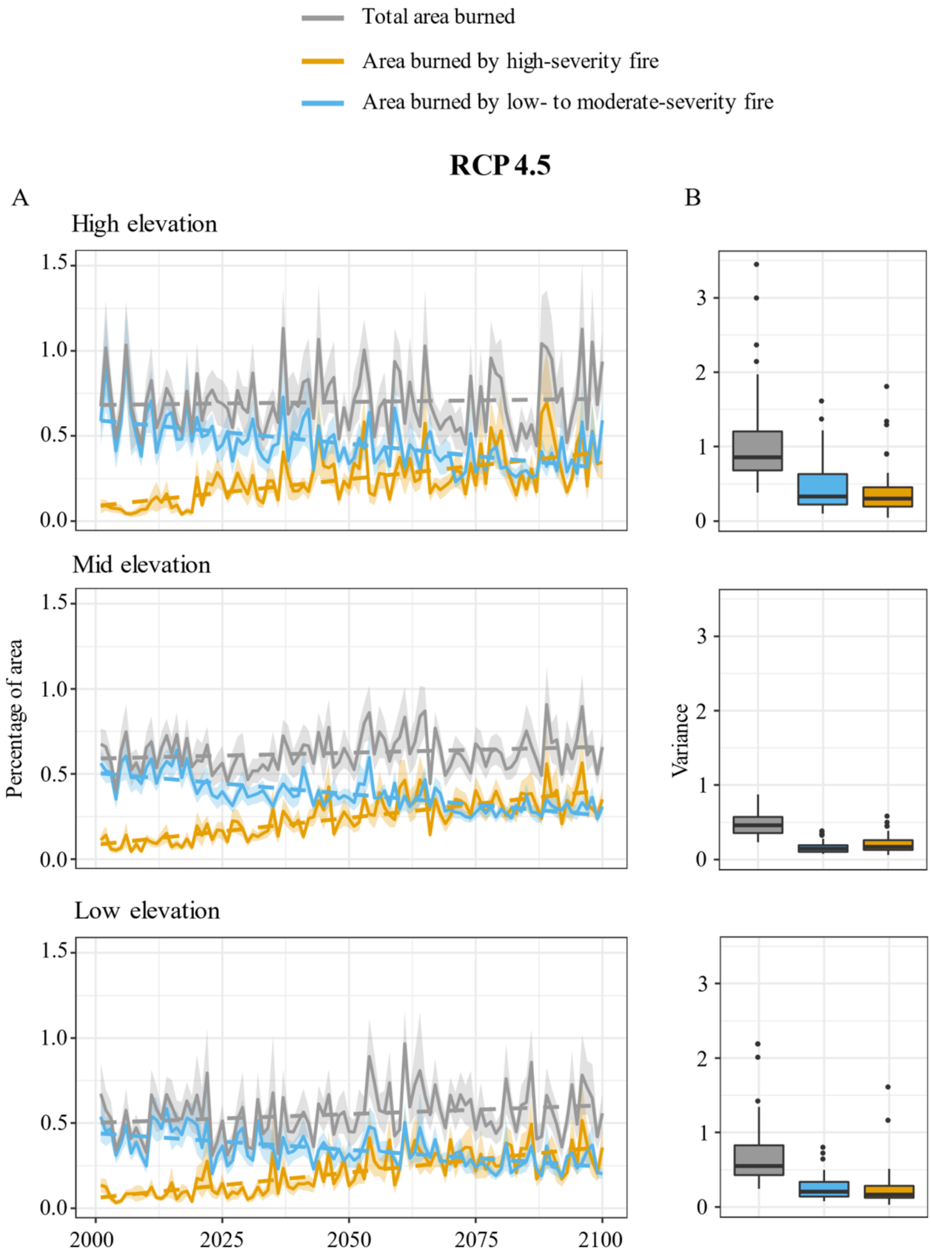

Figure 2 Projected area burned by low- to moderate- and high-fire severity by elevation in the upper Rio Grande watershed during the twenty-first century (**A**, **C**) and the variance (**B**, **D**) under projected climate forced with RCP 4.5 and RCP 8.5. Values correspond to annual averages from 40 replicate simulations. Dotted lines correspond to linear regression (see Table S2 for intercept, slope, and mean values)

When simulations included wildfire, the greatest amount of change occurred at high elevation, which accounted for most of the change reflected in the correlations for the entire landscape (Table S3). These differences are reflected in differences in biomass and

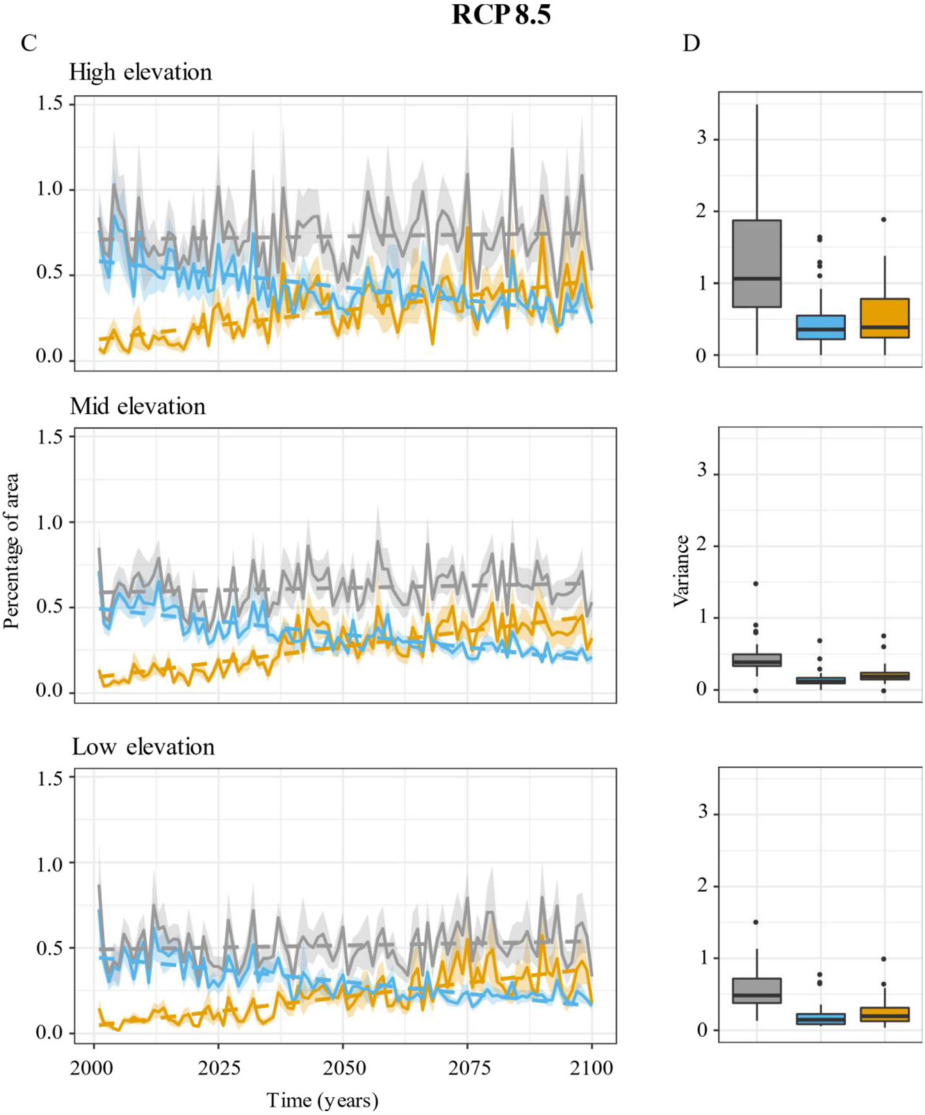

Figure 2 continued.

