

Landscape-scale restoration minimizes tree growth vulnerability to 21st century drought in a dry forest

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Abstract. Increasing aridity is a challenge for forest managers and reducing stand density to minimize competition is a recognized strategy to mitigate drought impacts on growth. In many dry forests, the most widespread and common forest management programs currently being implemented focus on restoration of historical stand structures, primarily to minimize fire risk and enhance watershed function. The implications of these restoration projects for drought vulnerability are not well understood. Here, we examined how planned restoration treatments in the Four Forests Restoration Initiative, the largest forest restoration project in the United States, would alter landscape-scale patterns of forest growth and drought vulnerability throughout the 21st century. Using drought–growth relationships developed within the landscape, we considered a suite of climate and treatment scenarios and estimated average forest growth and the proportion of years with extremely low growth as a measure of vulnerability to long-term decline. Climatic shifts projected for this landscape include higher temperatures and shifting seasonal precipitation that promotes lower soil moisture availability in the early growing season and greater hot-dry stress, conditions negatively associated with tree growth. However, drought severity and the magnitude of future growth declines were moderated by the thinning treatments. Compared to historical conditions, proportional growth in mid-century declines by ~40% if thinning ceases or continues at the status quo pace. By comparison, proportional growth declines by only 20% if the Four Forest Restoration Initiative treatments are fully implemented, and <10% if stands are thinned even more intensively than currently planned. Furthermore, restoration treatments resulted in dramatically fewer years with extremely low growth in the future, a recognized precursor to forest decline and eventual tree mortality. Benefits from density reduction for mitigating drought-induced growth declines are more apparent in mid-century and under RCP4.5 than under RCP8.5 at the end of the century. Future climate is inherently uncertain, and our results only reflect the climate projections from the representative suite of models examined. Nevertheless, these results indicate that forest restoration projects designed for other objectives also have substantial benefits for minimizing future drought vulnerability in dry forests and provide additional incentive to accelerate the pace of restoration.

Key words: climate change; forest management; *Pinus Ponderosa*; resilience; semiarid regions; water balance.

INTRODUCTION

Rising temperatures and enhanced 21st century drought severity may undermine the sustainability of dry forests. Forests are crucial components of dryland regions because they exert a disproportionately large influence over climate regulation (via C storage and albedo modification; Jackson and Baker 2010), water cycle modulation (Ellison et al. 2012), habitat diversity

(Watling and Donnelly 2006), and resource and recreational use (Irland et al. 2001). However, semiarid regions that support dry forests are generally becoming drier (Polade et al. 2014) and these trends toward enhanced aridity are expected to continue throughout the 21st century (Dai 2013). Even in dry forests areas where total precipitation is projected to increase in coming decades, drought stress may also increase as hotter temperatures enhance evapotranspiration rates (Tohver et al. 2014). Prolonged drought stress can leave dry forests vulnerable to rapid species turnover or loss. As a result, the sustainability of dryland forests in a warming climate is highly uncertain because mounting evidence

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suggests that drought-induced tree mortality is rising and will continue to increase in the future (Allen et al. 2010, Allen et al. 2015). Simultaneously, disturbance and extreme events, such as severe wildfires, droughts or heat waves, can also catalyze rapid shifts in forest structure and composition by killing established, large trees. Increases in storm intensity (Polade et al. 2017) may promote greater water loss to deep drainage in spring months and longer and hotter periods of dry soils in summer (Palmquist et al. 2016, Schlaepfer et al. 2017). Indeed, forest transitions have already been observed and are expected to continue across western North America and other dry areas (Breshears et al. 2009, Allen et al. 2010, Williams et al. 2013, Stevens-Rumann et al. 2017).

As a result of the challenge represented by increasing aridity, managers are seeking strategies to maximize forest sustainability by promoting stand structures and/or species compositions that are suitable for future conditions (Stein et al. 2014, Bradford et al. 2018). Changes in climate, and particularly elevated climatic extremes, represent a major challenge facing forest managers, policy makers, and forest scientists today (Millar et al. 2007, Bosworth et al. 2008, Seppälä et al. 2009, Littell et al. 2012, Webster et al. 2012). In particular, severe drought events cause widespread tree mortality and decreased growth in forest habitats across the globe, including areas with cool and mesic climates where drought impacts are not widely recognized (Allen et al. 2010, McDowell et al. 2011, Peng et al. 2011, Choat et al. 2012, Vicente-Serrano et al. 2013). As the reality of climate change and increasing drought frequency and severity become clear (Field et al. 2012), forest managers need proven approaches to increase adaptation capacity. Specifically, approaches that promote forest resistance (minimizing negative impacts during the drought) and resilience (maximizing recovery rates following drought; Spittlehouse and Stewart 2004, Blate et al. 2009).

Reducing forest density is one strategy to enhance the resistance and resilience of forests to drought. Manipulating forest stocking and composition using thinning and regeneration methods are engrained in the forestry profession as scientifically sound approaches to achieve timber- and wildlife-habitat-related objectives, such as increasing tree growth or establishing new individuals of desired species (Smith et al. 1997). Use of these tools to increase resistance and resilience to drought, although backed by ecophysiological research (e.g., Bréda et al. 1995, McDowell et al. 2006) and demonstrated in operational-scale experiments (e.g., Linder 2000, D'Amato et al. 2013, Magruder et al. 2013, Bottero et al. 2017, Bradford et al. 2017, Gleason et al. 2017), has yet to be widely incorporated into forest management practices or applied at large spatial scales. During a severe drought, trees experience growth declines, and potentially mortality, as a result of some combination of hydraulic failure and/or carbon starvation (McDowell et al. 2008). Forest treatments that decrease the density of stands can reduce this stress by moderating competition for scarce water

resources during a severe drought and hastening the resumption of growth after the drought.

Ecological restoration is a widely recognized objective of dry forest management that involves treating forest stands primarily for the purpose of promoting stand structural conditions consistent with the historical range of variability, and moderating fire regimes (Covington et al. 1997, Schultz et al. 2012), although the potential for interactions between ecological restoration and global climate change is largely unexplored (Harris et al. 2006, Fulé 2008). Dry forest restoration involves modifying the spatial patterns of trees, and typically includes objectives related to maintaining lower overall forest basal area density (Covington et al. 1997). Reducing basal area is a recognized strategy for adapting to climate change (Linder 2000, D'Amato et al. 2013, Magruder et al. 2013, Bottero et al. 2017, Bradford et al. 2017, Gleason et al. 2017), so these dry forest restoration treatments may enhance the resilience of tree growth to drought, climate change, and other stressors (e.g., insects and fire) by reducing competition for water. However, the magnitude and consistency of these benefits across landscapes with heterogeneous forest structures and restoration treatments are unknown.

The Four Forests Restoration initiative (4FRI) is the largest forest restoration project currently being implemented in the United States (U.S. Department of Agriculture 2015). The primary objective of 4FRI is landscape-scale restoration that results in reduced risk of severe fire effects and improved forest function and health including improved watershed function, plant biodiversity, wildlife habitat, and soil productivity (U.S. Department of Agriculture 2014). The first phase of 4FRI is currently being implemented over >175,000 ha of primarily ponderosa pine (*Pinus ponderosa*) forests in Northern Arizona (Fig. 1). Restoration thinning treatments prescribed by 4FRI may also have the additional benefit of creating stand structural conditions that are more resilient to drought. However, those ancillary drought resistance and resilience benefits have not been assessed. Within the 4FRI region, increasingly severe drought and associated reductions in water availability to plants and ecosystems have emerged as predominant characteristics of regional climate at the beginning of the 21st century (Cayan et al. 2010, Seager and Vecchi 2010, Cook et al. 2015). Based on ensemble climate change projections, drying conditions will characterize the region through the remainder of the century (Seager and Vecchi 2010). In fire-adapted ecosystems like ponderosa pine forests, prior management and fire suppression has created high density stands that are susceptible to stand-replacing wildfire (Covington et al. 1997). Drought and heat stress often promote more frequent and intense fires and insect outbreaks leading to widespread plant mortality (Savage and Mast 2005, Hicke and Jenkins 2008, Wu and Kim 2013). As climate change exacerbates the severity of drought conditions in these dryland forests, understanding the long-term benefits, and potential

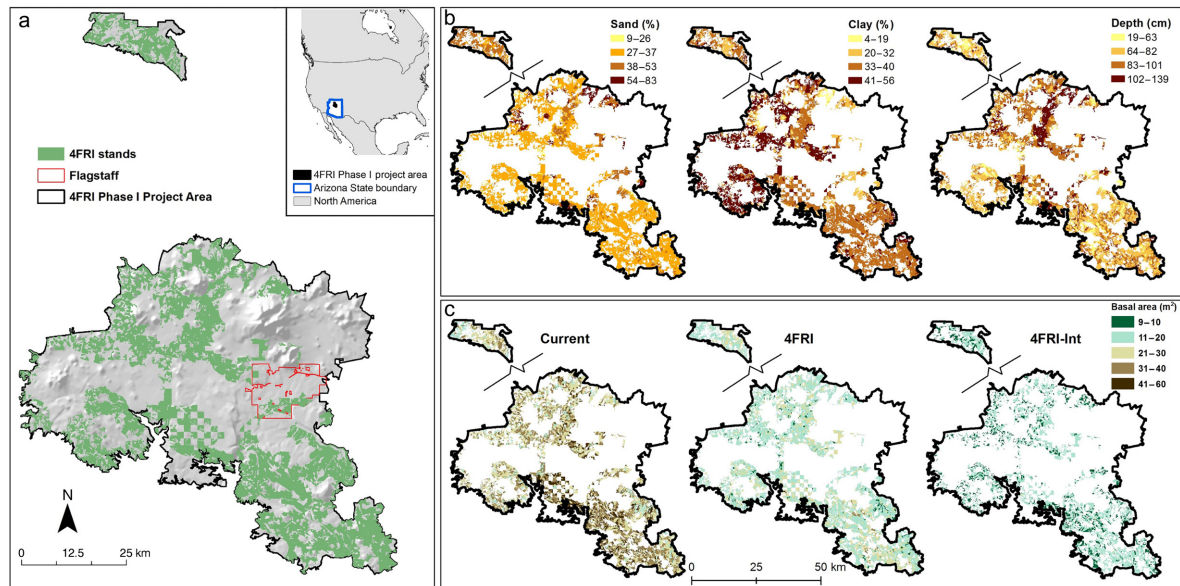


FIG 1. Location (left), soil conditions (top right), and basal area under alternative thinning treatments (bottom right) of forest stands examined within the Four Forests Restoration Initiative (4FRI) landscape in Northern Arizona, USA. Basal area values (m^2/ha) include current, 4FRI planned (4FRI), and a reduction more intensive than 4FRI (4FRI-Int). The line between polygons illustrates that the northern portion of the restoration landscape was moved closer to the rest of the area, for depiction purposes.

