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A changing climate is snuffing out post-fire recovery in montane forests

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Abstract

Aim: Climate warming is increasing fire activity in many of Earth's forested ecosystems. Because fire is a catalyst for change, investigation of post-fire vegetation response is critical to understanding the potential for future conversions from forest to non-forest vegetation types. We characterized the influences of climate and terrain on post-fire tree regeneration and assessed how these biophysical factors might shape future vulnerability to wildfire-driven forest conversion.

Location: Montane forests, Rocky Mountains, USA.

Time period: 1981–2099.

Taxa studied: *Pinus ponderosa*; *Pseudotsuga menziesii*.

Methods: We developed a database of dendrochronological samples ($n = 717$) and plots ($n = 1,301$) in post-fire environments spanning a range of topoclimatic settings. We then used statistical models to predict annual post-fire seedling establishment suitability and total post-fire seedling abundance from a suite of biophysical correlates. Finally, we reconstructed recent trends in post-fire recovery and projected future dynamics using three general circulation models (GCMs) under moderate and extreme CO_2 emission scenarios.

Results: Though growing season (April–September) precipitation during the recent period (1981–2015) was positively associated with suitability for post-fire tree seedling establishment, future (2021–2099) trends in precipitation were widely variable among GCMs, leading to mixed projections of future establishment suitability. In contrast, climatic water deficit (CWD), which is indicative of warm, dry conditions, was negatively associated with post-fire seedling abundance during the recent period and was projected to increase throughout the southern Rocky Mountains in the future. Our findings suggest that future increases in CWD and an increased frequency of extreme drought years will substantially reduce post-fire seedling densities.

Main conclusions: This study highlights the key roles of warming and drying in declining forest resilience to wildfire. Moisture stress, driven by macroclimate and topographic setting, will interact with wildfire activity to shape future vegetation patterns throughout the southern Rocky Mountains, USA.

KEYWORDS
climate change, conifer forests, dry forests, ecosystem resilience, montane zone, tree regeneration, western United States, wildfire

1 | INTRODUCTION

Climate warming is driving changes in vegetation phenology (Piao et al., 2019), increases in tree mortality rates (van Mantgem et al., 2009), and shifts in species distributions (Chen et al., 2011). Given the tremendous importance of plant life to Earth's ecosystems and humanity, a better understanding of these effects is needed to facilitate adaptation and mitigation planning. Statistical models that relate species presence or abundance to bioclimatic predictors are a common approach to understanding and projecting the influence of climate on plant species (Franklin, 2010; Pearson & Dawson, 2003). Traditionally, such models have often focused on the mature individuals of a species in undisturbed settings (e.g. McKenney et al., 2011). Yet for many tree species, juveniles have a narrower climatic niche than mature individuals (Bell et al., 2014; Dobrowski et al., 2015), and the existing distribution of mature individuals may reflect the environment they experienced in early life stages rather than the current environment (Grubb, 1977). Indeed, the patterns of new tree establishment may provide an early indication of the impacts of a changing climate (Sittaro et al., 2017). Intact forests maintain an element of system inertia that can mask this signal because mature trees moderate the environment experienced by juveniles (Davis et al., 2018; Dobrowski et al., 2015). Thus, the direct impacts of a changing climate may take decades to centuries to cause substantial shifts in undisturbed forest communities.

Wildland fire is a crucial indirect pathway by which climate can affect forests (Coop et al., 2020; Johnstone et al., 2016). High-severity fires, in combination with a changing climate, interrupt system inertia and 'break the legacy lock' (*sensu* Johnstone et al., 2010) of the prior system state, driving rapid shifts in local vegetation. Fire activity has increased throughout forests of the western United States since the 1980s, and much of this increase has been attributed to decreases in summer precipitation (Holden et al., 2018) and increasing aridity driven by anthropogenic climate change (Abatzoglou & Williams, 2016). Continued increases in weather conducive to fire ignition and spread are likely in many parts of North America (Kitzberger et al., 2017). A warming climate also hinders post-fire forest recovery, and severely burned areas are less likely to recover to a forested state when burning is followed by warm, dry periods (Davis et al., 2019; Stevens-Rumann et al., 2018). The integration of fire activity and post-fire recovery in projections of future vegetation dynamics is needed to effectively predict climate-driven changes in forested ecosystems.

We synthesized two complementary and spatially extensive field datasets that span the montane zone of the southern Rocky Mountains, USA, to develop models of annual post-fire seedling establishment and total post-fire seedling abundance. These models characterize spatio-temporal variation in forest resilience to wildfire 1981–2099 by incorporating 60-m terrain variables and 250-m climate surfaces. Specifically, we focused on the juvenile life stage of two widely distributed tree species (ponderosa pine – *Pinus ponderosa* var. *scopulorum* and Douglas-fir – *Pseudotsuga menziesii* var. *glauca*). We also incorporated interannual climate variability in the models, as extreme events can have lasting influences on forest structure (Andrus et al., 2018; Law et al., 2019). We asked the following questions: (a) How do annual patterns of post-fire tree seedling establishment in recent fires relate to interannual climate variability and time since fire? (b) What biophysical factors are most strongly associated with total post-fire seedling densities in recent fires? (c) What percentage of the montane zone in the southern Rocky Mountains was climatically suitable for post-fire seedling establishment in the recent (1981–2015) period, and how might this change throughout the remainder of the 21st century (2021–2099)? (d) How do recent post-fire seedling densities compare to projected densities in the remainder of the 21st century under moderate and extreme CO_2 emission scenarios?

2 | METHODS

2.1 | Study area

This study focuses on the montane zone of the Southern Rocky Mountains Ecoregion (SRME; United States Environmental Protection Agency Level III Ecoregion 21). The SRME spans *c*. 145,000 km^2 of topographically complex terrain in southern Wyoming, central and western Colorado, and northern New Mexico, USA (Figure 1). Here, we define the montane zone as vegetation types including a component of ponderosa pine, pine–oak, or mixed-conifer forests in the environmental site potential layer from the Landscape Fire and Resource Management Planning Tools program, which represents the potential natural vegetation on a site in the absence of disturbance (Rollins, 2009; Supporting Information Appendix S1). Forested landscapes cover 56.3% of the SRME and the montane zone spans 49.9% of the total forested area (Figure 1; Supporting Information Appendix S1). Dominant tree species in the montane zone include ponderosa pine, Douglas-fir, white fir (*Abies concolor* var. *concolor*), lodgepole pine (*Pinus contorta* var. *latifolia*), quaking aspen (*Populus tremuloides*), Gambel oak (*Quercus gambelii*) and blue spruce (*Picea pungens*), with relative abundances varying throughout the region.