tree species richness between the two scenarios (Table 1). Starting biomass and tree species richness varied between the RCPs due to non-similar historical (1950–2000) climate conditions. Climate change only simulations had a much larger increase in biomass at high elevation (RCP4.5: 62 ± 9, RCP8.5: 101 ± 17 Mg. ha^{-1}) than at mid- (RCP4.5: 56 ± 7, RCP8.5: 86 ± 15 Mg. ha^{-1}) or low elevation (RCP4.5: 43 ± 4, RCP8.5: 58 ± 9 Mg. ha^{-1}). When combined with wildfire, the majority of the increased biomass that we simulated with warmer temperatures at high-elevation in the climate change only scenario was lost, especially under RCP 4.5 (Table 1). Species richness increased with decreasing elevation under both scenarios, with larger increases in the climate change only RCP 4.5 scenario (Table 1).

Table 1 Changes in projected biomass and tree species richness through the end of the twenty-first century by elevation band under the climate change only and climate change with wildfire scenarios. Biomass is the mean aboveground biomass for the elevation band. Richness is the mean number of tree species per grid cell (9 ha) in the elevation band. Stars indicate p value < 0.001 of student's t test between current and projected values. † indicates not significant differences between values from RCP 4.5 and 8.5 projections

	Elevation	Current (2000)	Projected climate without fire (2099)	Projected climate with fire (2099)
Biomass (Mg ha^{-1})				
RCP 4.5	High	168	+ 62 ± 9 *,†	+ 2 ± 14,†
	Mid	132	+ 56 ± 7 *	+ 26 ± 8 *
	Low	62	+ 43 ± 4 *	+ 27 ± 5 *
	High	131	+ 101 ± 17 *,†	+ 36 ± 18 *,†
RCP 8.5	Mid	116	+ 86 ± 15 *	+ 53 ± 14 *
	Low	57	+ 58 ± 9 *	+ 42 ± 9 *
	Tree species richness (number of species)			
	High	2.97	+ 0.96 ± 0.04 *	+ 0.47 ± 0.17 *
RCP 4.5	Mid	3.20	+ 1.63 ± 0.04 *	+ 1.07 ± 0.10 *
	Low	2.23	+ 1.72 ± 0.02 *,†	+ 1.18 ± 0.12 *,†
	High	3.01	+ 0.77 ± 0.06 *	+ 0.22 ± 0.18 *
RCP 8.5	Mid	3.22	+ 1.44 ± 0.05 *	+ 0.87 ± 0.12 *
	Low	2.21	+ 1.75 ± 0.02 *,†	+ 1.23 ± 0.13 *,†

3.3 Species dynamics

Within each elevation range, the effect of fire severity, frequency, and size on the dominant species varied substantially (Fig. 3A, C). At both mid and high elevation, all three fire attributes promoted *P. tremuloides* regeneration, but increasing fire frequency and severity were especially beneficial for *P. tremuloides* (+32 % high elevation, +13% mid-elevation compared to the scenario without fire by 2099; Fig. 3B, D). At high elevation, *P. engelmannii* decreased the most after large and frequent fires, especially under RCP 8.5, while the decreases in *A. lasiocarpa*, *P. menziesii*, *A. concolor*, and *P. flexilis* were more or less due to any type of fire (Fig. 3A). At mid-elevation, the distributions of the most abundant species *P. ponderosa* and *Q. gambelii* were not impacted by fire (Fig. 3A, C). The other species abundances decreased, mostly due to large fires, except for *A. concolor* which showed sensitivity to all types of fire. At low elevation, decreases in abundance of the most common species were primarily due to fire size (Figure 3A, C).

Overall, high-severity fires had a less negative impact on tree regeneration than large and/or frequent fire, with the exception of firs (*A. lasiocarpa* and *A. concolor*). Large fire was the key driver of the decrease in dominant species abundances all along the elevation gradient. However, of the importance of fire frequency was either similar to higher than fire size for several of the common species at high elevation (e.g., *A. concolor* and *lasiocarpa*., *P. flexilis*, *P. aristata*, *P. pungens*).

4 Discussion

Broadly, projected increasing high-severity fire patch sizes combined with climate change are expected to catalyze large vegetation shifts in forest ecosystems in the coming decades (Davis et al. 2019; Hansen et al. 2018; Parks et al. 2019; Singleton et al. 2019; Stevens-Rumann and