limitations, of the planned 4FRI treatments will provide useful insight into their value and may identify how and where they could be modified to maximize long-term forest resilience to rising aridity.

Our overall goal was to assess the potential consequences of the planned 4FRI treatments for forest growth resilience in the context of climate change. Specifically, we quantified the impacts of planned 4FRI restoration treatments and projected 21st-century climate conditions on (1) stand-level growth, represented by both basal area increment (BAI, a useful measure of potential wood product yield) and proportional growth rates, quantified as BAI divided by basal area (BA), which provides a perspective on the stand vigor), and (2) tree drought stress, represented by the proportion of years with extremely low growth rates, a recognized precursor to eventual drought-driven tree mortality (Suarez et al. 2004, Vanoni et al. 2016, Cailleret et al. 2017, DeSoto et al. 2020). The 4FRI project is an ideal experiment for evaluating the potential landscape-scale, drought-resilience benefits of density reduction in dry forests for two reasons. First, the broad area encompassed by 4FRI includes substantial landscape heterogeneity, which allows for assessment of patterns and drivers of vulnerability within the landscape. Although this heterogeneity has multiple recognized benefits, including ecological value, restricted potential for spread of insects, disease, and fire, the potential benefits of 4FRI heterogeneity for drought resilience are unknown. Second, and perhaps most important, the treatments prescribed in 4FRI were developed through a long-term, multi-agency, collaborative process (U.S. Department of Agriculture 2014) to

meet a diverse set of objectives that are valued by the communities within the 4FRI landscape. Quantifying the impacts of 4FRI on drought resilience will provide useful insight into the benefits of restoration treatments for adapting vulnerable ecosystems to climate change both within the 4FRI landscape and in dry forests across western North America.

METHODS

Description of the 4FRI study area and treatment overview

The 4FRI landscape (Fig. 1) is located on the Coconino and Kaibab National Forests in Northern Arizona. The landscape is dominated by ponderosa pine forest types, and ranges from 1,780 to 3,850 m elevation with a mean of 2,190 m. Over the past century, ponderosa pine forests in this region have experienced fire suppression, harvesting, and episodic regeneration events that resulted in densification from a more open historical condition to high concentration of small diameter trees (Covington et al. 1997). The 4FRI project will restore >430,000 acres across >6,000 stands with mechanical thinning and apply prescribed fire to restore an additional 586,110 acres of ponderosa pine forest and grasslands (U.S. Department of Agriculture 2015).

Growth estimation

We estimated stand-level annual BAI for each stand under various combinations of restoration treatment

and time period using a predictive relationship for growth (Eq. 1) developed in Northern Arizona ponderosa pine stands in the Taylor Woods long-term growing stock level experiment (described in Bailey 2008) that includes stands with basal areas ranging from <10 to >50 m²/ha (Andrews et al. 2020)

$$\begin{aligned} \text{BAI} = & 0.9822 - 0.00081(\text{BA}) - 0.0154(\text{Temp}_{\text{AnnMax}}) \\ & - 0.0285(\text{Temp}_{\text{Ann}}) + 0.92219(\text{Moisture}_{0\text{YA}}) \\ & + 0.1606(\text{Moisture}_{1\text{YA}}) + 0.0099(\text{Stress}_{2\text{YA}}) \\ & + 0.0922(\text{BA} \times \text{Moisture}_{0\text{YA}}) - 0.0015(\text{BA} \\ & \times \text{Stress}_{2\text{YA}}) \end{aligned} \quad (1).$$

Eq. 1 estimates annual, stand-level, forest growth as a function of stand structure, weather, and ecological drought conditions. This includes negative growth impacts of BA, annual temperature (Temp_{Ann}, °C) and annual maximum temperature (Temp_{AnnMax}, °C), and two detailed measures of ecological drought severity. These effects are developed and described in Andrews et al. (2020), and were shown to be strongly linked to growth in ponderosa pine forests of the region (Andrews et al. 2020). Briefly, the first ecological drought metric is relative moisture availability, assessed for both the current growing season (Moisture_{0YA}) and the previous growing season (Moisture_{1YA}). Relative moisture availability is positively related to growth and is quantified as the ratio of soil water availability (SWA) to potential evapotranspiration (PET). SWA is defined as total soil water content in the soil profile minus soil water content at -3.9 MPa, which is a threshold for potential maximum water extraction of dryland plants (Sperry and Hacke 2002). The second ecological drought metric is exposure to hot-drought stress over the previous two years (Stress_{2YA}). Stress_{2YA} is negatively related to growth and is quantified as the number of days with both extremely high temperature (>28°C) and very dry soils (<-2.2 MPa). This predictive equation for annual growth also includes interactions between basal area and both Moisture_{0YA} and Stress_{2YA}.

Using this framework, stand-level growth is represented by BAI (e.g., annual change in basal area; BAI, m²·ha⁻¹·yr⁻¹) and proportional growth (BAI/BA). To estimate the vulnerability of these stands to extremely low growth rates, we quantified how often each stand will experience extremely low proportional growth rates. We defined extremely low growth as proportional growth rate observed in the lowest 5% of years (e.g., 1 in 20 yr; Appendix S1: Fig. S1) and derived this metric from stand-level, annual, proportional growth rates that were calculated from dendrochronology (described in Bottero et al. 2017, Gleason et al. 2017) at Taylor Woods. Because Taylor woods includes a very broad gradient of total basal areas, including un-thinned stands with extremely high basal area and low proportional growth rates (Andrews et al. 2020), the proportion of

years meeting this criteria for extremely low growth in the 4FRI landscape was less than 5%.

Restoration treatments and landscape scenarios

Our objective was to assess future forest growth under climate change and alternative landscape-scale forest management scenarios, which are defined by stand-level restoration thinning treatments applied within climatic time periods. We examined three climatic time periods: historical (1970–2010), near-term future (2020–2059), and long-term future (2060–2099). We evaluated four different stand-level restoration thinning treatments defined by stand BA reduction: no harvest (BA maintained at the value estimated for 2010 by the U.S. Forest Service), status quo (current pace of thinning), 4FRI (based on the stand-specific BA reduction proposed in the 4FRI implementation plan), and 4FRI intensive (hereafter 4FRI-I; a further reduction in 4FRI BA of 0.56). This 0.56 reduction was not meant to represent any actual planned restoration treatment but meant to assess the differences between the proposed 4FRI BA and BA representative of the historical range of variability in this region and forest type (Reynolds et al. 2013). We used BA and density (trees/ha) as our units of measure for applying treatment differences to individual stands. For the historical time period, all stands were assumed to be at the untreated basal area level. Future stand-level BA was defined to represent each of the above landscape-scale management scenarios (Appendix S1: Table S1.1). In the “no-harvest” scenario, all stands remain at the historical basal area. In the status quo scenario, treatment continues at the recent actual pace of treatment application; in the near term (2020–2059), 10% of stands are treated to 4FRI BA (90% are at untreated BA) and, in the long term (2060–2099), 30% of stands treated to 4FRI BA while 70% remain at untreated BA. To avoid making assumptions about which stands will be treated and which will remain untreated for each time window, we estimated future growth for all stands under all potential basal area treatments, and then estimated stand-level growth for alternative landscape scenarios from a weighted average of the different stand-level treatments. For example, in the status-quo landscape scenario, 2020–2059 growth for each stand is an average of historical BA (weighted 90%) and 4FRI BA (weighted 10%). Likewise, under status-quo restoration 2060–2099 growth is weighted 30% historical and 70% 4FRI. The third and fourth scenarios are termed 4FRI and 4FRI-I because 100% of stands are assumed to be at the 4FRI and 4FRI-I BA in both future time periods and do not require weighted averages to estimate stand-level growth. Our estimates of future basal area conditions assume basal area will be maintained at no harvest levels or the prescribed levels after forest restoration is complete. We do not evaluate demographic processes that change basal area such as recruitment or mortality. This assumption is consistent with

the overall 4FRI restoration strategy, which calls for prescribed burns following initial mechanical thinning treatments to maintain basal area reductions at the prescribed level.