2.2 | Field data

We combined data from six studies that described annual post-fire tree seedling (i.e. all juvenile trees originating following fire) establishment or total post-fire seedling abundance across a range of fire severities, climatic conditions and topographic settings (Chambers et al., 2016,

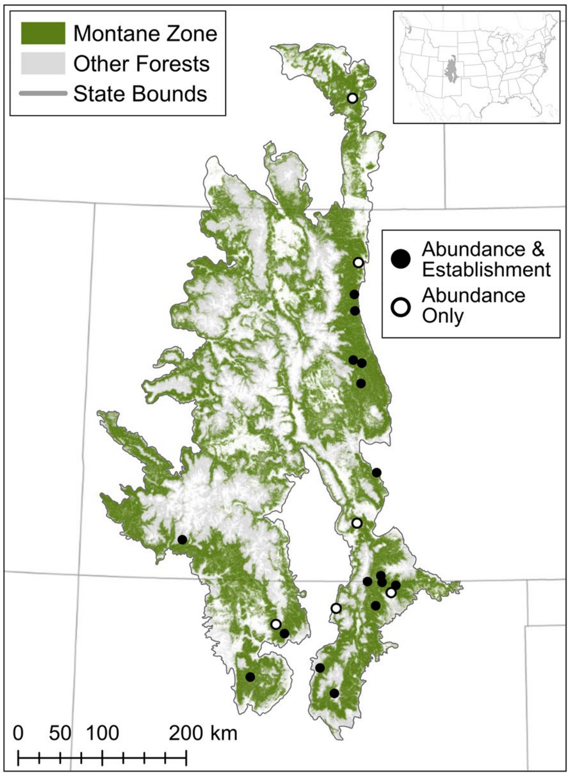

FIGURE 1 Site map showing the locations of the 22 surveyed fires in the Southern Rocky Mountains Ecoregion. All sites included post-fire conifer seedling abundance surveys, while sites with 'abundance and establishment' also included destructive samples of post-fire seedlings dated to the year of germination

unpublished data; Ouzts et al., 2015; Rodman, Veblen, Chapman, et al., 2020; Rother & Veblen, 2016, 2017) to develop a regionally extensive database of post-fire forest recovery in the montane zone of the SRME. All surveyed fires occurred 1988–2010, with a range of 7–29 years between fire occurrence and the timing of field sampling. Specifically, we focused on two important montane conifer species (i.e. ponderosa pine and Douglas-fir) that vary in shade-, drought- and fire-tolerance. In total, these data comprise (a) 717 post-fire seedlings dated to the year of establishment (ponderosa pine $n = 624$; Douglas-fir $n = 93$) from 16 fires, and (b) 1,301 plots used to survey post-fire abundance for 22 fires (Figure 1). The 717 post-fire seedlings were destructively sampled and dated following the protocols of Rother and Veblen (2017). Dating errors using these methods have been reported to be *c.* 0.3 years (Hankin et al., 2018), enabling analyses at an annual resolution. Post-fire conifer seedling abundance was assessed somewhat differently among studies, but all data included observations of abundance for ponderosa pine and Douglas-fir, as well as forest structural attributes and biophysical predictors.

2.3 | Spatial data

Gridded climate data are typically developed at coarse spatial resolutions that do not reflect the topoclimatic variation inherent to mountainous areas (Franklin et al., 2013). To address this limitation of data resolution, we developed annual gridded climate datasets for the recent (1981–2015) and future (2021–2099) periods at 250-m resolution using spatial gradient and inverse distance squared interpolation (GIDS; Flint & Flint, 2012) of data from the Gridded Surface Meteorological (Abatzoglou, 2013) and Multivariate Adaptive Constructed Analogs datasets (Abatzoglou & Brown, 2012). We used 30-m digital elevation models (DEMs; United States Geological Survey, 1999) and 250-m water balance metrics of Holden et al. (2019) as ancillary data in downscaling (Supporting Information Appendix S2). Gridded climate data are inherently uncertain, but GIDS-interpolated outputs have been shown to closely match local climatic conditions in complex terrain (McCullough et al., 2016). Future climate projections were based on outputs from 19 general circulation models (GCMs) under two CO_2 emissions scenarios (i.e. representative concentration pathways; RCPs) from phase five of the Coupled Model Intercomparison Project (CMIP5). In CMIP5, RCPs estimate changes in radiative forcing (Δ W/m^2) at the top of the troposphere from years 1750–2100. RCP 4.5 assumes moderate increases in emissions through 2040, followed by declines, while RCP 8.5 assumes substantial increases in emissions through 2100 (Riahi et al., 2011). Due to computational limitations, we reduced the number of GCMs used in final analyses to three (under two RCPs for a total of six potential trajectories) that span the range of projected changes in climate throughout the 21st century (Supporting Information Appendix S2).

We used annual actual evapotranspiration (AET), annual climatic water deficit (CWD), and growing season (i.e. April–September) precipitation as potential climatic predictors of post-fire establishment and abundance. AET identifies areas with the simultaneous availability of energy and moisture and is an indicator of site productivity; CWD is the difference between potential and actual evapotranspiration and is an indicator of drought stress (Stephenson, 1998). Growing season precipitation influences tree establishment across a broad elevational range in the SRME (Andrus et al., 2018; Rother & Veblen, 2017). We analysed trends in 1981–2015 and 2021–2099 AET, CWD, and growing season precipitation using Mann–Kendall trend tests with the variance correction approach of Hamed and Rao (1998) to address serial autocorrelation.

We also developed or acquired spatial data describing terrain, soils, and fire severity for use as predictors in statistical models of seedling abundance (Table 1, Supporting Information Appendix S3). Using *c.* 30-m DEMs, we calculated topographic position index (TPI; Weiss, 2001) and heat load index (HLI; McCune & Keon, 2002) – potential indicators of site moisture and solar heating, respectively. We acquired spatial data describing clay content and soil pH from the Probabilistic Remapping of SSURGO (POLARIS) database (Chaney et al., 2016), and Landsat-derived fire severity data from the Monitoring Trends in Burn Severity (MTBS) program (Eidenshink et al. 2007). We projected terrain, soil, and fire severity data to Universal Transverse Mercator (UTM) Zone 13N and aggregated these data to a 60-m spatial resolution to correspond with the designs of field surveys.