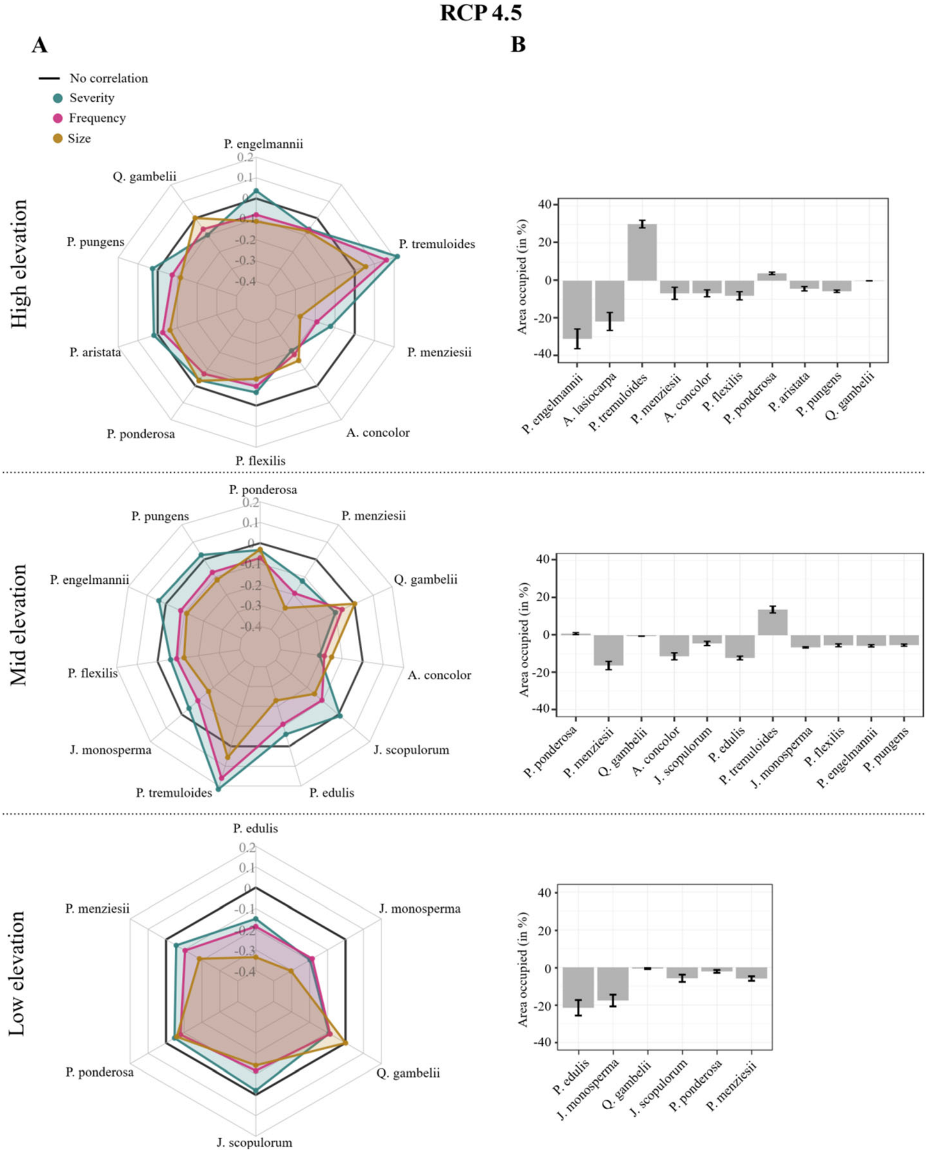

Figure 3 Pearson's correlations of individual species presence/absence between 2000 and 2099 and fire metrics (severity, frequency, and size) in each elevation band (**A**, **C**) and the difference in area occupied by each species at time 2099 between the climate change only and climate change and wildfire scenarios (**B**, **D**) for both projected climate conditions RCP 4.5 and 8.5. Only species covering more than 10% of the elevation bands at 2000 or 2099 are shown. Species are sorted from most to least abundant at time 2000 (clockwise for the radar chart and from the left for the bar chart). Correlations were calculated at the grid cell scale using burned grid cells from the 40 replicates. All Pearson's correlations are significant (p value < 0.05), with the exception of *P. engelmannii* and fire severity at high elevation. Differences in area occupied by species between both scenarios are the mean and standard deviation from the 40 replicate simulations. See Table S1 for detailed values

Morgan 2019). Similar to the current observed trends of increasing high-severity fire, we found a steady increase in area burned by high severity though the twenty-first century, and

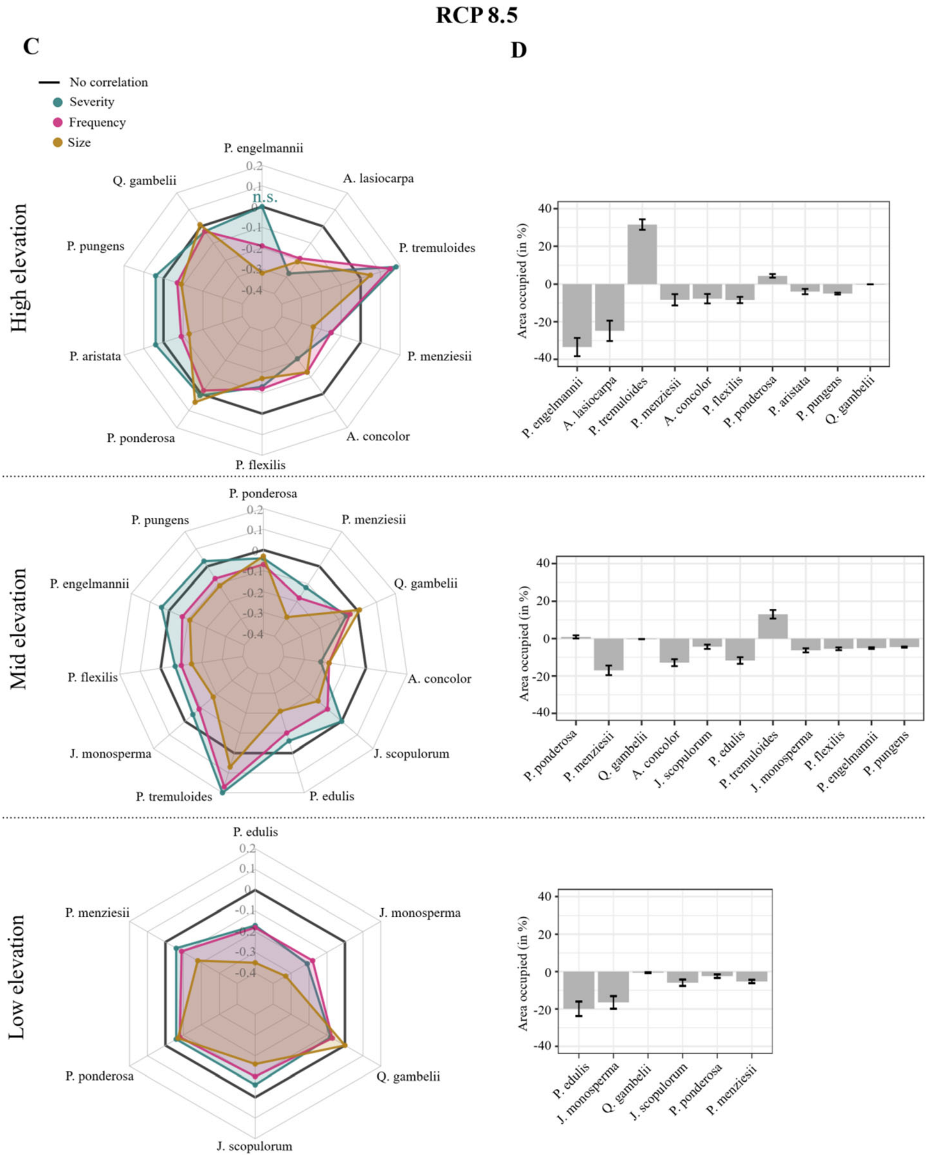

Figure 3 continued.

our results demonstrate that the interaction between fire and climate change caused larger changes in species distributions than climate change alone (Fig. 2, Table S3).

Overall, projected warming driven by increasing carbon dioxide and other greenhouse gases is expected to increase forest growth and tree species richness in the absence of disturbances during the twenty-first century (Flatley and Fulé 2016; Iverson and Prasad 2001). Our results support this and show an increase in biomass productivity and tree species richness along the elevation gradient under projected climate (Table 1). In the absence of wildfire, we observed an increase in the abundance of all species, except *P. tremuloides* and

Q. gambelii at mid and high elevations (Table S1). However, ongoing climate change is a driver of increased fire activity, and the compound effects of changing climate and wildfire are likely to reshape ecosystems (Liang et al. 2017b; Marshall and Falk 2020; Westerling 2016). We expected that simulated fire activity would cause the largest changes at low elevation because warmer, drier conditions reduce postfire tree regeneration (Donato et al. 2016; Kemp et al. 2019; Parks et al. 2019). However, we found the largest changes were in the high-elevation mixed-conifer and spruce-fir forests, even though tree species richness remained relatively constant over time (Table 1, S3).