Climate, stand structure and soil moisture data

To simulate the effects of forest BA on soil moisture and to calculate the indices of moisture availability and hot-drought stress necessary for our growth equation, we used SOILWAT2. SOILWAT2 is a daily time-step, multiple-soil-layer, process-based, CO₂-sensitive, simulation model of ecosystem water balance that has been tested in several dryland ecosystems (Schlaepfer et al. 2012, Bradford et al. 2014), including forests (Petrie et al. 2017, Andrews et al. 2020). The model accounts for vegetation structure through monthly measures of biomass (kg/ha), leaf area index (LAI), and litter biomass (kg/ha) for four different plant functional types (trees, shrubs, grasses, and shrubs). Stand-level BA and TPH were acquired from the U.S. Forest Service Common Stand Exam inventory data and used to calculate stand-level forest biomass (data available online).² To calculate forest biomass from BA/TPH, a mean diameter at breast height (DBH) for a stand was calculated and then converting DBH to biomass using equations found in Jenkins et al. (2003). Other tree species are present in the inventory data, including pinyon pine (*Pinus edulis*), multiple juniper species, Gambel oak (*Quercus gambelii*), and mixed conifer species, but since the representation of these species was minor compared to ponderosa pine, we did not include them in the BA and TPH calculations. In addition, we excluded any stands that had less than 70% ponderosa pine proportionally. LAI was calculated based on equations found in Flathers et al. (2016) and is constant for a given basal area and TPH. SOILWAT2 was used to model treatment-specific interactions between forest BA, soil conditions, and climate. We extracted information on soil depths and textures from 117 soil map units found within the study area from the Terrestrial Ecosystem Surveys of the Coconino and Kaibab National Forests (U.S. Department of Agriculture 1991, 1995). The soil data were derived from field surveys of soil pits dug to bedrock that were representative of the soil map unit. Because the horizon depths varied across soil units, we used weighted averaging to standardize all these soil metrics to the standard depths of up to 18 soil horizons used in SOILWAT2: 5-cm depth layers between 0 and 30 cm, 10-cm layers between 30 and 120, 15-cm layers between 120 and 150 cm, and a 50-cm layer to 200 cm. For each forest stand, we used the soil unit(s) that overlapped with at least 50% of the boundary. In the case where two soil units were required to reach this 50% threshold, we averaged soil metrics of the standardized soils. Soil data were not available for 1% of the stands and these were removed from the

analysis. Bulk density information was not available from the Forest Service soil surveys; instead we used average bulk densities for forest stand using a 250-m resolution soil gridded dataset (Hengl et al. 2017).

We explored how shifting water availability due to climate change would impact growth using global circulation models (GCMs) and Eq. 1 (Andrews et al. 2020) identified above. For historical condition, daily climate data were taken from Livneh et al. (2013) at 1/16th degree resolution (Fig. 2). For future conditions, we extracted climate as monthly time-series for two time periods, 2020–2059 (mid-century) and 2060–2099 (late-century), from one-half degree downscaled and bias-corrected products of the fifth phase of the Climate Model Intercomparison Project (CMIP5; Taylor et al. 2011). Data were extracted from the Downscaled CMIP3 and CMIP5 Climate and Hydrology Projections archive (Maurer et al. 2007). We combined historical daily data (Livneh et al. 2013) with monthly GCM predictions of historical and future conditions with a hybrid-delta downscaling approach to obtain future daily forcing at 1/16th degree resolution (Hamlet et al. 2010, Dickerson-Lange and Mitchell 2014, Tohver et al. 2014). Eleven GCMs were selected from those models included in CMIP5 to comprise both the most independent (Knutti et al. 2013) and best performing GCMs for the western United States (Rupp et al. 2013). GCMs examined included CanESM2, CESM1-CAM, CNRM-CM, CSIRO-Mk3-6-0, FGOALS-g2, FGOALS-s2, GISS-E2-R, HadGEM2-ES, Inmcm4, IPSL-CM, and MIROC-ESM. GCM data were utilized from representative concentration pathways (RCPs): families 4.5, which represent a relatively low emissions scenario, and families 8.5, which represent the highest emissions scenarios (Moss et al. 2010, Taylor et al. 2011).

Climate projections for these forest stands suggest rising temperatures that are reasonably consistent across climate models and throughout the year. Mean annual temperature (MAT) was 8.1°C between 1970–2010 and is projected to increase to 10.3°C (GCM range 9.2–11.4°C) during 2020–2059 and to 13°C (11.2–15.1°C) during 2060–2099 in the median model under RCP8.5 (Fig. 2 and Appendix S1: Fig. S2). Projected changes in precipitation, by contrast, are more variable than temperature. Mean annual precipitation was 652 mm between 1970 and 2010, and increased to 679 mm (GCM range 412–802 mm) during 2020–2059 and to 672 mm (344–854 mm) during 2060–2099. Climate models varied substantially in projections for monthly precipitation, and models disagree about the direction of precipitation change for all months (Fig. 2), with the exception of May, when all models project slight decreases in precipitation. Variation among climate models in monthly precipitation is generally larger in 2060–2099 than 2020–2059, particularly during the monsoon season (July through September.) Data generated during this study are available from the USGS Science-Base-Catalog (Andrews and Bradford 2020).

² <https://www.fs.fed.us/nrm/fsveg/>

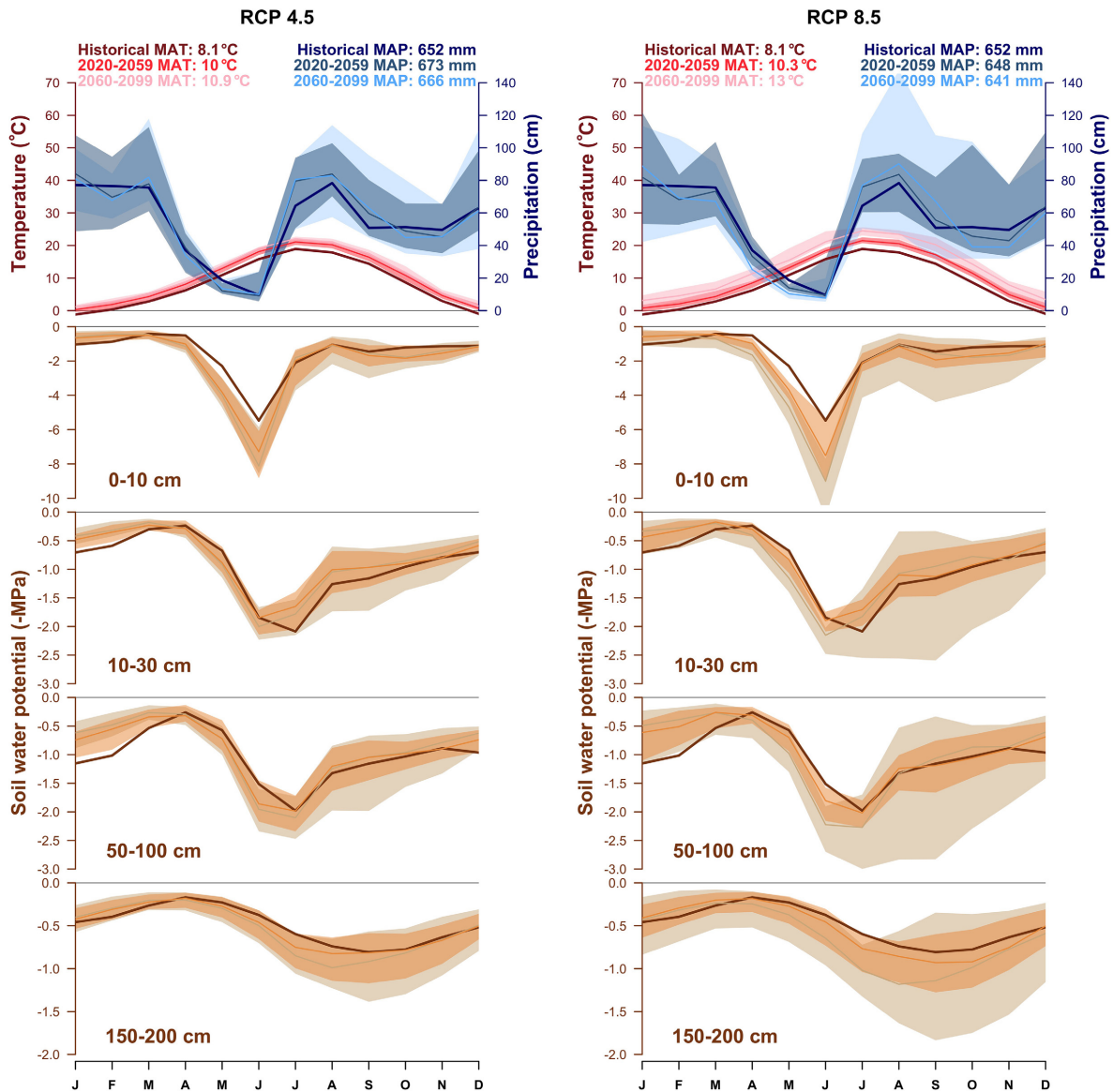


FIG. 2. Mean monthly climate (top panels; MAT, mean annual temperature; MAP, mean annual precipitation) and soil moisture conditions (bottom panels) under historical and future climate for representative concentration pathway (RCP) 4.5 (left) and RCP 8.5 (right) across all stands within the focal landscape. Dark lines for temperature (red, top panels), precipitation (blue, top panels), and soil moisture (brown, bottom panels) are mean monthly historical climate conditions. Thinner lines for each variable show projections from the median general circulation model (GCM) and shaded areas show variation among the all GCMs examined for two future time periods: 2020–2059 (darker line and darker shaded area) and 2060–099 (lighter line and lighter shaded area).