TABLE 1 A summary of predictor variables tested for inclusion in models of post-fire seedling abundance

Fire	
Minimum distance to seed tree	Distance (m) to the closest surviving conifer. Values were square-root transformed before analysis to incorporate a nonlinear effect. Greater distance to seed source may lead to a decrease in seed availability and seedling density.
Relative differenced normalized burn ratio (RdNBR)	RdNBR is a continuous index of fire severity derived from pre- and post-fire Landsat imagery (Miller & Thode, 2007). High fire severity might reduce overall seedling densities, but smaller high-severity patches may also increase ponderosa pine density by modifying the seedbed and increasing light availability.
Time since fire	The number of years between fire occurrence and the time of field surveys. Increasing time since fire may allow for increases in seedling density over time.
Topography/terrain	
Heat load index (HLI)	HLI combines slope, aspect and latitude to estimate terrain-driven differences in solar heating, with higher values indicative of warmer sites (McCune & Keon 2002: eq. 2). We expected that cooler and wetter terrain (i.e. low HLI) would have greater seedling densities, particularly at low elevations.
Topographic position index (TPI)	TPI is the difference between the elevation of a site and the average elevation of its surroundings (Weiss, 2001). We calculated this metric in 3-cell and 15-cell neighbourhoods, representing fine-scale and broader-scale topographic settings, respectively. We expected that both species would have higher densities in valley bottoms (i.e. negative TPI), particularly at low elevations.
Soils	
Percent clay content	A measure of soil texture derived from the Probabilistic Remapping of SSURGO (POLARIS) database (Chaney et al., 2016). Lower clay content was expected to be positively associated with seedling densities due to a reduction in shrink-swell potential.
Soil pH	A measure of the acidity and alkalinity of soils derived from the POLARIS database (Chaney et al., 2016). Lower soil pH may be positively associated with seedling density as a reflection of both parent material and the wetter climates associated with acidic soils.
Average climate	
Average actual evapotranspiration (AET)	Average annual AET (in mm; 1981–2010) based on monthly water balance models (Supporting Information Appendix S2). Higher AET, generally associated with higher productivity sites, was expected to have a positive relationship with seedling density.
Average climatic water deficit (CWD)	Average annual CWD (in mm; 1981–2010) based on monthly water balance models (Supporting Information Appendix S2). CWD, indicative of moisture limitation experienced by plants, was expected to have a negative or nonlinear relationship with seedling density, with higher densities at sites with intermediate to low CWD.
Average Apr-Sep precipitation (PPT)	Average precipitation (in mm; 1981–2010) in the April–September growing season. We expected a positive or nonlinear relationship between precipitation and seedling density, with higher densities at sites with intermediate to high precipitation.
Post-fire climate	
Post-fire AET[a]	Mean, minimum and maximum (separate variables) annual AET from the 5 years following fire occurrence. Higher post-fire AET may increase the chances of seedling establishment and survival.
Post-fire CWD[a]	Mean, minimum and maximum (separate variables) annual CWD from the 5 years after fire occurrence. Higher post-fire CWD may decrease the chances of initial seedling establishment and survival.
Post-fire Apr-Sep PPT[a]	Mean, minimum and maximum (separate variables) total precipitation from April–September in the 5 years following fire occurrence. Above-average precipitation during the growing season may be beneficial to seedling establishment.

Note.: Further descriptions of each variable are provided in Supporting Information Appendices S2 and S3.

[a]All post-fire climate variables were scaled and centred to z-scores specific to each 250-m grid cell (relative to 1981–2015 values) before analysis, thus indicating site-specific variation from longer-term averages.

2.4 | Models of annual post-fire seedling establishment

We developed models of annual suitability for post-fire seedling establishment based on interannual climate variability and time since fire using boosted regression trees (BRTs). BRTs outperformed generalized linear mixed models (GLMMs) and other statistical approaches in spatially stratified cross-validation (not shown; 16 folds in which one fire was withheld as a test set in each fold). For the response variable in BRTs, we aggregated counts of establishing seedlings (by year) to the level of individual fires to accommodate variation in plot design among studies; also, we combined counts for the two species because of the low sample size for Douglas-fir and because preliminary analyses indicated similar climate responses for the two species. We scaled and centred (i.e. z-score transformation) seedling counts using the series-wide mean and standard deviation in each fire, such that positive values in a given year had above-average post-fire establishment in a given fire. This transformation was useful as it standardized the response variable across fires and accounted for differences in sample depth. We extracted annual AET, annual CWD, and growing season precipitation within each fire perimeter, and scaled and centred values of each predictor based on the baseline period of 1981–2015. We selected the number of trees in the final model (i.e. 2,325) using the 'gbm.step' function in the 'dismo' package (Hijmans et al., 2017) in R version 3.5.0 (R Core Team, 2018). We used a Gaussian loss function, a learning rate of 0.001, a step size of 5 and a complexity of 2, allowing for two-way variable interactions (Elith et al., 2008). We assessed BRT accuracy by comparing observed and predicted establishment suitability (i.e. z-scores of seedling counts), both in the entire dataset and in spatially stratified cross-validation. We determined the percent relative influence of each predictor in final BRTs based on the average decrease in mean squared error.

2.5 | Models of total post-fire seedling abundance

To predict post-fire ponderosa pine and Douglas-fir seedling abundances, we developed GLMMs using the 'glmmTMB' package (Brooks et al., 2017) in R. We used zero-inflated models with a generalized Poisson error structure and a nested random intercept term of subarea within fire (see Supporting Information Appendix S4 for further discussion). We modelled post-fire seedling counts by species in each field plot with an offset term of 'log(plot area)' to account for differences in plot size. We selected variables for the final GLMMs and assessed predictive accuracy using spatially stratified cross-validation (22 folds in which one fire was withheld as a test set in each fold). We included potential predictors – related to time since fire, surviving forest cover, terrain, soils, average climate and post-fire climate (Table 1) – in the final GLMMs if they increased accuracy in cross-validation and predicted realistic relationships that matched prior understanding in the published literature. We then predicted density (i.e. post-fire seedlings/ha) using fitted GLMMs of seedling abundance. For accuracy assessment and variable selection in cross-validation, we square-root transformed observed and predicted seedling densities before comparison to limit the influence of extreme outliers.