Fires in the southwestern USA were actively suppressed by public land management agencies during the majority of the twentieth century, leading to an increase in fuel loads and fuel connectivity and favoring the expansion of species not adapted to fire (Fulé et al. 2002; Margolis et al. 2007; Mast and Wolf 2004; Strahan et al. 2016). In mixed-conifer forests, fine surface fuels are typically sparse and ladder fuels more abundant than in ponderosa pine forests, which historically caused more infrequent and larger mixed-severity fires (Schoennagel et al. 2004). Our results from early in the simulation period approximate this historic condition well, with high interannual variability in area burned and a mix of low- and moderate-severity coupled with high-severity fire (Fig. 2). These high-severity fire patches create larger canopy openings favoring the regeneration of early seral species that are capable resprouting or wind dispersal, such as *P. tremuloides* (Campbell and Shinneman 2017; Shive et al. 2018). As the climate continued to warm, the proportion of area burned at high-severity increased, causing declines in the dominant species *P. engelmannii* and *A. lasiocarpa*, which are not fire resistant (Bigler et al. 2005; Stevens et al. 2020). The increase in high-severity fire and resultant change in dominant species caused a large biomass loss, despite the positive effect of projected climate change on biomass productivity at high elevation (Table 1, Fig. 3). Moreover, this decrease in biomass due to wildfires is not compensated by warmer conditions under RCP 4.5 simulations, because temperature increases are insufficient to cause substantial increases in growth. The large and high-severity fires, in addition to promoting the establishment of *P. tremuloides*, allowed the establishment of *P. ponderosa*, which is adapted to more frequent fire and tolerant of warmer and drier conditions than the previously dominant *P. engelmannii* and *A. lasiocarpa* (Fig. 4). This finding indicates that fire can act to catalyze changes in species distributions by creating conditions that allow establishment of lower elevation species as the climate continues to change. However, warmer conditions and fires tend to limit the tree species diversification promoted by future climate conditions at regional scale (Table 1).

At low and mid-elevations, total area burned and the number of years with extreme fire activity were lower than at high elevation, and species composition and biomass were less impacted by wildfire (Tables 1 and S3, Figs. 2 and 3). At mid-elevation, two of the most common species, *P. ponderosa* and *P. menziesii*, are fire resistant, and another common species, *Q. gambelii*, resprouts following fire and can persist in both tree and shrub form (Guiterman et al. 2018; Kemp et al. 2016; Stoddard et al. 2015). At low elevation, pinyon-juniper woodlands are less productive, and even though *P. edulis* and *J. monosperma* are two species sensitive to fire, fuel limitations on fire size caused fires to be consistently smaller than at high elevation, reducing fire impacts (Koniak 1985; Parks et al. 2018; Poulos et al. 2020b).

High-elevation mixed-coniferous forests have been resilient to a broad range of climatic conditions and fire regimes over the past 6,000 years (Anderson et al. 2008; Higuera et al. 2014; Morris et al. 2015). Further, the prevailing hypothesis regarding climate change impacts on forests has been that impacts will be greatest at the lower elevation boundary or trailing edge of an ecosystem or species' distribution, leading to a focus on lower elevation pinyon-juniper woodlands and ponderosa pine forests (Davis et al. 2019; Kemp et al. 2019; Parks et al. 2019; Stevens-Rumann et al. 2017). While these lower elevation systems are certainly susceptible to vegetation change because of the combined effects of wildfire and climate, our simulations suggest that fire activity at high elevation, combined with ongoing climate change, could have significant impacts on both species distributions and biomass density (Coop et al. 2020; Keyser et al. 2020; O'Connor et al. 2020; Stevens-Rumann and Morgan 2019). Future fire regime changes will increase the chance that what is currently spruce-fir forest (*P. englemanii* and *A. lasiocarpa*), with a low-frequency fire regime, will become less common, especially under projected climate conditions associated with RCP 8.5. At higher rates of warming, this high-elevation forest type is replaced by *P. tremuloides*, a post-disturbance successional species, and species more common at mid-elevation (*P. ponderosa*, *P. menziesii*) (Fig. 3). Empirical observations through the last decade in the Grand Canyon National Park also show a shift in species dominance towards ponderosa pine in both the mixed-conifer and spruce-fir forests (Stoddard et al. 2020). Previous work on the Kaibab Plateau in Northern Arizona simulated widespread loss of more mesic conifer species and transition toward species more tolerant of warm, dry conditions with projected climate change (Flatley and Fulé 2016). The influence of topography on both climate and fire refugia are the likely cause of the persistence of more mesic conifer species in our topographically complex landscape compared to the Kaibab Plateau (Dobrowski 2011; Krawchuk et al. 2020).

There are three primary sources of uncertainty that could have influenced our results. First, the spatial resolution of the projected climate data we used in this study (~ 6-km grid) does not capture the fine-scale variability that occurs in a topographically complex system and is responsible for high spatial vegetation variability (Franklin et al. 2013). The average elevation range covered by each projected climate grid cell in our study area was 510 ± 280 m, which in a steep elevation gradient can mask substantial changes in temperature and precipitation. Further, approximately half of annual precipitation occurs during the summer monsoon, which has high spatial variability (Petrie et al. 2014). We attempted to minimize the effects of the projected climate data resolution by stratifying our landscape by elevation bands. However, the potential still exists for lags in species movement. Second, extreme drought events and insect outbreaks are also important disturbances in these ecosystems and can interact to cause widespread mortality (Anderegg et al. 2015; Ganey and Vojta 2011; Huang and Anderegg 2012; Kane et al. 2017; Williams et al. 2010). We did not simulate insect outbreaks, which can be an important driver of mortality during drought, and there is evidence that fine-scale processes influence the frequency and magnitude of extreme events (Diffenbaugh et al. 2005; Fei et al. 2019; Kolb et al. 2016). As a result of these limitations, our results may be optimistic about the resilience of these ecosystems to climate change. Finally, we parameterized the number of ignitions and fire size distribution from empirical data (2000–2019), and the simulated number of fires and fire sizes cannot exceed these values (Fig. S3). Given the link between climate and area burned, our simulations likely underestimate area burned (Westerling 2016). A feedback between vegetation and fire can reduce subsequent fire size, but this effect is dependent upon the rate of vegetation regrowth (Hurteau et al. 2019). In our landscape, low and mid-elevation areas could become fuel limited with ongoing warming and drying, but sustained productivity at high-elevation likely means we have underestimated the area burned. The effect of all three of these sources of uncertainty is a bias toward resiliency in the system. As a result, the ecosystem changes we expect to see under future conditions could be substantially larger than our result.