RESULTS

Basal area

Under the planned Four Forests Restoration Initiative (4FRI) treatments, basal area in these forest stands will decrease considerably, and the hypothetical 4FRI-intensive (4FRI-I) treatment would further reduce basal area. Historical basal area (BA) ranges from 13 to 57 m²/ha, averages 30 m²/ha (median 26), and is bimodally distributed (Fig. 3). One group of

stands has basal area values ranging from ~35 to ~42 m²/ha, while another group of stands ranges from ~27 down to 15 m²/ha. Treatment to the 4FRI prescriptions creates a more unimodal distribution of basal areas with a mean (and median) of 17 m²/ha and a range of 9–44 m²/ha. By contrast, application of the 4FRI-I prescription results in mean basal area of 10 m²/ha (median 9 m²/ha) and a range of 5–25 m²/ha (Fig. 3). Patterns of biomass for these stands are similar among treatments and time periods to patterns of basal area (Appendix S1: Fig. S3).

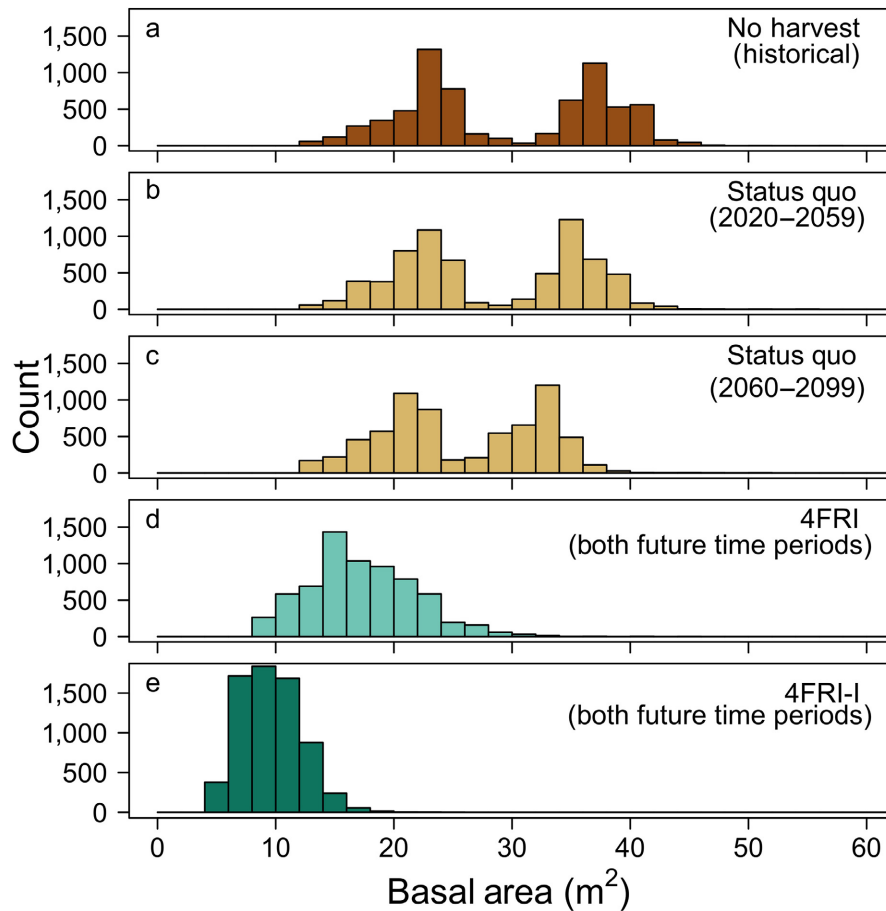


FIG 3. Basal area of all stands within the Four Forests Restoration Initiative under (a) no-harvest scenario (historical basal area) and (b and c) future basal area assuming thinning at the status-quo scenario, (d) the 4FRI scenario, and (e) the 4FRI-intensive scenario.

Soil moisture projections

Our results suggest that the projected changes in temperature and precipitation from GCMs will alter soil moisture availability. Historically, soil moisture at these sites displayed clear seasonal patterns, with highest average soil moisture in April after snowmelt followed by a rapid decline to the lowest average soil moisture in July (Fig. 2). Average soil moisture increased sharply in August during the monsoon and continued to increase slightly until stabilizing between November and February and increasing again in March and April. Future climate conditions alter these seasonal patterns in a few important ways, notably producing wetter soils during the winter (December–March), earlier peak moisture (March in the future vs. April historically), and earlier decline to a seasonal minimum in June and in July in deep soils that are lower than the historical July minimum. Like increasing temperature, these altered seasonal soil moisture patterns for both RCP 4.5 and RCP 8.5 are reasonably consistent across climate models (e.g., consistent across climate models; Bradford et al. 2020),

strongly suggesting that these forests will experience a longer, hotter dry soil period in late spring and early summer. Soil moisture during the monsoon season and into the fall is generally similar to historical conditions, but highly variable among climate models.

Growth patterns

We quantified growth as stand-level basal area increment (BAI; estimated from Eq. 1), proportional growth (BAI/BA), and biomass growth (Appendix S1: Fig. S4). Historic mean BAI averaged 0.64 m²/ha across all stands (median 0.60), and varied among stands from 0.10 to 1.5 m²/ha (Fig. 4). Estimated growth under future climatic and drought conditions is projected to decrease BAI across all thinning scenarios. BAI is strongly determined by stand BA; stands with low BA will have commensurately low stand BAI (Appendix S1: Fig. S5), although often they also have high proportional BAI (Fig. 5). Likewise, BAI increases with BA, except for extremely high BA conditions (Andrews et al. 2020), when severe competition inhibits growth and promotes self-thinning.

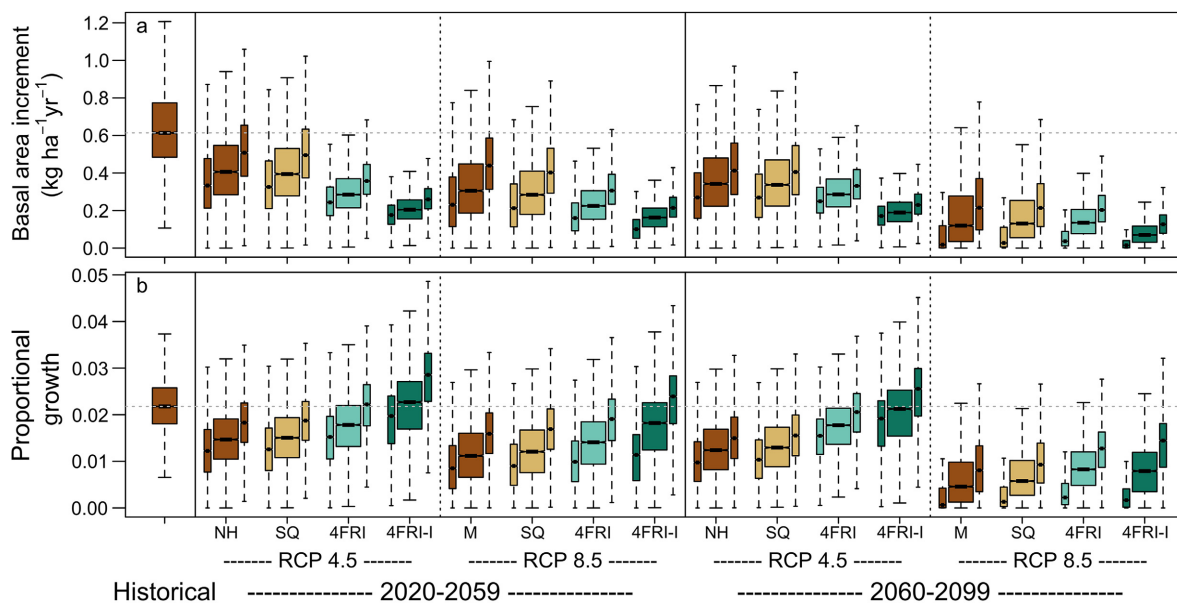


FIG 4. Distributions of annual stand-level (a) basal area growth and (b) proportional growth under historical and future conditions and alternative thinning scenarios for all stands in the Four Forests Restoration Initiative. Each group of three bars includes results for three general circulation models (GCMs): the minimum GCM (left), the median GCM (middle), and the maximum GCM (right). Future thinning scenario abbreviations are NH, no harvest; SQ, status quo; 4FRI, 4FRI prescription; and 4FRI-I, 4FRI intensive prescription. Box plot components are midline, median; box edges, interquartile range; and whiskers, ± 2.67 SD.

Thus, the largest decreases in BAI are expected in the 4FRI and 4FRI-I scenarios (Fig. 4a). In the no-harvest scenario, BAI for the median GCM between 2020 and 2059 is projected to decline by 34% to an average of $0.42 \text{ m}^2 \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$ (GCM range $0.35\text{--}0.53$) under RCP 4.5 and by 43% to $0.36 \text{ m}^2 \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$ (GCM range $0.29\text{--}0.43$) under RCP 8.5. Projected BAI between 2020 and 2059 in the status quo scenario also declines by 35% to $0.41 \text{ m}^2 \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$ ($0.34\text{--}0.51$) under RCP 4.5 and by 44% to $0.36 \text{ m}^2 \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$ (GCM range $0.29\text{--}0.43$) under RCP 8.5. For the 4FRI scenario, by 2020–2059 BAI declines 53% to $0.30 \text{ m}^2 \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$ under both RCPs (GCM range $0.25\text{--}0.37$ for RCP 4.5 and $0.26\text{--}0.35$ for RCP 8.5). Among the landscape restoration scenarios, BAI changes were greatest in 4FRI-I, in which BAI declines 67% to $0.21 \text{ m}^2 \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$ under RCP 4.5 ($0.18\text{--}0.27$) and by 69% to $0.20 \text{ m}^2 \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$ in the 4FRI-I under RCP 8.5 ($0.18\text{--}0.24$).