2.6 | Recent and future seedling establishment suitability using annual establishment models

We used fitted BRTs to project annual establishment suitability at a 250-m resolution (corresponding to the resolution of downscaled climate data) for ponderosa pine and Douglas-fir throughout the SRME in each year of the 1981–2015 period, as well as 2021–2099 in GCM projections. In spatial models for each year, we assumed that establishment was occurring in the year following fire occurrence (i.e. a constant value of 1 for 'time since fire'). We summarized establishment suitability in each year as the percent surface area of the montane zone in the SRME with above-average conditions for establishment (i.e. predicted z-scores greater than zero). Thus, high values in a given year are indicative of climatic conditions beneficial to post-fire establishment of ponderosa pine and Douglas-fir across much of the montane zone. We analysed temporal trends in the percentage of the montane zone with above-average establishment suitability in the 1981–2015 period and 2021–2099 GCM projections using Mann–Kendall trend tests with variance correction.

2.7 | Recent and future seedling densities using total post-fire abundance models

We used fitted GLMMs to make projections of post-fire seedling densities of ponderosa pine and Douglas-fir at a 60-m resolution – incorporating average climate, interannual climate variability, and terrain effects – across the montane zone for each year in 1981–2010 and each GCM and RCP combination in 2021–2080. We restricted our analyses to these years for the direct comparison of three 30-year periods (i.e. 1981–2010, 2021–2050, 2051–2080). Topographic variables were held constant across years in projections, based on existing conditions. Minimum distance to seed tree was set at a constant value of 10 m in all 60-m cells in each year to focus the analysis on the limitations of the biophysical environment while assuming the availability of a nearby seed source. In 1981–2010, average climate variables were based on cell-specific averages from these years, and thus average climate did not vary in this 30-year period. For future scenarios of 2021–2080, we used a 30-year running mean (centred around the focal year) of each climate variable in each cell in each year. Maximum post-fire CWD was taken as the highest z-score (relative to cell-specific mean and standard deviation in 1981–2015) of CWD in the 5 years following the focal year. We resampled (using the average value of all 250-m cells intersecting a new 60-m cell) and aligned 250-m gridded climate data to the 60-m grids of terrain variables.

We assessed the potential for resilience to fire in each year by comparing GLMM predictions in each 60-m cell to 19th-century tree density thresholds of 50 ponderosa pine/ha and 15 Douglas-fir/ha. We developed these thresholds by compiling data from three studies that reconstructed 19th-century forest densities and species compositions throughout the SRME (Battaglia et al., 2018; Fulé et al., 2009; Rodman et al., 2017; Supporting Information Appendix S5), before the widespread impacts of industrialization. We used the 25th percentile of ponderosa pine and Douglas-fir 19th-century densities, including only plots where the respective species were present. We selected these numbers as a means of assessing resilience because they represent the lower range of what might still be considered montane forests. Using these thresholds, we quantified the number of years in each 30-year period (1981–2010, 2021–2050, 2051–2080) in which a 60-m cell was projected to have seedling densities exceeding 19th-century tree density thresholds. In 2021–2080, we did this separately in each GCM, and values in each 60-m cell were taken as the mean value across GCMs, within a given RCP. For a simple comparison of projected values among the three 30-year periods, we define 'suitability' as the percentage of the montane zone that was predicted to exceed 19th-century tree density thresholds in more than half of the years in a 30-year period (i.e. greater than 15 years).

3 | RESULTS

3.1 | Recent trends and projected future changes in AET, CWD, and growing season precipitation

In 1981–2015, annual CWD increased (Kendall's correlation $\tau = .30$, $p < .01$), while annual AET ($\tau = -.14$, $p = .24$) and growing season precipitation ($\tau = -.25$, $p < .01$) declined across the SRME (Figure 2). Future climate scenarios exhibited a wide range of projected trends. Of the 19 GCMs initially studied, 18 predicted 21st-century increases in CWD in RCP 4.5, and all predicted increases in CWD in RCP 8.5 (Supporting Information Table S2.2). Future trends in annual AET were more muted (Supporting Information Table S2.1). Of the 19 GCMs, 17 predicted moderate increases in annual AET in both RCP 4.5 and 8.5, with the greatest increases at higher elevations and northern latitudes (Supporting Information Figure S2.3). GCM projections of growing season precipitation were mixed, with roughly half of GCMs projecting increases in each RCP (Supporting Information Table S2.3). In general, GCMs projected increases in growing season precipitation in northern latitudes and declines in southern latitudes in the SRME (Supporting Information Figure S2.3). The selected GCMs that were downscaled and used for further analysis were the Commonwealth Scientific and Industrial Research Organization (CSIRO) MK3.6.0, Geophysical Fluid Dynamics Laboratory (GFDL) ESM2G, and Institut Pierre Simon Laplace (IPSL) CM5A MR (hereafter 'CSIRO', 'GFDL' and 'IPSL', respectively). These GCMs span the range of 21st-century climate projections in the SRME (Supporting Information Appendix S2).

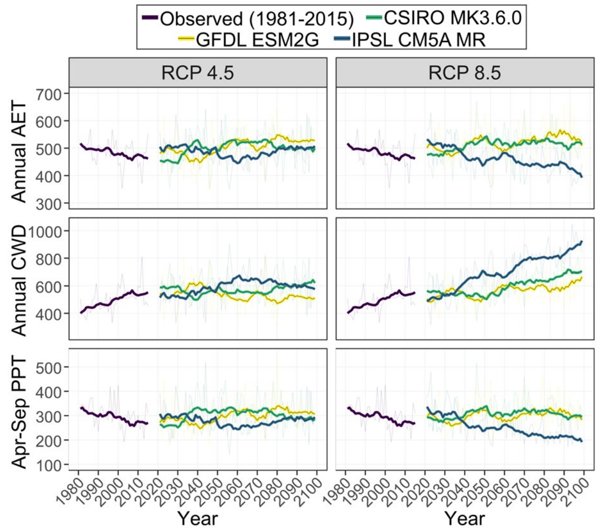

FIGURE 2 A summary of past climate and future climate projections for the Southern Rocky Mountains Ecoregion. Lines show observed (1981–2015) and projected future (2021–2099) trends in annual actual evapotranspiration (AET), climatic water deficit (CWD) and growing season precipitation (Apr-Sep PPT). Future trends are based on three general circulation models – the Commonwealth Scientific and Industrial Research Organization (CSIRO) MK3.6.0, Geophysical Fluid Dynamics Laboratory (GFDL) ESM2G, and Institut Pierre Simon Laplace (IPSL) CM5A MR – and two representative concentration pathways (RCPs 4.5 and 8.5). Values given are the mean of a climate variable within the regional boundary (in mm/year). Transparent lines give annual values, while solid lines give 10-year running means