5 Conclusion

Changing climatic conditions are likely to alter species and ecosystem distributions, and, in the southwestern USA, these changes will occur over relatively short distances because of steep elevational gradients. By isolating climate change from the interaction of climate change and fire, our results indicate that the amount of distributional change and change in biomass is influenced heavily by fire size, severity, and frequency. This finding is especially true for high-elevation forests, which we expected to be more resilient to changing climate. Future research should prioritize understanding the processes controlling dispersal and establishment of higher-elevation tree species and climatic limitations on lower-elevation species establishing at higher elevation. These factors are likely to influence the amount and composition of forest cover at higher elevations in the southwestern USA as the climate continues to warm and dry and ecosystems become more flammable.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10584-021-03140-x.

Acknowledgements This work is supported by the Interagency Carbon Cycle Science program grant no. 2017-67004-26486/ project accession no. 1012226 from the USDA National Institute of Food and Agriculture and the Joint Fire Science Program under Project JFSP 16-1-05-8. We thank Scott L. Collins for his participation in the development of the project.

References

Abatzoglou JT, Williams AP (2016) Impact of anthropogenic climate change on wildfire across western US forests. Proc Natl Acad Sci U S A 42(113):11770–11775

Abatzoglou JT, Dobrowski SZ, Parks SA, Hegewisch KC (2018) TerraClimate, a high-resolution global dataset of monthly climate and climatic water balance from 1958–2015. Sci Data 5(1):170191. https://doi.org/10.1038/sdata.2017.191

Aber J, Ollinger S, Federer C, Reich P, Goulden G, Kicklighter D, Melillo J, Lathrop R (1995) Predicting the effects of climate change on water yield and forest production in the northeastern United States. Clim Res 05(3):207–222. https://doi.org/10.3354/cr005207

Ahlström A, Xia J, Arneth A, Luo Y, Smith B (2015) Importance of vegetation dynamics for future terrestrial carbon cycling. Environ Res Lett 10(5):054019. https://doi.org/10.1088/1748-9326/10/5/054019

Allen CD, Breshears DD, McDowell NG (2015) On underestimation of global vulnerability to tree mortality and forest die-off from hotter drought in the Anthropocene. Ecosphere 6(8):art129. https://doi.org/10.1890/ES15-00203.1

Anderegg LDL, HilleRisLambers J (2015) Drought stress limits the geographic ranges of two tree species via different physiological mechanisms. Glob Chang Biol 22(3):1029–1045. https://doi.org/10.1111/gcb.13148

Anderegg WRL, Hicke JA, Fisher RA, Allen CD, Aukema J, Bentz B, Hood S, Lichstein JW, Macalady AK, McDowell N, Pan Y, Raffa K, Sala A, Shaw JD, Stephenson NL, Tague C, Zeppel M (2015) Tree mortality from drought, insects, and their interactions in a changing climate. New Phytol 208(3):674–683

Anderson RS, Allen CD, Toney JL, Jass RB, Bair AN (2008) Holocene vegetation and fire regimes in subalpine and mixed conifer forests, southern Rocky Mountains, USA. Int J Wildland Fire 17(1):96–114. https://doi.org/10.1071/WF07028

Anderson-Teixeira KJ, Miller AD, Mohan JE, Hudiburg TW, Duval BD, DeLucia EH (2013) Altered dynamics of forest recovery under a changing climate. Glob Chang Biol 19(7):2001–2021. https://doi.org/10.1111/gcb.12194

Bigler C, Kulakowski D, Veblen TT (2005) Multiple disturbance interactions and drought influence fire severity in rocky mountain subalpine forests. Ecology 86(11):3018–3029. https://doi.org/10.1890/05-0011

Breshears DD, Barnes FJ (1999) Interrelationships between plant functional types and soil moisture heterogeneity for semiarid landscapes within the grassland/forest continuum: a unified conceptual model. Landsc Ecol 14(5):465–478. https://doi.org/10.1023/A:1008040327508

Britton CM, Dodd JD (1976) Relationships of photosynthetically active radiation and shortwave irradiance. Agric Meteorol 17(1):1–7. https://doi.org/10.1016/0002-1571(76)90080-7

Campbell JL, Shinneman D (2017) Potential influence of wildfire in modulating climate-induced forest redistribution in a central Rocky Mountain landscape. In Ecological Processes 6 7 117. https://doi.org/10.1186/s13717-017-0073-9

Chapin FS, Randerson JT, McGuire AD, Foley JA, Field CB (2008) Changing feedbacks in the climate–biosphere system. Front Ecol Environ 6(6):313–320. https://doi.org/10.1890/080005

Chen I-C, Hill JK, Ohlemüller R, Roy DB, Thomas CD (2011) Rapid range shifts of species associated with high levels of climate warming. Science 333(6045):1024–1026. https://doi.org/10.1126/science.1206432

Christian JR, Arora VK, Boer GJ, Curry CL, Zahariev K, Denman KL, Flato GM, Lee WG, Merryfield WJ, Roulet NT, Scinocca JF (2010) The global carbon cycle in the Canadian Earth system model (CanESM1): preindustrial control simulation. J Geophys Res Biogeosci 115(G3). https://doi.org/10.1029/2008JG000920

Collins, WJ, Bellouin N, Doutriaux-Boucher M, Gedney N, Hinton T, Jones CD, Liddicoat S, Martin G, O'Connor F, Rae J, Senior C, Totterdell I, Woodward S, Reichler T., Kim J (2008). Evaluation of the HadGEM2 model. Met Office Hadley Centre Technical Note (HCTN 74). http://www.metoffice.gov.uk/publications/HCTN/index.html

Coop JD, Parks SA, Stevens-Rumann CA, Crausbay SD, Higuera PE, Hurteau MD, Tepley A, Whitman E, Assal T, Collins BM, Davis KT, Dobrowski S, Falk DA, Fornwalt PJ, Fulé PZ, Harvey BJ, Kane VR, Littlefield CE, Margolis EQ, North M, Parisien M-A, Prichard S, Rodman KC (2020) Wildfire-driven forest conversion in Western North American landscapes. BioScience 70(8):659–673

Cooper CE, Muir JP, Morgan CLS, Moore GW (2018) Tortoise or hare: will resprouting oaks or reseeding pines dominate following severe wildfire? For Ecol Manag 408:54–66. https://doi.org/10.1016/j.foreco.2017.10.044

Crookston NL, Finley AO (2008). yaImpute: an R package for kNN imputation. J Stat Software 23(10) 16. https://www.fs.usda.gov/treesearch/pubs/29365

Crookston NL, Rehfeldt GE, Warwell MV (2007) Using forest inventory and analysis data to model plant-climate relationships. In: McRoberts RE, Reams GA, Van Deusen PC, McWilliams WH (eds) Proceedings of the Seventh Annual Forest Inventory and Analysis Symposium; October 3-6, 2005; Portland, ME. Gen. Tech. Rep. WO-77, vol 77. U.S. Department of Agriculture, Forest Service, Washington, DC, pp 243–250

Dale VH, Joyce LA, McNulty S, Neilson RP (2000) The interplay between climate change, forests, and disturbances. Sci Total Environ 262(3):201–204. https://doi.org/10.1016/S0048-9697(00)00522-2