For all restoration scenarios and both RCPs, projected declines in BAI were largest for the long-term future under RCP 8.5. Between 2060–2099, estimated average BAI for the no-harvest, status quo, 4FRI, and 4FRI-I scenarios decreased by 49%, 53%, 53%, and 67%, respectively, under RCP4.5, and by 73%, 74%, 76%, and 86%, respectively, under RCP8.5. Biomass growth displayed similar patterns as basal area across scenarios and time periods (Appendix S1: Fig. S4).

Similar to BAI, projected declines in proportional growth are estimated to be greatest in the long-term future period and under RCP 8.5. However, proportional

growth displays opposite patterns than BAI across the different treatment scenarios. Historic mean proportional growth averaged 2.2% per year across all stands (median 2.2%) and ranged between 0.5% and 4.7%. Estimates of proportional growth under future climate and drought conditions suggest declines, with the greatest declines in the no-harvest and status quo scenarios and the smallest declines in the 4FRI-I scenario (Fig. 4b). Between 2020 and 2059 under RCP 4.5, proportional growth for the median GCM averages 1.5% (GCM range $1.2\text{--}1.8\%$) under the no-harvest scenario, 1.5% ($1.3\text{--}1.9\%$) under the status quo scenario, 1.8% ($1.5\text{--}2.2\%$) for the 4FRI scenario, and 2.2% ($1.9\text{--}2.8\%$) for the 4FRI-I scenario. Under RCP 8.5 during the same time period, proportional growth averages 1.2% ($1.0\text{--}1.5\%$) for no-harvest, 1.3% (GCM range $1.1\text{--}1.5\%$) for status quo, 1.8% ($1.5\text{--}2.0\%$) for 4FRI, and 2.1% ($1.8\text{--}2.5$) for 4FRI-I.

Between 2060 and 2099, proportional growth declines further, especially under RCP 8.5. During this time period for the no-harvest scenario proportional growth averaged 1.1% ($0.9\text{--}1.6\%$) under RCP 4.5 and 0.6% ($0.2\text{--}0.9\%$) under RCP 8.5. For the status quo scenario, proportional growth between 2060 and 2099 averaged 1.2% ($0.9\text{--}1.7\%$) under RCP 4.5 and 0.7% ($0.3\text{--}1.0\%$) under RCP 8.5. In the 4FRI restoration scenario for this time period, proportional growth averaged 1.4% ($1.0\text{--}1.9\%$) under RCP 4.5 and 0.8% ($0.3\text{--}1.3\%$) under RCP 8.5. Under the 4FRI-I restoration scenario, proportional growth averaged 1.8% ($1.1\text{--}2.3\%$) under RCP 4.5 and 0.8% ($0.3\text{--}1.4\%$) under RCP 8.5.

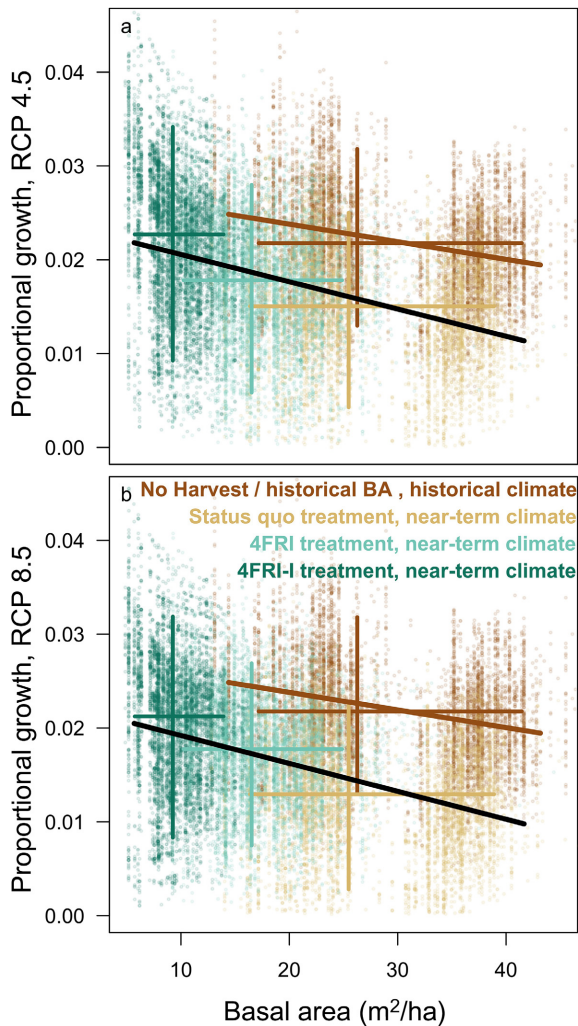


FIG 5. Relationship between proportional growth and stand basal area. Brown line and points show proportional growth vs. historical stand basal area under historical climate condition. Future proportional growth vs. basal area in three alternative basal area treatment scenarios under future (2020–2059) climate conditions (black line) for (a) RCP 4.5 and (b) RCP 8.5. Points for status quo, 4FRI, and 4FRI-I treatments shown in light brown, light green, and dark green, respectively. Colored lines depict the distribution of 90% of points for each scenario (no harvest, status quo, 4FRI, and 4FRI-I) relative to both basal area on the y-axis and proportional growth on the x-axis.

Our results suggest that higher stand-level basal area is associated with lower proportional growth under historical and future conditions (Fig. 5). For example, from 2020 to 2059 under RCP8.5, the 4FRI-I and 4FRI scenarios result in proportional growth rates of similar magnitudes to historical (e.g., recent) conditions (only 8% and 22% reductions, respectively, from historical rates). However, in the no-harvest and status quo scenarios during the same time period, proportional growth declines 46% and 44%, respectively.

Drought stress

Under historical conditions, these stands experienced extremely low growth in an average of only 1.6% of years (Fig. 6 and Appendix S1: Fig. S6). From 2020 to 2059, we projected the mean percent of years with extremely low growth in the no-harvest scenario to increase to 16% (GCM range 7–26%) under RCP 4.5 or 23% (14–35%) under RCP 8.5. In the status quo restoration scenario, mean percentage of years with low growth increases to 15% (6–25%) under RCP 4.5 and 22% (13–33%) under RCP 8.5. In the 4FRI scenario, it increases to 9% (3–16%) under RCP 4.5 and 6.6% (2.3–12%) under RCP 8.5. Among scenarios, mean percent of years with low growth increased the least in the 4FRI-I scenario, with estimates of 4% (0.8–9%) under RCP 4.5 and 5.4% (1.7–10%) under RCP 8.5.

Historically, 71% of stands did not have any years with extremely low growth, while 4% of stands experienced low growth an average of 1 in 10 yr (Appendix S1: Fig. S6). From 2020–2059 for the median GCM, the percent of stands that experience no years with extremely low growth drops from 71% to 25% or 12% (median GCM for RCP 4.5 and 8.5, respectively) for the no-harvest and status quo scenarios, to 55% or 51% in the 4FRI scenario, and to 70% or 61% in the 4FRI-I scenario. In contrast, the proportion of stands with low growth at least 1 in 10 yr increases from 4% historically to 40% or 52% (RCP 4.5 or RCP 8.5) in the no-harvest scenario, to 34% (both RCPs) in the status quo scenario, to 22% or 18% in the 4FRI scenario, and to 12% or 15% in the 4 FRI-I scenario.

From 2060 to 2099, the average percentage of years with extremely low growth increases even further, to 28% or 59% (RCP 4.5 or RCP 8.5, respectively) in the no-harvest scenario, 25% or 53% under status quo, 18% or 40% in the 4FRI scenario, and 11% or 45% in 4FRI-I. During this time period, the percent of stands with no low growth years drops from 71% to 13% or 0% (RCP 4.5 or 8.5, respectively) for the no-harvest and status-quo scenarios, to 35% or 3% for 4FRI, and to 50% or 6% for 4FRI-I. Likewise, the proportion of stands experiencing low growth at least 1 in 10 yr increases to 58% or 90% (RCP 4.5 or 8.5, respectively) for no-harvest, 52% or 87% for status quo, 40% or 78% for 4FRI, and 26% or 83% for 4FRI-I.