3.2 | Predictors of annual post-fire seedling establishment suitability

Final BRT models of the combined establishment of ponderosa pine and Douglas-fir seedlings included time since fire, growing season precipitation, and annual AET (Figure 3). The most influential predictor in BRTs was time since fire (relative influence = 45.0%), but growing season precipitation (30.0%) and annual AET (25.0%) during the germination year still had strong relationships with establishment suitability. Seedling establishment was most likely from 1–10 years after fire occurrence, with a peak at 3–7 years following a fire (Figure 3a). Post-fire establishment was also more likely during wet years with above-average growing season precipitation and higher annual AET (Figure 3b,c). Correlations between observed and predicted establishment suitability from the final BRT model were .60 in the full dataset and .43 in spatially stratified cross-validation.

3.3 | Predictors of post-fire seedling abundance

For both species, wetter sites and those closer to surviving trees had higher post-fire seedling densities (Figure 4). For example, sites with low average CWD (i.e. cool and wet) had higher ponderosa pine and Douglas-fir seedling densities (Figure 4b,f). Extreme drought years

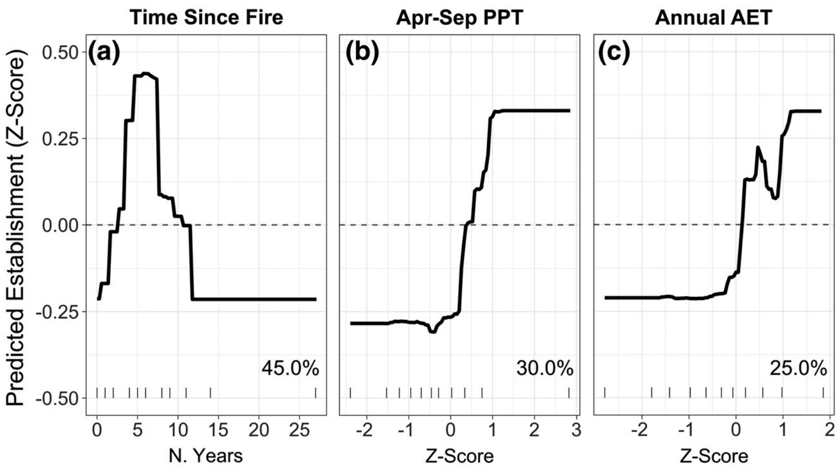

FIGURE 3 The influence of (a) time since fire, (b) growing season precipitation (Apr-Sep PPT), and (c) annual actual evapotranspiration (AET) on annual establishment suitability for ponderosa pine and Douglas-fir combined. Derived from boosted regression tree analyses, each subfigure shows the marginal influence of a given predictor (*y* axis) across the range of values observed in the data (*x* axis). *x* axis values at which a solid line is above zero indicate a positive relationship between that variable and counts of established seedlings, while values at which the solid line is below zero indicate a negative relationship. Percentages in each subpanel give the relative influence of each variable in final models and tick marks at the bottom of each subfigure give deciles of observed data

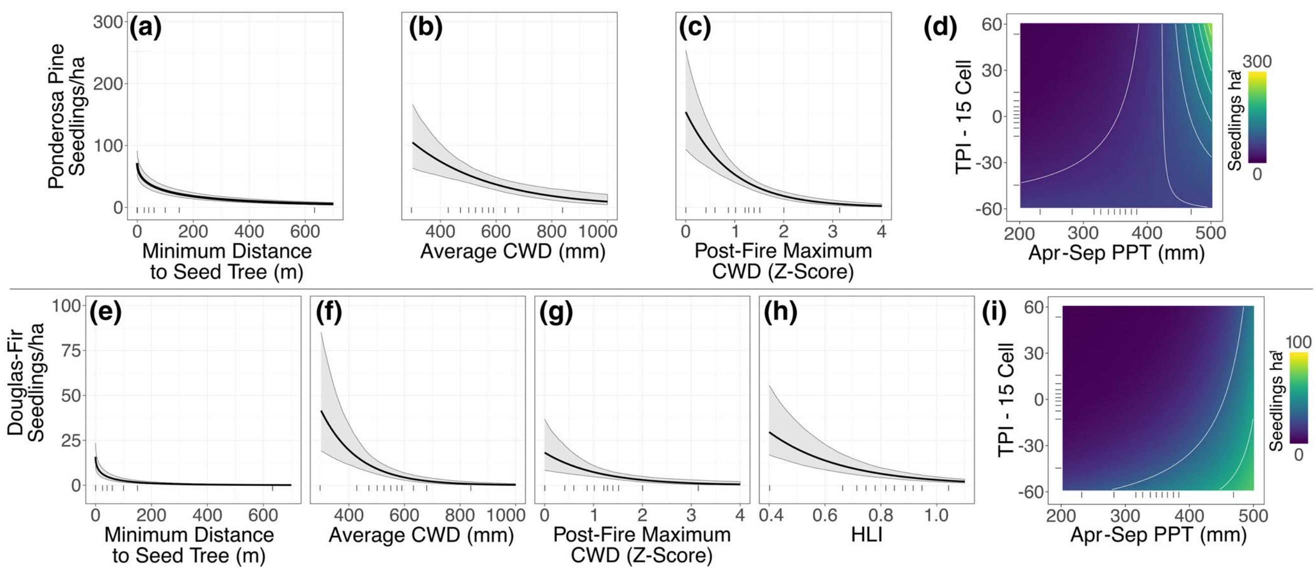

FIGURE 4 Predicted values of post-fire ponderosa pine and Douglas-fir seedling densities from generalized linear mixed models. Black lines give predicted seedling densities across the range of a specified variable, conditional on the mean value of random effects and of other predictors. Shaded regions around each line show one standard error of the prediction. The (d, i) coloured contour plots show the interaction between topographic position index (TPI) and growing season (Apr-Sep) precipitation (PPT) for each species, where the effect of TPI on seedling density is contingent upon Apr-Sep PPT. Note that scales differ by species. Tick marks in each subfigure identify decile values of the observed data. CWD = climatic water deficit; HLI = heat load index