Davis KT, Dobrowski SZ, Higuera PE, Holden ZA, Veblen TT, Rother MT, Parks SA, Sala A, Maneta MP (2019) Wildfires and climate change push low-elevation forests across a critical climate threshold for tree regeneration. Proc Natl Acad Sci 116(13):6193–6198. https://doi.org/10.1073/pnas.1815107116

de Bruijn A, Gustafson EJ, Sturtevant BR, Foster JR, Miranda BR, Lichti NI, Jacobs DF (2014) Toward more robust projections of forest landscape dynamics under novel environmental conditions: embedding PnET within LANDIS-II. Ecol Model 287:44–57. https://doi.org/10.1016/j.ecolmodel.2014.05.004

Diffenbaugh NS, Pal JS, Trapp RJ, Giorgi F (2005) Fine-scale processes regulate the response of extreme events to global climate change. Proc Natl Acad Sci 102(44):15774–15778. https://doi.org/10.1073/pnas.0506042102

Dobrowski SZ (2011) A climatic basis for microrefugia: the influence of terrain on climate. Glob Chang Biol 17(2):1022–1035. https://doi.org/10.1111/j.1365-2486.2010.02263.x

Donato DC, Harvey BJ, Turner MG (2016) Regeneration of montane forests 24 years after the 1988 Yellowstone fires: a fire-catalyzed shift in lower treelines? Ecosphere 7(8):e01410. https://doi.org/10.1002/ecs2.1410

Fei S, Morin RS, Oswalt CM, Liebhold AM (2019) Biomass losses resutling from insect and disease invasions in US forests. Proc Natl Acad Sci 116(35):17371–17376. https://doi.org/10.1073/pnas.1820601116

Flatley WT, Fulé PZ (2016) Are historical fire regimes compatible with future climate? Implications for forest restoration. Ecosphere 7(10):e01471. https://doi.org/10.1002/ecs2.1471

Franklin J, Davis FW, Ikegami M, Syphard AD, Flint LE, Flint AL, Hannah L (2013) Modeling plant species distributions under future climates: how fine scale do climate projections need to be? Glob Chang Biol 19(2):473–483. https://doi.org/10.1111/gcb.12051

Franklin J, Serra-Diaz JM, Syphard AD, Regan HM (2016) Global change and terrestrial plant community dynamics. Proc Natl Acad Sci 113(14):3725–3734. https://doi.org/10.1073/pnas.1519911113

Fulé PZ, Covington WW, Moore MM, Heinlein TA, Waltz AEM (2002) Natural variability in forests of the Grand Canyon, USA. J Biogeogr 29(1):31–47. https://doi.org/10.1046/j.1365-2699.2002.00655.x

Ganey JL, Vojta SC (2011) Tree mortality in drought-stressed mixed-conifer and ponderosa pine forests, Arizona, USA. For Ecol Manag 261(1):162–168. https://doi.org/10.1016/j.foreco.2010.09.048

Gratani L (2014) Plant phenotypic plasticity in response to environmental factors. Adv Botany 2014:208747. https://doi.org/10.1155/2014/208747

Guiterman CH, Margolis EG, Allen CD, Falk DA, Swetnam TW (2018) Long-term persistence and fire resilience of oak subfields in dry conifer forests of Northern New Mexico. Ecosystems 21:943–959. https://doi.org/10.1007/s10021-017-0192-2

Hansen WD, Braziunas KH, Rammer W, Seidl R, Turner MG (2018) It takes a few to tango: changing climate and fire regimes can cause regeneration failure of two subalpine conifers. Ecology 99(4):966–977. https://doi.org/10.1002/ecy.2181

Higuera PE, Briles CE, Whitlock C (2014) Fire-regime complacency and sensitivity to centennial-through millennial-scale climate change in Rocky Mountain subalpine forests, Colorado, USA. J Ecol 102(6): 1429–1441. https://doi.org/10.1111/1365-2745.12296

Huang C-Y, Anderegg WRL (2012) Large drought-induced aboveground live biomass losses in southern Rocky Mountain aspen forests. Glob Chang Biol 18(3):1016–1027. https://doi.org/10.1111/j.1365-2486.2011.02592.x

Hurteau MD, Liang S, Westerling AL, Wiedinmyer C (2019) Vegetation-fire feedback reduces projected area burned under climatechange. Scientific Reports 9(1)

IPCC ARS WGl (2013), Stocker TF, et al. eds. Climate change 2013: the physical science basis. Working Group l (WGl) Contribution to the Intergovernmental Panel on Climate Change (IPCC) 5th Assessment Report (ARS), Cambridge University Press

Iverson LR, Prasad AM (2001) Potential changes in tree species richness and forest community types following climate change. Ecosystems 4(3):186–199. https://doi.org/10.1007/s10021-001-0003-6

Jenkins JC, Chojnacky DC, Heath LS, Birdsey RA (2003) National-scale biomass estimators for United States tree species. For Sci 49(1):12–35. https://doi.org/10.1093/forestscience/49.1.12

Kane JM, Varner JM, Metz MR, van Mantgem PJ (2017) Characterizing interactions between fire and other disturbances and their impacts on tree mortality in western U.S. Forests. For Ecol Manag 405(1):188–199. https://doi.org/10.1016/j.foreco.2017.09.037

Kattge J, Díaz S, Lavorel S, Prentice IC, Leadley P, Bönisch G, Garnier E, Westoby M, Reich PB, Wright IJ, Cornelissen JHC, Violle C, Harrison SP, Bodegom PMV, Reichstein M, Enquist BJ, Soudzilovskaia NA, Ackerly DD, Anand M et al (2011) TRY – a global database of plant traits. Glob Chang Biol 17(9):2905–2935. https://doi.org/10.1111/j.1365-2486.2011.02451.x

Kelly AE, Goulden ML (2008) Rapid shifts in plant distribution with recent climate change. Proc Natl Acad Sci 105(33):11823–11826

Kemp KB, Higuera PE, Morgan P (2016) Fire legacies impact conifer regeneration across environmental gradients in the U.S. northern Rockies. Landsc Ecol 31(3):619–636. https://doi.org/10.1007/s10980-015-0268-3

Kemp KB, Higuera PE, Morgan P, Abatzoglou JT (2019) Climate will increasingly determine post-fire tree regeneration success in low-elevation forests, Northern Rockies, USA. Ecosphere 10(1):e02568. https://doi.org/10.1002/ecs2.2568

Keyser AR, Krofcheck DJ, Remy CC, Allen CD, Hurteau MD (2020) Simulated increases in fire activity reinforce shrub conversion in a southwestern US forest. Ecosystems. https://doi.org/10.1007/s10021-020-00498-4

Kitzberger T, Falk DA, Westerling AL, Swetnam TW (2017) Direct and indirect climate controls predict heterogeneous early-mid 21st century wildfire burned area across western and boreal North America. PLoS One 12(12):e0188486. https://doi.org/10.1371/journal.pone.0188486