Our growth estimates utilize relationships derived from the same area (Andrews et al. 2020) and applying these relationships to all stands within this landscape (>6,000) provides insight into potential spatial patterns and heterogeneity of drought vulnerability under future climate conditions (Fig. 6). Much of the spatial heterogeneity is a result of variability in target basal area, which is negatively related to proportional growth and varies substantially among stands within each restoration scenario (Figs 3 and 5). Proportional growth is lower in stands with low soil moisture and high hot-dry stress, and reductions in stand density can minimize the

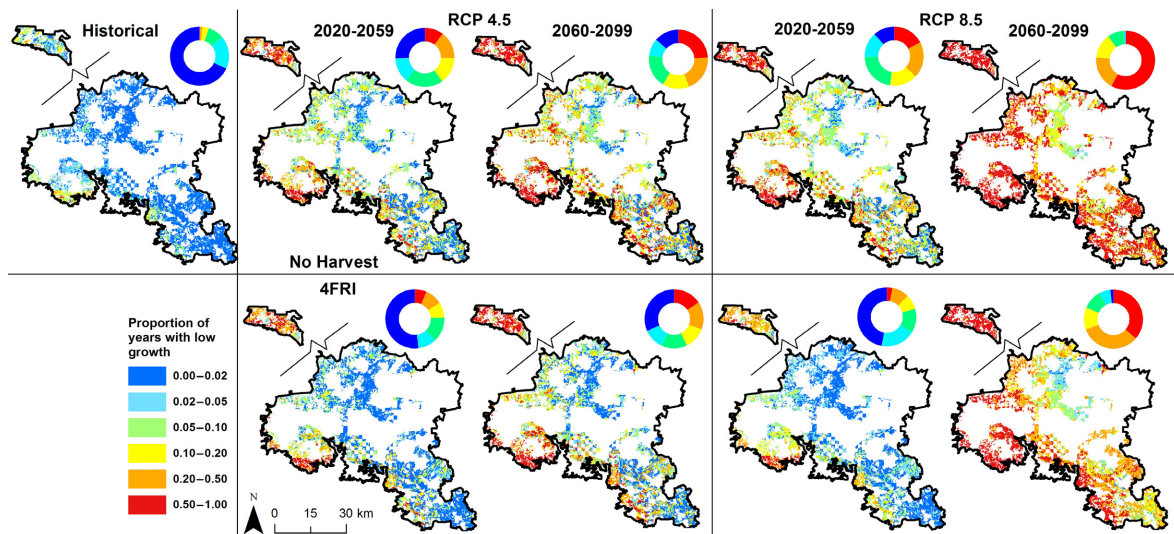


FIG 6. Geographic patterns in the proportion of years with extremely low growth across the Four Forest Restoration Initiative landscape illustrating the impact of two basal area conditions (top row, No Harvest; bottom row, 4FRI treatments) and five climate conditions (left column, historical climate; second and third columns, 2020–2059 and 2060–2099 for representative concentration pathway 4.5; fourth and fifth columns, 2020–2059 and 2060–2099 for representative concentration pathway 8.5). Donut plots for each map panel depict the proportion of the landscape within each range of extreme low growth proportion. The line between polygons illustrates that the northern portion of the restoration landscape was moved closer to the rest of the area, for depiction purposes.

severity of these conditions and thus mitigate future expectations for declining growth (Appendix S1: Fig. S8). This landscape heterogeneity is also driven by inherent site characteristics including soil conditions. Note that locations with shallow or sandy soils (Fig. 1) along the southwest margin of the project area as well as the disjunct northern piece have a higher percentage of years with extremely low growth even under 4FRI thinning in the moderate RCP 4.5 scenario (Fig. 6). This characteristic is apparent across the project area; stands on deep soils that can store more total water are projected to have significantly less years with extremely low growth rates than shallower soils (Appendix S1: Fig. S7).

DISCUSSION

Although proven strategies for adapting ecosystems to climate change are rare, our results suggest that landscape-scale restoration treatments are likely to have substantial benefits related to minimizing growth vulnerability in dry forests in addition to meeting established restoration objectives. In the context of global environmental change, ecosystem restoration has emerged as a widely accepted goal, as illustrated by the United Nations Decade on Ecosystem Restoration (UN Environment Program 2019). Ecological restoration is endorsed as a strategy to rehabilitate degraded ecosystems, minimize further degradation, mitigate rising atmospheric CO₂ levels, and enhance food security, water supply, and biodiversity. In dry, fire-adapted

forests, restoration projects often focus on recreating historical stand structures and applying prescribed fire to promote disturbance regimes similar to historical patterns (Covington et al. 1997). These restoration practices have been shown to have numerous benefits, including mitigated extreme fire behavior (Finney et al. 2005), enhanced run-off (Robles et al. 2014), improved habitat (Waltz and Wallace Covington 2004), moderated bark beetle activity and tree mortality (Wallin et al. 2008), and increased long-term ecosystem carbon storage (McCauley et al. 2019). Despite these numerous benefits, the relevance of ecological restoration for creating dry forest systems that are adapted to future climate conditions is unclear (Fulé 2008).

Here, we evaluated the impact of planned restoration treatments on average stand-level basal area increment (BAI), proportional growth (BAI/BA), and the percent of years that each stand is expected to experience extremely low growth. Although both BAI and proportional growth generally decline under future scenarios, the influence of treatment and resulting stand density differ substantially between these two growth metrics. BAI, as well as total biomass (Appendix S1: Fig. S3) and annual biomass increment (Appendix S1: Fig. S4), are greatest in the no-harvest and status quo scenarios that maintain stands at high basal area. However, the higher estimated BAI, biomass, and biomass increment for these scenarios are accompanied by two important caveats. First, maintaining the landscape in this high-density condition will involve elevated forest health risk (e.g., insect-related mortality) and risk of high severity wildfires with

substantial carbon emissions and potential to transform these forests into non-forested systems (Hurteau et al. 2008, Stevens-Rumann et al. 2017, Loehman et al. 2018, McCauley et al. 2019). Second, these future growth estimates assume that the high basal areas prescribed in the no-harvest and status quo scenarios are not reduced due to either inhibited potential tree regeneration under high-density situations (Flathers et al. 2016, Kolb et al. 2020) or elevated tree mortality promoted by high competition (Das et al. 2011, Van Gunst et al. 2016, Bradford and Bell 2017). Moreover, hotter and drier conditions under climate change are predicted to increase recruitment failure (Petrie et al. 2017) and mortality of pine species in dryland forests and woodlands (McDowell et al. 2015, Breshears et al. 2018) suggesting that forests under these high basal area conditions are not sustainable.

The results of this study indicate that proportional growth is likely a more appropriate metric for assessing the vulnerability of individual trees to drought-induced growth declines and eventual mortality (Bigler and Bugmann 2004). Our projections for substantially higher future proportional growth in either 4FRI or 4FRI-I restoration scenarios, compared to the no-harvest or status quo scenarios, illustrate the potential drought benefits of additional density reduction for minimizing drought vulnerability. Similarly, our results regarding the percentage of years with extremely low proportional growth rates highlight the potential benefits of the 4FRI and 4FRI-I scenarios and provide perspective on how these forest restoration scenarios may impact drought-driven tree mortality. Although decreases in forest growth are expected under future climate conditions regardless of treatment, the higher proportional growth rates estimated under the 4FRI and 4FRI-I treatments, compared to the status quo treatment, imply that those low-density stands are likely to be substantially more resistant and resilient to growth declines through the middle of the century. Although the effectiveness of restoration treatments at maintaining proportional growth at rates similar to historical conditions is sustained throughout the 21st century under RCP 4.5, those benefits decrease during the end of the century time period under RCP 8.5 (Fig. 4b), which includes substantially higher temperature projections (Fig. 2 and Appendix S1: Fig. S2).

Slow tree growth is a recognized precursor to tree mortality (Suarez et al. 2004, Vanoni et al. 2016, Caillet et al. 2017) and, while low growth years are projected to increase for all scenarios, the percentage of years with low growth is several times higher in the no-harvest and status quo scenarios (23% and 22%, respectively, during 2020–2059 under RCP 8.5) compared to the 4FRI and 4FRI-I scenarios (7% and 5%, respectively). These differences are also apparent in the more moderate climate change conditions of RCP 4.5, in which the percentage of years with low growth averages 16% and 15% in no-harvest and status quo, respectively,

compared to 9% and 4% under 4FRI or 4FRI-I treatments. Higher future proportional growth, and relatively few years with extremely low proportional growth, under conditions prescribed by forest restoration treatments implies that these two scenarios may be able to sustain overall tree growth vigor through the middle of the 21st century.

Because proportional growth rates decline with basal area under both historical and future conditions (Fig. 5), maintaining stands at low basal areas appears to be even more important for sustaining growth in the future than it has been historically. Thus, applying these restoration treatments and maintaining stands at low density shows potential to obtain the original benefits considered in the restoration planning, namely minimization of catastrophic fire risk, as well as promote decreased vulnerability to future drought-induced growth reduction and forest decline. In our analysis, differences in vulnerability among restoration scenarios are driven by both higher estimated competition in dense stands (represented by the negative basal area coefficient in Eq. 1) and by the direct influence of forest structure on patterns of drought severity (Andrews et al. 2020). Specifically, our water balance modeling suggested that the slower rates of transpiration in lower density stands result in higher moisture availability and less frequent hot-dry stress under future climate conditions, thus moderating the hotter and drier spring and early summer conditions noted earlier (Appendix S1: Fig. S2). The only exception to the general relationship of lower basal area associated with higher proportional growth and lower percent of years with extremely low growth is during 2060–2099 under RCP 8.5, when our results suggest slightly higher proportion of years with low growth in the 4FRI-I scenario compared to the 4FRI scenario (Appendix S1: Fig. S6). In these climate conditions, the 4FRI-I treatments experience slightly more especially unfavorable years than the 4FRI treatment (but not less favorable conditions on average.) This is a consequence of our water balance model estimating that the very low 4FRI-I BA levels create slightly higher levels of the $Stress_{2YA}$ during the warmest years within 2060–2099 under RCP8.5 than 4FRI (Appendix S1: Fig. S2e). Because temperatures during in this time period and RCP are dramatically different from those observed in our training data set (temperatures during the hottest year are $\sim 7^{\circ}\text{C}$ higher than present; Appendix S1: Fig. S2a), our projections for both drought stress (e.g., $Stress_{2YA}$) and resulting tree growth need to be confirmed by additional observational studies.