in the first 5 years after fire (i.e. high values of maximum post-fire CWD) were associated with low seedling densities for each species (Figure 4c,g). Heat load index (HLI) improved predictions for Douglas-fir, where densities were highest on north-easterly aspects with lower HLIs (Figure 4h). An interaction term between growing season precipitation and topographic position index (TPI; 15-cell neighbourhood) improved GLMM predictions for both ponderosa pine and Douglas-fir. For ponderosa pine, valley bottoms (i.e. low values of TPI) were positively associated with seedling density in drier sites (i.e. low growing season precipitation). At wetter sites, ridgetops had higher ponderosa pine seedling densities than did valley bottoms (Figure 4d). For Douglas-fir, valley bottoms were associated with increased seedling densities across the entire gradient of growing season precipitation; however, low TPIs were more important to Douglas-fir densities on dry sites (Figure 4i). Time since fire, Landsat-derived fire severity (i.e. relative differenced normalized burn ratio, RdNBR), soil variables, and annual AET did not improve GLMM predictions for either species. Observed and predicted

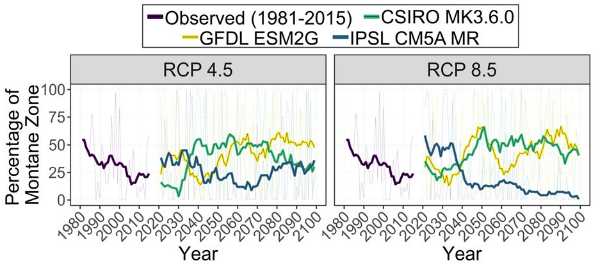

FIGURE 5 The percent surface area of the montane zone in the Southern Rocky Mountains Ecoregion predicted to have above-average conifer establishment suitability based on boosted regression tree models presented in Figure 3. Values for 1981–2015 are reconstructed from the observed climate. Future trends (2021–2099) are based on three general circulation models– the Commonwealth Scientific and Industrial Research Organization (CSIRO) MK3.6.0, Geophysical Fluid Dynamics Laboratory (GFDL) ESM2G, and Institut Pierre Simon Laplace (IPSL) CM5A MR –and two representative concentration pathways (RCPs 4.5 and 8.5). Transparent lines give annual values, while solid lines give 10-year running means

ponderosa pine seedling densities had a correlation of .70 in the full dataset and .22 in spatially stratified cross-validation. Observed and predicted Douglas-fir densities had a correlation of .80 in the full dataset and .34 in cross-validation.

3.4 | Past and future trends in annual suitability for seedling establishment

Establishment suitability declined in the 1981–2015 period ($\tau = -.22$, $p < .01$), but also varied through time (Figure 5). The mid-1980s, late 1990s and 2014–2015 were the years most suitable for post-fire establishment throughout the SRME, while the late 1980s and early 2000s were least suitable. Projected future trends in establishment suitability varied by GCM and emissions scenario. In RCP 4.5, the moderate emissions scenario, two of the three GCMs predicted little change in establishment suitability in the 2021–2099 period (CSIRO: $\tau = .09$, $p = .23$; IPSL: $\tau = .01$, $p = .91$), while one GCM predicted increases (GFDL: $\tau = .19$, $p < .01$). In RCP 8.5, two GCMs predicted slight increases in establishment suitability throughout the montane zone (CSIRO: $\tau = .14$, $p = .08$; GFDL: $\tau = .13$, $p = .04$), while the third GCM predicted substantial declines (IPSL: $\tau = -.32$, $p < .01$). Importantly, future projections of establishment suitability were dependent upon trends in growing season precipitation, but projected precipitation trends in the SRME differ considerably among GCMs.

3.5 | Spatio-temporal models of susceptibility to regeneration failure in the 21st century

Assuming the availability of a seed source, much of the montane zone was predicted to have post-fire seedling densities exceeding 19th-century tree density thresholds of 50 ponderosa pine/ha and 15 Douglas-fir/ha in portions of the 1981–2010 period (Figure 6). Specifically, 49.9% of the montane zone was predicted to exceed the ponderosa pine threshold in more than half of the years (greater than 15 years; hereafter 'suitable') in 1981–2010. For Douglas-fir, 37.7% of the montane zone was considered suitable in 1981–2010. However, we projected broad declines in post-fire seedling densities for ponderosa pine and Douglas-fir across the SRME throughout the remainder of the 21st century (Figure 6; Supporting Information Appendix S5). From 2021–2050, post-fire densities were projected to decline (relative to 1981–2010 levels) under both RCPs. From 2021–2050 under RCP 4.5, 12.3% and 13.5% of the montane zone was considered suitable for ponderosa pine and Douglas-fir, respectively. With RCP 8.5 in the 2021–2050 time period, 19.2% (ponderosa pine) and 18.4% (Douglas-fir) of the montane zone was considered suitable. A strong divergence between RCPs occurred after 2050. RCP 4.5 projected slight increases in the percentage of the montane zone considered suitable from 2051–2080 (relative to 2021–2050 levels) to 17.5% for each species. In contrast, GCMs using RCP 8.5 projected continued and drastic declines in post-fire seedling densities from 2051–2080 (Figure 6) – 3.5 and 6.3% of the montane zone was considered suitable for ponderosa pine and Douglas-fir, respectively. Increases in average CWD and post-fire CWD were the primary reasons for the projected declines in resilience to fire.

4 | DISCUSSION

Increasing wildfire activity and declining forest resilience to wildfire have the potential to drive widespread conversions from forested to non-forested vegetation types (e.g. grasslands, xeric shrublands, mesic shrublands) across many ecosystems in western North America (Coop et al., 2020; Johnstone et al., 2016). Herein, we assessed the potential for fire-driven forest conversions in the montane zone of the SRME using statistical models of post-fire seedling establishment and post-fire seedling abundance for two widely distributed conifers. Both sets of models were developed using extensive field datasets and high-resolution climate surfaces. Further, post-fire abundance models were refined using terrain variables. We confirmed expectations that (a) increasing climate aridity has contributed to declines in forest resilience to wildfire over the 1981–2015 period, and (b) further declines in resilience are likely, but with substantial differences among GCMs and RCPs.