Kolb TE, Fettig CJ, Ayres MP, Bentz BJ, Hicke JA, Mathiasen R, Stewart JE, Weed AS (2016) Observed and anticipated impacts of drought on forest insects and diseases in the United States. For Ecol Manag 380(15): 321–334. https://doi.org/10.1016/j.foreco.2016.04.051

Koniak S (1985) Succession in pinyon-juniper woodlands following wildfire in the Great Basin. Great Basin Nat 45(3):556–566

Krawchuk MA, Meigs GW, Cartwright JM, Coop JD, Davis R, Holz A, Kolden C, Meddens AJH (2020) Disturbance refugia within mosaics of forest fire, drought, and insect outbreaks. Front Ecol Environ 18(5): 235–244. https://doi.org/10.1002/fee.2190

Krofcheck DJ, Hurteau MD, Scheller RM, Loudermilk EL (2017) Restoring surface fire stabilizes forest carbon under extreme fire weather in the Sierra Nevada. Ecosphere 8(1):e01663. https://doi.org/10.1002/ecs2.1663

Krofcheck DJ, Hurteau MD, Scheller RM, Loudermilk EL (2018) Prioritizing forest fuels treatments based on the probability of high-severity fire restores adaptive capacity in Sierran forests. Glob Chang Biol 24(2):729–737. https://doi.org/10.1111/gcb.13913

Krofcheck DJ, Loudermilk EL, Hiers JK, Scheller RM, Hurteau MD (2019) The effects of management on long-term carbon stability in a southeastern U.S. forest matrix under extreme fire weather. Ecosphere 10(3): e02631. https://doi.org/10.1002/ecs2.2631

Lenoir J, Gégout JC, Marquet PA, de Ruffray P, Brisse H (2008) A significant upward shift in plant species optimum elevation during the 20th century. Science 320(5884):1768–1771. https://doi.org/10.1126/science.1156831

Liang S, Hurteau MD, Westerling AL (2017a) Response of Sierra Nevada forests to projected climate–wildfire interactions. Glob Chang Biol 23(5):2016–2030. https://doi.org/10.1111/gcb.13544

Liang S, Hurteau MD, Westerling AL (2017b) Potential decline in carbon carrying capacity under projected climate-wildfire interactions in the Sierra Nevada. Sci Rep 7:2420. https://doi.org/10.1038/s41598-017-02686-0

Long MC, Lindsay K, Peacock S, Moore JK, Doney SC (2013) Twentieth-century oceanic carbon uptake and storage in CESM1(BGC). J Clim 26(18):6775–6800. https://doi.org/10.1175/JCLI-D-12-00184.1

Margolis EQ, Swetnam TW, Allen CD (2007) A stand-replacing fire history in upper montane forests of the southern Rocky Mountains. Can J For Res 37(11):2227–2241. https://doi.org/10.1139/X07-079

Marshall LA, Falk DA (2020) Demographic trends in community functional tolerance reflect tree responses to climate and altered fire regimes. Ecol Appl 30(8):e02197. https://doi.org/10.1002/eap.2197

Mast JN, Wolf JJ (2004) Ecotonal changes and altered tree spatial patterns in lower mixed-conifer forests, Grand Canyon National Park, Arizona, U.S.A. Landsc Ecol 19(2):167–180. https://doi.org/10.1023/B:LAND.0000021718.20058.36

Millar CI, Stephenson NL (2015) Temperate forest health in an era of emerging megadisturbance. Science 349(6250):823–826. https://doi.org/10.1126/science.aaa9933

Miller DA, White RA (1998) A conterminous United States multilayer soil characteristics dataset for regional climate and hydrology modeling. Earth Interact 2(2):1–26. https://doi.org/10.1175/1087-3562(1998)002<0001:ACUSMS>2.3.CO;2

Miller JD, Safford HD, Crimmins M, Thode AE (2009) Quantitative evidence for increasing forest fire severity in the Sierra Nevada and southern Cascade mountains, California and Nevada, USA. Ecosystems 12(1):16–32. https://doi.org/10.1007/s10021-008-9201-9

Morin X, Viner D, Chuine I (2008) Tree species range shifts at a continental scale: new predictive insights from a process-based model. J Ecol 96(4):784–794. https://doi.org/10.1111/j.1365-2745.2008.01369.x

Morris JL, DeRose RJ, Brunelle AR (2015) Long-term landscape changes in a subalpine spruce-fir forest in central Utah, USA. Forest Ecosyst 2(1):35. https://doi.org/10.1186/s40663-015-0057-0

O'Connor CD, Falk DA, Garfin GM (2020) Projected climate-fire interactions drive forest to shrubland transition on an Arizona Sky Island. Front Environ Sci 8:137. https://doi.org/10.3389/fenvs.2020.00137

Ohmann JL, Gregory MJ (2002) Predictive mapping of forest composition and structure with direct gradient analysis and nearest- neighbor imputation in coastal Oregon, U.S.A. Can J For Res 32(4):725–741. https://doi.org/10.1139/x02-011

Overpeck JT, Rind D, Goldberg R (1990) Climate-induced changes in forest disturbance and vegetation. Nature 343(6253):51–53. https://doi.org/10.1038/343051a0

Parks SA, Dobrowski SZ, Panunto MH (2018) What drives low-severity fire in the Southwestern USA? Forests 9(4):165. https://doi.org/10.3390/f9040165

Parks SA, Dobrowski SZ, Shaw JD, Miller C (2019) Living on the edge: trailing edge forests at risk of fire-facilitated conversion to non-forest. Ecosphere 10(3):e02651. https://doi.org/10.1002/ecs2.2651

Pecl GT, Araújo MB, Bell JD, Blanchard J, Bonebrake TC, Chen I-C, Clark TD, Colwell RK, Danielsen F, Evengård B, Falconi L, Ferrier S, Frusher S, Garcia RA, Griffis RB, Hobday AJ, Janion-Scheepers C, Jarzyna MA, Jennings S et al (2017) Biodiversity redistribution under climate change: impacts on ecosystems and human well-being. Science 355(6332):eaai9214. https://doi.org/10.1126/science.aai9214

Petrie MD, Collins SL, Gutzler DS, Moore DM (2014) Regional trends and local variability in monsoon precipitation in the northern Chihuahuan Desert, USA. J Arid Environ 103:63–70. https://doi.org/10.1016/j.jaridenv.2014.01.005

Petrie MD, Wildeman AM, Bradford JB, Hubbard RM, Lauenroth WK (2016) A review of precipitation and temperature control on seedling emergence and establishment for ponderosa and lodgepole pine forest regeneration. For Ecol Manag 361:328–338. https://doi.org/10.1016/j.foreco.2015.11.028

Pierce DW, Cayan DR, Thrasher BL (2014) Statistical downscaling using localized constructed analogs (LOCA). J Hydrometeorol 15(6):2558–2585. https://doi.org/10.1175/JHM-D-14-0082.1