Managing natural resources in the context of climate change is complicated by uncertainty in future climate trajectories, and a focus on integrative measures of ecological drought may help minimize that uncertainty. Climate uncertainty is especially challenging for dryland ecosystems that are strongly dependent on and limited by water, because projected changes in precipitation are less consistent than temperature. Climate projections for

these forests, as for most drylands, include robust estimates (e.g., consistent across climate models) for increasing temperature and more frequent extreme weather (Collins et al. 2013, Knutti and Sedlacek 2013, Trenberth et al. 2015, Diffenbaugh et al. 2017), but generally more variable estimates for changes in precipitation (Burke and Brown 2008, Collins et al. 2013, Padrón et al. 2019). Here, we worked to minimize some of the uncertainty related to divergent precipitation projections by estimating ecological drought metrics that integrate the effects of temperature and soil moisture availability. We identified shifts in seasonal soil moisture that are both robust across models and likely to be important for understanding the response of these dry forests to climate change. The projections for changes in soil moisture patterns that are robust across climate models are, for the most part, those driven by rising temperature. Specifically, all climate models under both RCPs agree about the projections for wetter winter soils, earlier spring soil drying, and longer spring-summer dry periods (Fig. 3). Although the consistent signal for slightly lower precipitation in May likely contributes to the longer dry periods, much of these changes are logical outcomes of higher temperatures. Warmer future temperatures result in more water entering the soil during the winter, rather than accumulating as snow, enhancing soil moisture during the winter. More rapid evapotranspiration created by higher temperatures also promotes earlier spring soil drying that results in longer dry periods occurring in the spring and early summer with higher temperatures than experienced historically. By contrast, large variability among models in projected changes in monsoon precipitation results in large soil moisture variability during the late summer and fall.

Our analysis is limited in several important ways that suggest potential opportunities for improvement in subsequent studies. First, our estimation of growth rates is derived from the historical Taylor Woods long-term forest management experiment (Bailey 2008) that includes several levels of stand density in monospecific, even-aged ponderosa pine stands. While this experiment provides an excellent perspective on the type and strength of interactions between stand density and drought conditions (Andrews et al. 2020) that are consistent with similar sites in other long-term forest management experiments (Bottero et al. 2017, Gleason et al. 2017), it represents only a single soil type and climate (Bailey 2008). Our drought metrics utilize soil water potential to quantify moisture availability, which should be more easily applied to other soils with different particle sizes than metrics relying upon volumetric water content. However, the influence of soils on growth from non-moisture conditions, notably fertility, are not represented in our analysis and warrant further investigation. Consistent with Taylor Woods, most 4FRI stands are almost entirely ponderosa pine, although the landscape includes minor components of oak, pinyon, and juniper species whose dynamics are not represented by our results (U.S.

Department of Agriculture 2014). Likewise, some stands consist of mixed age cohorts that may display different stand-level growth responses to drought (U.S. Department of Agriculture 2014). Over time, variability in individual tree growth among mixed size classes or age cohorts within a heterogeneous stand may exacerbate divergence in tree sizes and create more favorable conditions for the largest dominant trees than would be predicted based on total stand basal area, although we have no means for assessing this in our data. Second, our estimation of future growth rates required applying a statistical model with linear relationships for growth outside of the range of climatic and soil moisture conditions in which it was developed. While the values for moisture availability declined slightly under future climate conditions but generally remain within the range of historical variation, climate change projections indicate higher values for annual mean temperature, annual maximum temperature, and hot-dry stress especially under RCP8.5 from 2060–2099 than have been observed within this landscape under historical conditions (Fig. 2 and Appendix S1: S2). We utilized data from a suite of climate models selected to represent the full variation among models in CMIP5, but long-term climate conditions are nevertheless inherently uncertain, and our insights about future drought and tree growth vulnerability are conditioned on the climate projections that we considered. Thus, the impacts of climate change for these forests should be reconsidered as awareness of climate trajectories is improved. Regardless of the source for future climate conditions, confirming the appropriateness of specific soil moisture metrics and the relationship of those metrics to annual stand-level ponderosa pine growth on other soil types and in a broader range of climate conditions is an important next step. Another limitation of our analysis is that our approach to estimating growth does not include effects from factors other than temperature and moisture, notably potential limitation by availability of nitrogen or other nutrients. Despite these limitations, our results illustrate that dry forest treatments planned for restoration goals are likely to have substantial additional benefits for minimizing drought vulnerability.

Our projections of 21st-century forest growth and the influence of restoration treatments display important differences between RCP 4.5 and RCP 8.5 and between 2020–2059 and 2060–2099 time frames. Most notably, the 4FRI forest restoration project maintains proportional growth and the percentage of low growth years similar to historical levels under RCP 4.5 climate throughout the 21st century, or under RCP 8.5 climate for the near term. By contrast, in the long-term climate conditions expected for RCP 8.5, average growth rates under all restoration scenarios are <40% of their historical means, while extremely low growth rates are expected in more than one-third of years even in the 4FRI-I scenario (Appendix S1: Fig. S6). Clear differences between RCP 4.5 and RCP 8.5 are most pronounced in the long-

term timeframe (Fig. 4). The RCP 4.5 climate simulations show that growth and drought vulnerability at the end of the 21st century (2060–2099) are relatively similar to values estimated for RCP 8.5 in the near-term future, 2020–2059 (Figs 4 and 6). These differences highlight an important long-term divergence in climate change impacts on these dry forests between RCP 4.5, in which forest management can help moderate drought vulnerability throughout the 21st century, and RCP 8.5, in which growth declines substantially, and low growth years increase markedly under all treatment options. This implies that the benefits of these restoration scenarios for minimizing drought vulnerability and enhancing forest growth resistance and resilience to drought may last decades longer under the lower emissions RCP 4.5 pathway.

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LITERATURE CITED

- Allen, C. D., et al. 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *Forest Ecology and Management* 259:660–684.
- Allen, C. D., D. D. Breshears, and N. G. McDowell. 2015. On underestimation of global vulnerability to tree mortality and forest die-off from hotter drought in the Anthropocene. *Ecosphere* 6(8):art129.
- Andrews, C. M., and J. B. Bradford. 2020. Ecosystem water balance and ecological drought patterns under historical and future climate conditions for the Four Forest Restoration Initiative (4FRI) Landscape. U.S. Geological Survey data release. <https://doi.org/10.5066/P937Z0R9>
- Andrews, C. M., A. W. D'Amato, S. Fraver, B. Palik, M. A. Battaglia, and J. B. Bradford. 2020. Low stand density moderates growth declines during hot-droughts in semi-arid forests. *Journal of Applied Ecology* 57:1089–1102.
- Bailey, J. D. (2008). Forty years later at Taylor Woods: Merging the old and new. Pages 100–105 in S. D. Olberding and M. M. Moore, editors. *Fort Valley Experimental Forest—a century of research 1908–2008*. Conference Proceedings; August 7–9, 2008; Flagstaff, Arizona. Proceedings RMRS-P-55. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado, USA.
- Bigler, C., and H. Bugmann. 2004. Predicting the time of tree death using dendrochronological data. *Ecological Applications* 14:902–914.
- Blate, G. M., L. A. Joyce, J. S. Littell, S. G. McNulty, C. I. Millar, S. C. Moser, R. P. Neilson, K. O'Halloran, and D. L. Peterson. 2009. Adapting to climate change in United States national forests. *Unasylva* 231:57–62.
- Bosworth, D., R. Birdsey, L. Joyce, and C. Millar. 2008. Climate change and the nation's forests: Challenges and opportunities. *Journal of Forestry* 106:214–221.
- Bottero, A., A. W. D'Amato, B. J. Palik, J. B. Bradford, S. Fraver, M. A. Battaglia, and L. A. Asherin. 2017. Density-dependent vulnerability of forest ecosystems to drought. *Journal of Applied Ecology* 54:1605–1614.
- Bradford, J. B., et al. 2017. Future soil moisture and temperature extremes imply expanding suitability for rainfed agriculture in temperate drylands. *Scientific Reports* 7:12923.
- Bradford, J. B., and D. M. Bell. 2017. A window of opportunity for climate-change adaptation: easing tree mortality by reducing forest basal area. *Frontiers in Ecology and the Environment* 15:11–17.
- Bradford, J. B., J. L. Betancourt, B. J. Butterfield, S. M. Munson, and T. E. Wood. 2018. Anticipatory natural resource science and management for a changing future. *Frontiers in Ecology and the Environment* 16:295–303.
- Bradford, J. B., D. R. Schlaepfer, and W. K. Lauenroth. 2014. Ecohydrology of adjacent sagebrush and lodgepole pine ecosystems: The consequences of climate change and disturbance. *Ecosystems* 17:590–605.
- Bradford, J. B., D. R. Schlaepfer, W. K. Lauenroth, and K. A. Palmquist. 2020. Robust ecological drought projections for drylands in the 21st century. *Global Change Biology* 26(7):3906–3919.
- Bréda, N., A. Granier, and G. Aussenac. 1995. Effects of thinning on soil and tree water relations, transpiration and growth in an oak forest (*Quercus petraea* (Matt.) Liebl.). *Tree Physiology* 15:295–306.
- Breshears, D. D., et al. 2018. A dirty dozen ways to die: Metrics and modifiers of mortality driven by drought and warming for a tree species. *Frontiers in Forests and Global Change* 1:4.
- Breshears, D. D., O. B. Myers, C. W. Meyer, F. J. Barnes, C. B. Zou, C. D. Allen, N. G. McDowell, and W. T. Pockman. 2009. Tree die-off in response to global change-type drought: mortality insights from a decade of plant water potential measurements. *Frontiers in Ecology and the Environment* 7:185–189.
- Burke, E. J., and S. J. Brown. 2008. Evaluating Uncertainties in the Projection of Future Drought. *Journal of Hydrometeorology* 9:292–299.
- Cailleret, M., et al. 2017. A synthesis of radial growth patterns preceding tree mortality. *Global Change Biology* 23:1675–1690.
- Cayan, D. R., T. Das, D. W. Pierce, T. P. Barnett, M. Tyree, and A. Gershunov. 2010. Future dryness in the southwest US and the hydrology of the early 21st century drought. *Proceedings of the National Academy of Sciences USA* 107(50):21271–21276.
- Choat, B., et al. 2012. Global convergence in the vulnerability of forests to drought. *Nature* 491:752–755.
- Collins, M., et al. 2013. Long-term climate change: projections, commitments and irreversibility. Pages 1029–1136 in T. F. Stocker, D. Qin, G.-K. Plattner, M. Tignor, S. K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex, and P. M. Midgley, editors. *Climate change 2013: the physical science basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge, UK.
- Cook, B. I., T. R. Ault, and J. E. Smerdon. 2015. Unprecedented 21st century drought risk in the American Southwest and Central Plains. *Science Advances* 1:e1400082.
- Covington, W. W., P. Z. Fulé, M. M. Moore, S. C. Hart, T. E. Kolb, J. N. Mast, S. S. Sackett, and M. R. Wagner. 1997. Restoration of ecosystem health in southwestern ponderosa pine forests. *Journal of Forestry* 95:23–29.
- Dai, A. 2013. Increasing drought under global warming in observations and models. *Nature Climate Change* 3:52–58.
- D'Amato, A. W., J. B. Bradford, S. Fraver, and B. J. Palik. 2013. Effects of thinning on drought vulnerability and climate