Seedling establishment suitability for ponderosa pine and Douglas-fir was highest in the first 10 years after fire occurrence and years with above-average growing season precipitation and AET. Observed declines in growing season precipitation from 1981–2015 were associated with declines in establishment suitability during this same period. Yet 2021–2099 projections of seedling establishment suitability were mixed because of the wide range of GCM-projected trends in growing season precipitation. Growing season precipitation also has a strong influence on annual area burned throughout the western United States (Holden et al., 2018), and uncertainty surrounding future trends in precipitation

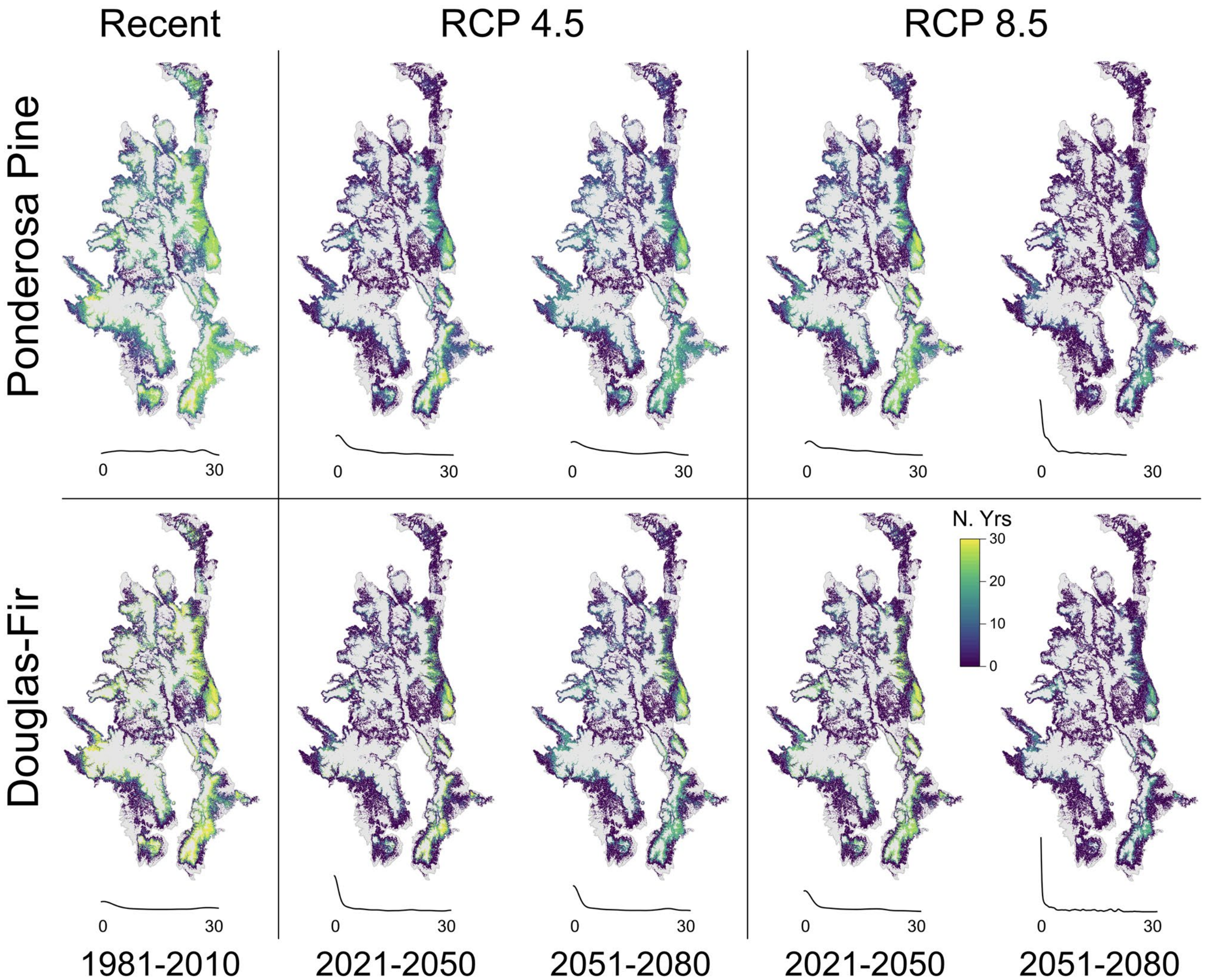

FIGURE 6 Summary of spatial models predicting post-fire seedling densities across the montane zone of the Southern Rocky Mountains Ecoregion in 1981–2010 (based on the observed climate) and 2021–2080 (potential climate scenarios from three general circulation models – the Commonwealth Scientific and Industrial Research Organization (CSIRO) MK3.6.0, Geophysical Fluid Dynamics Laboratory (GFDL) ESM2G, and Institut Pierre Simon Laplace (IPSL) CM5A MR – and two representative concentration pathways (RCPs 4.5 and 8.5). Areas outside the montane zone are shown in light grey. We modelled post-fire seedling densities across the region at a 60-m resolution in each year 1981–2010 and 2021–2080 based on the fitted models in Figure 4. Map colours and density plots (below each map) show the number of years in which each 60-m cell was predicted to exceed 19th-century tree density thresholds (50 ponderosa pine/ha and 15 Douglas-fir/ha) in each 30-year time period

is a key limitation to predicting fire-driven shifts in vegetation (Coop et al., 2020). Despite uncertainties in individual climate parameters, models incorporating interannual climate variability to understand and predict infrequent demographic events are a useful approach to assessing sensitivity to a warming climate (Law et al., 2019; Petrie et al., 2017). Infrequent years with climate conditions conducive to seed germination and seedling survival may have critical implications for subsequent forest trajectories (Davis et al., 2019; Rother & Veblen, 2017).