Pierce DW, Cayan DR, Maurer EP, Abatzoglou JT, Hegewisch KC (2015) Improved bias correction techniques for hydrological simulations of climate change. J Hydrometeorol 16(6):2421–2442. https://doi.org/10.1175/JHM-D-14-0236.1

Poulos HM, Barton AM, Berlyn GP, Schwilk DW, Faires CE, McCurdy WC (2020a) Differences in leaf phisiology among juvenile pines and oaks following high-severity wildfire in an Arizona Sky Island Mountain range. For Ecol Manag 457(1):117704. https://doi.org/10.1016/j.foreco.2019.117704

Poulos HM, Reemts CM, Wogan KA, Karges JP, Gatewood RG (2020b) Multiple wildfires with minimal consequences: low severity wildfire effects on West Texas piñon-juniper woodlands. For Ecol Manag 473:118293. https://doi.org/10.1016/j.foreco.2020.118293

R Core Team (2019) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. URL http://www.R-project.org/

Reclamation 2013 Downscaled CMIP3 and CMIP5 Climate and hydrology projections: release of downscaled CMIP5 climate projections, comparison with preceding information, and summary of user needs', prepared by the U.S. Department of the Interior, Bureau of Reclamation, Technical Services Center, Denver, Colorado. 47

Remy CC, Krofcheck DJ, Keyser AR, Litvak ME, Collins SL, Hurteau MD (2019) Integrating Species-specific information in models improves regional projections under climate change. Geophys Res Lett 46(12):6554–6562. https://doi.org/10.1029/2019GL082762

Riahi K, Grübler A, Nakicenovic N (2007) Scenarios of long-term socio-economic and environmental development under climate stabilization. Technol Forecast Soc Chang 74(7):887–935. https://doi.org/10.1016/j.techfore.2006.05.026

Scheller RM, Domingo JB, Sturtevant BR, Williams JS, Rudy A, Gustafson EJ, Mladenoff DJ (2007) Design, development, and application of LANDIS-II, a spatial landscape simulation model with flexible temporal and spatial resolution. Ecol Model 201(3):409–419. https://doi.org/10.1016/j.ecolmodel.2006.10.009

Schoennagel T, Veblen TT, Romme WH (2004) The interaction of fire, fuels, and climate across rocky mountain forests. BioScience 54(7):661–676. https://doi.org/10.1641/0006-3568(2004)054[0661:TIOFFA]2.0.CO;2

Sheppard PR, Comrie AC, Packin GD, Angersbach K, Hughes MK (2002) The climate of the US Southwest. Clim Res 21(3):219–238. https://doi.org/10.3354/cr021219

Shive KL, Preisler HK, Welch KR, Safford HD, Butz RJ, O'Hara KL, Stephens SL (2018) From the stand scale to the landscape scale: predicting the spatial patterns of forest regeneration after disturbance. Ecol Appl 28(6):1626–1639. https://doi.org/10.1002/eap.1756

Singleton MP, Thode AE, Sánchez Meador AJ, Iniguez JM (2019) Increasing trends in high-severity fire in the southwestern USA from 1984 to 2015. For Ecol Manag 433:709–719. https://doi.org/10.1016/j.foreco.2018.11.039

Stevens JT, Kling MM, Schwilk DW, Varner JM, Kane JM (2020) Biogeography of fire regimes in western U.S. conifer forests: a trait-based approach. Glob Ecol Biogeogr 29(5):944–955. https://doi.org/10.1111/geb.13079

Stevens-Rumann CS, Morgan P (2019) Tree regeneration following wildfires in the western US: a review. Fire Ecology 15(1):15. https://doi.org/10.1186/s42408-019-0032-1

Stevens-Rumann CS, Kemp KB, Higuera PE, Harvey BJ, Rother MT, Donato DC, Morgan P, Veblen TT (2017) Evidence for declining forest resilience to wildfires under climate change. Ecol Lett 21(2):243–252. https://doi.org/10.1111/ele.12889

Stoddard MT, Sánchez Meador AJ, Fulé PZ, Korb JE (2015) Five-year post-restoration conditions and simulated climate-change trajectories in a warm/dry mixed-conifer forest, southwestern Colorado, USA. For Ecol Manag 356:253–261. https://doi.org/10.1016/j.foreco.2015.07.007

Stoddard MT, Fulé PZ, Huffman DW, Sánchez Meador AJ, Roccaforte JP (2020) Ecosystem management applications of resource objective wildfires in forests of the Grand Canyon National Park, USA. Int J Wildland Fire 29(2):190–200. https://doi.org/10.1071/WF19067

Strahan RT, Meador AJS, Huffman DW, Laughlin DC (2016) Shifts in community-level traits and functional diversity in a mixed conifer forest: a legacy of land-use change. J Appl Ecol 53(6):1755–1765. https://doi.org/10.1111/1365-2664.12737

Sturtevant BR, Scheller RM, Miranda BR, Shinneman D, Syphard A (2009) Simulating dynamic and mixed-severity fire regimes: a process-based fire extension for LANDIS-II. Ecol Model 220(23):3380–3393. https://doi.org/10.1016/j.ecolmodel.2009.07.030

The Commonwealth Scientific and Industrial Research Organisation; Bureau of Meteorology (2017) WCRP CMIP5: the CSIRO-BOM team ACCESS1-0 model output collection. Centre for Environmental Data Analysis, 07/31/2020. http://catalogue.ceda.ac.uk/uuid/98a933094fa44e8cb886649cf3f5ba4c

Thom D, Rammer W, Seidl R (2017) Disturbances catalyze the adaptation of forest ecosystems to changing climate conditions. Glob Chang Biol 23(1):269–282. https://doi.org/10.1111/gcb.13506

Trumbore S, Brando P, Hartmann H (2015) Forest health and global change. Science 349(6250):814–818. https://doi.org/10.1126/science.aac6759

van Mantgem PJ, Nesmith JCB, Keifer M, Knapp EE, Flint A, Flint L (2013) Climatic stress increases forest fire severity across the western United States. Ecol Lett 16(9):1151–1156. https://doi.org/10.1111/ele.12151

Westerling AL (2016) Increasing western US forest wildfire activity: sensitivity to changes in the timing of spring. Philos Trans R Soc B 371(1696):20150178. https://doi.org/10.1098/rstb.2015.0178

Williams AP, Allen CD, Millar CI, Swetnam TW, Michaelsen J, Still CJ, Leavitt SW (2010) Forest responses to increasing aridity and warmth in the southwestern United States. Proc Natl Acad Sci 107(50):21289–21294. https://doi.org/10.1073/pnas.0914211107

Zhu K, Woodall CW, Clark JS (2011) Failure to migrate: lack of tree range expansion in response to climate change. Glob Chang Biol 18(3):1042–1052. https://doi.org/10.1111/j.1365-2486.2011.02571.x

Affiliations

Cécile C. Remy[1] • Alisa R. Keyser[1] • Dan J. Krofcheck[1] • Marcy E. Litvak[1] • Matthew D. Hurteau[1]

✉ Matthew D. Hurteau
mhurteau@unm.edu

[1] Department of Biology, University of New Mexico, Albuquerque, NM, USA