- communities: climate change consequences for soil water resources. *Ecology* 97:2342–2354.
- Peng, C., Z. Ma, X. Lei, Q. Zhu, H. Chen, W. Wang, S. Liu, W. Li, X. Fang, and X. Zhou. 2011. A drought-induced pervasive increase in tree mortality across Canada's boreal forests. *Nature Climate Change* 1:467–471.
- Petrie, M. D., J. B. Bradford, R. M. Hubbard, W. K. Lauenroth, C. M. Andrews, and D. R. Schlaepfer. 2017. Climate change may restrict dryland forest regeneration in the 21st century. *Ecology* 98:1548–1559.
- Polade, S. D., A. Gershunov, D. R. Cayan, M. D. Dettinger, and D. W. Pierce. 2017. Precipitation in a warming world: Assessing projected hydro-climate changes in California and other Mediterranean climate regions. *Scientific Reports* 7:10783.
- Polade, S. D., D. W. Pierce, D. R. Cayan, A. Gershunov, and M. D. Dettinger. 2014. The key role of dry days in changing regional climate and precipitation regimes. *Scientific Reports* 4:4364.
- Reynolds, R. T., A. J. S. Meador, J. A. Youtz, T. Nicolet, M. S. Matonis, P. L. Jackson, D. G. DeLorenzo, and A. D. Graves. 2013. Restoring composition and structure in southwestern frequent-fire forests: a science-based framework for improving ecosystem resiliency. General Technical Report RMRS-GTR-310. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado, USA.
- Robles, M. D., R. M. Marshall, F. O'Donnell, E. B. Smith, J. A. Haney, and D. F. Gori. 2014. Effects of climate variability and accelerated forest thinning on watershed-scale runoff in southwestern USA ponderosa pine forests. *PLoS One* 9: e111092.
- Rupp, D. E., J. T. Abatzoglou, K. C. Hegewisch, and P. W. Mote. 2013. Evaluation of CMIP5 20th century climate simulations for the Pacific Northwest USA. *Journal of Geophysical Research: Atmospheres* 118:2013JD020085.
- Savage, M., and J. N. Mast. 2005. How resilient are southwestern ponderosa pine forests after crown fires? *Canadian Journal of Forest Research* 35:967–977.
- Schlaepfer, D. R., et al. 2017. Climate change reduces extent of temperate drylands and intensifies drought in deep soils. *Nature Communications* 8:14196.
- Schlaepfer, D. R., W. K. Lauenroth, and J. B. Bradford. 2012. Ecohydrological niche of sagebrush ecosystems. *Ecohydrology* 5:453–466.
- Schultz, C. A., T. Jedd, and R. D. Beam. 2012. The collaborative forest landscape restoration program: a history and overview of the first projects. *Journal of Forestry* 110:381–391.
- Seager, R., and G. A. Vecchi. 2010. Greenhouse warming and the 21st century hydroclimate of southwestern North America. *Proceedings of the National Academy of Sciences USA* 107:21277–21282.
- Seppälä, R., A. Buck, and P. Katila. 2009. Adaptation of forests and people to climate change—a global assessment report. *IUFRO World Series* 22:224.
- Smith, D. M., B. C. Larson, M. J. Kelty, and P. M. S. Ashton. 1997. *The practice of silviculture: applied forest ecology*. John Wiley and Sons, New York, New York, USA.
- Sperry, J. S., and U. G. Hacke. 2002. Desert shrub water relations with respect to soil characteristics and plant functional type. *Functional Ecology* 16:367–378.
- Spittlehouse, D. L., and R. B. Stewart. 2004. Adaptation to climate change in forest management. *Journal of Ecosystems and Management* 4:1–11.
- Stein, B. A., P. Glick, N. Edelson, and A. Staudt. 2014. Climate-smart conservation: putting adaption principles into practice. National Wildlife Federation, Washington, D.C., USA.
- Stevens-Rumann, C. S., K. B. Kemp, P. E. Higuera, B. J. Harvey, M. T. Rother, D. C. Donato, P. Morgan, and T. T. Veblen. 2017. Evidence for declining forest resilience to wildfires under climate change. *Ecology Letters* 21:243–252.
- Suarez, M. L., L. Ghermandi, and T. Kitzberger. 2004. Factors predisposing episodic drought-induced tree mortality in *Nothofagus*—site, climatic sensitivity and growth trends. *Journal of Ecology* 92:954–966.
- Taylor, K. E., R. J. Stouffer, and G. A. Meehl. 2011. An overview of CMIP5 and the experiment design. *Bulletin of the American Meteorological Society* 93:485–498.
- Tohver, I. M., A. F. Hamlet, and S.-Y. Lee. 2014. Impacts of 21st-century climate change on hydrologic extremes in the pacific northwest region of North America. *JAWRA Journal of the American Water Resources Association* 50:1461–1476.
- Trenberth, K. E., J. T. Fasullo, and T. G. Shepherd. 2015. Attribution of climate extreme events. *Nature Climate Change* 5:725–730.
- U.S. Department of Agriculture. 1991. Terrestrial ecosystem survey of the Kaibab National Forest. Department of Agriculture, Forest Service, Southwestern Region, Tempe, Arizona, USA.
- U.S. Department of Agriculture. 1995. Terrestrial ecosystem survey of the Coconino National Forest. Department of Agriculture, Forest Service, Southwestern Region, Tempe, Arizona, USA.
- U.S. Department of Agriculture. 2014. Final environmental impact statement for the four-forest restoration initiative. Coconino and Kaibab National Forests, Forest Service Southwestern Region, Tempe, Arizona, USA.
- U.S. Department of Agriculture. 2015. Record of decision for the four-forest restoration initiative. Forest Service Southwest Region, Coconino and Kaibab National Forests, Tempe, Arizona, USA.
- UN Environment Program. 2019. New UN Decade on Ecosystem Restoration offers unparalleled opportunity for job creation, food security and addressing climate change. <https://www.unenvironment.org/news-and-stories/press-release/new-un-decade-ecosystem-restoration-offers-unparalleled-opportunity>
- Van Gunst, K. J., P. J. Weisberg, J. Yang, and Y. Fan. 2016. Do denser forests have greater risk of tree mortality: A remote sensing analysis of density-dependent forest mortality. *Forest Ecology and Management* 359:19–32.
- Vanoni, M., H. Bugmann, M. Nötzli, and C. Bigler. 2016. Drought and frost contribute to abrupt growth decreases before tree mortality in nine temperate tree species. *Forest Ecology and Management* 382:51–63.
- Vicente-Serrano, S. M., et al. 2013. Response of vegetation to drought time-scales across global land biomes. *Proceedings of the National Academy of Sciences USA* 110:52–57.
- Wallin, K. F., T. E. Kolb, K. R. Skov, and M. Wagner. 2008. Forest management treatments, tree resistance, and bark beetle resource utilization in ponderosa pine forests of northern Arizona. *Forest Ecology and Management* 255:3263–3269.
- Waltz, A. E. M., and W. Wallace Covington. 2004. Ecological restoration treatments increase butterfly richness and abundance: mechanisms of response. *Restoration Ecology* 12:85–96.
- Watling, J. I., and M. A. Donnelly. 2006. Fragments as Islands: A synthesis of faunal responses to habitat patchiness. *Conservation Biology* 20:1016–1025.
- Webster, M., et al. 2012. Analysis of climate policy targets under uncertainty. *Climatic Change* 112:569–583.

Williams, P. A., et al. 2013. Temperature as a potent driver of regional forest drought stress and tree mortality. *Nature Climate Change* 3:292–297.

Wu, T., and Y.-S. Kim. 2013. Pricing ecosystem resilience in frequent-fire ponderosa pine forests. *Forest Policy and Economics* 27:8–12.

SUPPORTING INFORMATION

Additional supporting information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/eap.2238/full>

DATA AVAILABILITY STATEMENT

Data generated during this study are available from the USGS ScienceBase-Catalog (Andrews and Bradford 2020): <https://doi.org/10.5066/P937Z0R9>