Post-fire seedling abundance surveys, though more temporally coarse than annual establishment data, provided important insight into the complexity of forest ecosystem responses to wildfire across the southern Rocky Mountains. We found that distance to a seed source, average climate (i.e. annual CWD and growing season precipitation), individual post-fire drought years (i.e. maximum post-fire CWD), and terrain (i.e. HLI and TPI) were useful predictors of post-fire seedling densities for ponderosa pine and Douglas-fir. Our findings align with the results of several prior studies across the western United States that illustrate the importance of surviving trees, climate, and topography to post-fire regeneration processes in forests dominated by obligate seeding conifers (Korb et al., 2019; Stevens-Rumann & Morgan, 2019). Notably, we found that HLI and TPI may help to identify topographic conditions that moderate the influence of broad-scale climate on tree seedlings. Similar terrain variables also help to predict the locations in which trees are most likely to survive fire (Chapman et al. 2020; Meigs et al., 2020). Thus, topographic variables such as TPI and HLI may aid in locating climate change refugia that are less vulnerable to future changes in fire regimes (Krawchuk et al., 2020; Morelli et al., 2020).

Across a range of GCMs and emissions scenarios, we projected that further declines in post-fire seedling densities are likely across much of the SRME. It has been suggested that future warming will reduce conifer seedling establishment and density in many areas, but that increasing temperatures could benefit regeneration at the leading edge (Kemp et al., 2019; Petrie et al., 2017). Still, the combined effects of pre-fire species dominance and extreme drought events may constrain the potential for enhanced regeneration in cooler, wetter sites (Serra-Diaz et al., 2016; Young et al., 2019), and other research has projected near-universal declines in forest resilience to wildfire due to increasing moisture deficits (Tepley et al., 2017). Our projections suggested that increases in average CWD and post-fire drought stress (i.e. maximum post-fire CWD) would drive 21st-century declines in post-fire seedling densities across much of the region, particularly under the more extreme emissions scenario of RCP 8.5. Further warming in the southern Rocky Mountains is likely to lead to increases in overall moisture deficit and the frequency of extreme drought years, with broad-scale consequences for forest dynamics.

The velocity of climate change has the potential to exceed the capacities for migration and genetic adaptation of many plant species (Batllori et al., 2017; Nicotra et al., 2010). Tree species that are most likely to successfully migrate to newly suitable sites are those with light, wind-borne seeds capable of traveling long distances (Normand et al., 2011). Ponderosa pine, Douglas-fir and many other North American conifers have relatively heavy seeds that will not disperse broadly by wind or water (McCaughey et al., 1986). Ponderosa pine and Douglas-fir are long-lived (i.e. > 500 years in the absence of disturbance), and rates of genetic adaptation are comparatively slow for long-lived plant species. However, phenotypic plasticity, localized genetic differences already present in populations, and increases in intrinsic water use efficiency due to carbon fertilization may contribute an uncertain degree of adaptive capacity (Gea-Izquierdo et al., 2017; Nicotra et al., 2010). These uncertainties, combined with an incomplete understanding of the mechanisms facilitating migration – long-range dispersal events (i.e. jump dispersal), the influence of climate on seed production, and cold-temperature limitations to seedling establishment – currently hinder the ability to predict movement to new areas. Still, our projection of regional declines in post-fire resilience across the existing ranges of two dominant tree species is indicative of the potential for a broad-scale reorganization of forest ecosystems in this region, irrespective of potential migration to cooler sites at higher elevations and northern latitudes.

Two additional factors that were not considered in this study, but are relevant to future forest resilience to wildfire, are the influences of climate warming and human ignitions on fire regimes. While warm, dry climatic conditions are strongly related to the annual area burned in the western United States (Abatzoglou & Williams, 2016; Holden et al., 2018), the influence of climate on fire severity is less clear (Abatzoglou et al., 2017). Still, some studies have documented increases in fire severity in the SRME in recent years (i.e. 1984–2010s; Picotte et al., 2016; Singleton et al., 2019). Fire severity is a crucial parameter related to forest resilience because it influences patterns of surviving trees, thereby influencing propagule dispersal and seedling densities in recently burned areas. Across 23 recent fires in the montane zone of the SRME, 38% of the total area burned is distant from any surviving trees (Chapman et al., 2020). A lack of mature trees also leads to increased daytime temperatures and greater diurnal fluctuations (Davis et al., 2018), with potential impacts on tree seedlings. Currently, both human- and lightning-caused fires are common throughout the southern Rocky Mountains, yet humans are the most important ignition source in population-dense areas in other parts of the United States (Balch et al., 2017). Future population gains may increase the number of human ignitions throughout the SRME, and these changes would interact with fuel availability and weather conditions to drive complex changes in fire regimes (Bistinas et al., 2013). In our analyses, we isolated the influence of climate on post-fire recovery by assuming that fire frequency, size and severity were not limiting to tree establishment, a 'best-case scenario'. Future fire regimes, in combination with climate-driven changes in post-fire tree establishment, will have important influences on vegetation patterns throughout the Rocky Mountains (Parks et al., 2019).

One of our most striking findings was the difference in future projections of post-fire recovery between RCPs 4.5 and 8.5. While RCP 4.5 assumes moderate growth in carbon emissions through 2040, followed by declines, RCP 8.5 assumes rapid increases in emissions that continue through 2100 (Riahi et al., 2011). Models of annual establishment suitability and total post-fire seedling abundance indicated similar trends between RCP 4.5 and 8.5 through mid-century but showed strong divergence beyond that point. These findings echo those of prior research that has demonstrated the importance of emissions scenario to projected effects on tree regeneration (Petrie et al., 2017; Tepley et al., 2017). Continued warming is likely to lead to increases in wildfire activity and declines in post-fire resilience throughout the montane forests of the southern Rocky Mountains. However, the next two decades represent a crucial point of divergence between alternative emissions scenarios (IPCC, 2014; Riahi et al., 2011). Given the stark differences in projections of post-fire recovery under RCPs 4.5 and 8.5, there may be the potential to mitigate the most drastic climate impacts to forest resilience through emissions reductions before 2040.

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AUTHOR CONTRIBUTIONS

JRO, KCR, MEC and MTR collected the field data and MAB, PJF, TEK, and TTV helped plan fieldwork. ZAH contributed spatial data. KCR and TTV designed the study. KCR performed the statistical analyses and wrote the first draft of the manuscript. All authors contributed to manuscript revisions.

DATA AVAILABILITY STATEMENT

Field data, spatial data, gridded climate data, final statistical models, and example model outputs from this study are available in the Dryad Digital Repository (Rodman, Veblen, Battaglia, et al., 2020): https://doi.org/10.5061/dryad.qz612jmb7.

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BIOSKETCH

The authors in this research team have a diverse range of backgrounds and skillsets, including experience in field ecology, ecophysiology, dendrochronology, geospatial analysis, silviculture, and land management.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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