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Biomass stocks in California's fire-prone forests: mismatch in ecology and policy

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Abstract

Restoration of fire-prone forests can promote resiliency to disturbances, yet such activities may reduce biomass stocks to levels that conflict with climate mitigation goals. Using a set of large-scale historical inventories across the Sierra Nevada/southern Cascade region, we identified underlying climatic and biophysical drivers of historical forest characteristics and projected how restoration of these characteristics manifest under future climate. Historical forest conditions varied with climate and site moisture availability but were generally characterized by low tree density ($\sim$53 trees ha^{-1}), low live basal area ($\sim$22 m^2 ha^{-1}), low biomass ($\sim$34 Mg ha^{-1}), and high pine dominance. Our predictions reflected broad convergence in forest structure, frequent fire is the most likely explanation for this convergence. Under projected climate (2040–2069), hotter sites become more prevalent, nearly ubiquitously favoring low tree densities, low biomass, and high pine dominance. Based on these projections, this region may be unable to support aboveground biomass >40 Mg ha^{-1} by 2069, a value approximately 25% of current average biomass stocks. Ultimately, restoring resilient forests will require adjusting carbon policy to match limited future aboveground carbon stocks in this region.

1. Introduction

Fire-prone forests (those with historical fire intervals <35 years) have undergone drastic changes that render them more vulnerable to large-scale disturbances (Stephens *et al* 2013, 2018a, Singleton *et al* 2019, Hagmann *et al* 2021). Indeed, past management practices and over a century of aggressive fire suppression have resulted in increased tree density, shifts in species composition, and elevated fuels loads (Stephens *et al* 2009, Lydersen *et al* 2013, Knapp *et al* 2017, North *et al* 2021). The consequences of these changes on forest ecosystems are evident in California, where recent years of drought, insect outbreaks, and wildfires led to substantial levels of tree mortality (Stephens *et al* 2018a, Fettig *et al* 2019). With extreme drought and severe wildfire expected to increase in frequency and severity under projected future climate (Allen *et al* 2015, Kolb *et al* 2016, Williams *et al* 2019), there is greater likelihood of forest loss and the ecosystem services that they provide (Liang *et al* 2017b, Jones *et al* 2020).

In 2017, California re-authorized its landmark greenhouse gas reduction efforts and extended its goal of reducing greenhouse gas emissions to 40% below 1990 levels by 2030 (AB-398). To achieve this goal, the state has outlined restoration and conservation strategies designed to ensure that forests remain net sinks of carbon. The Sierra Nevada/southern Cascade region contains almost half of the forest carbon stocks in California, accounting for 46% of the total above ground live tree carbon across the state (Forest Climate Action Team 2018). However, the annual rate of carbon sequestration is declining. From 2018 to 2019, the region lost 1.1 MMT of carbon dioxide equivalent (CO2e)—a 35% decrease that is largely attributed to disturbance-related tree mortality (Christensen *et al* 2019). If these trends continue under climate change, the ability of the Sierra Nevada/southern Cascade region to remain a reliable carbon sink may be compromised (Liang *et al* 2017a).

The capacity of fire-prone forests to withstand or recover from disturbances can be improved with restoration treatments (Stephens *et al* 2020b, Hagmann *et al* 2021). Restoration is an attractive approach to forest management because it is based on structural and compositional characteristics that are reflective of the selective pressures driving evolutionary history (Franklin *et al* 2007). Improving the resiliency of California's forests is a shared and pressing goal for federal and state managers (California and United States Department of Agriculture, Forest Service 2020). Thus, implementing restoration on the landscape is a priority (Hessburg *et al* 2021). However, this charge raises a critical question—restoration to what?

Quantifying the patterns and processes of past ecosystems vitally informs the stewardship of contemporary ecosystems (Beller *et al* 2020). As such, land managers increasingly value well-documented reference conditions (Higgs *et al* 2014). These conditions are shaped by the complex interactions among climate, topography, and fire that result in variable conditions across multiple scales (Collins *et al* 2016, Jeronimo *et al* 2019). A concern with relying on reference conditions to inform restoration is that novel conditions under climate change may create uncharacteristic feedbacks between climate, vegetation, and disturbances that substantially diverge from the processes that drove forest dynamics in the past(Coop *et al* 2020). Under these circumstances, the value of using reference conditions as a relevant baseline for promoting resiliency must be evaluated against expectations of the types of forests that can be sustained under future conditions (Fulé 2008).

Using a set of large-scale historical (1911–1936) inventories conducted in California, we identified the underlying climatic and biophysical drivers of historical forest characteristics, and then project how these characteristics will be distributed across the region under future climate. These inventories provide detailed observations of a forest condition that was shaped by frequent fire, interacting with topography and local moisture availability (Hagmann *et al* 2018). As such, the reconstructed forest structure and composition captures reference conditions that can inform large-scale forest restoration. Given the similarities across a broad range of studies that quantified historical structure in fire-prone forests (Hagmann *et al* 2013, 2014, Collins *et al* 2015, Stephens *et al* 2015, Stephens *et al* 2018b, Collins *et al* 2021), we expect low aboveground live tree biomass (AGLB), low tree density, low basal area and pine dominance to be relatively common across a broad range of historical environmental conditions within the Sierra Nevada/southern Cascade region. However, some of these environments are unlikely to persist with climate change. Future resilient forests may therefore be different than what they were historically. Our overall goal is to provide information on the long-term sustainability of forest carbon stocks, which can be used to design spatially explicit restoration treatments for these altered forests into the future. This information may be particularly useful to policymakers and land managers for the development of realistic goals that reconcile the ecology of these systems under projected near-term climate with carbon mitigation goals.

2. Methods

2.1. Study area

The historical forest inventory data used covers a range of latitudes (36°–40°) and elevations (1046 m–2442 m), from the southernmost location in the southern Sierra Nevada to the northernmost location in the southern Cascade Range (supplementary figure 1 available online at stacks.iop.org/ERL/17/044047/mmedia). Prior to 1900, low- to moderate-severity fire was common across these areas ignited by lightning and Indigenous people, with median fire return intervals ranging from 5 to 20 years (Kilgore and Taylor 1979, Caprio and Swetnam 1993, Stephens and Collins 2004, Stephens *et al* 2007, Scholl and Taylor 2010, Taylor *et al* 2016, Skinner and Taylor 2018). There is no evidence that our study areas were impacted by management prior to the historical inventories, with the exception of a very small proportion of observations (<1%) (Collins *et al* 2015, Stephens *et al* 2015, 2018b) which we excluded from further analyses.

2.2. Historical inventory data

Our historical dataset consists of four separate inventories that were completed between 1911 to 1936 (supplementary table 1). Three inventories were conducted in federally-owned forests including the Sequoia National Forest (formerly Kern National Forest), the Stanislaus National Forest (including some areas of Yosemite National Park), and the El Dorado National Forest. One inventory located near the Plumas and Lassen National Forests was privately-owned and we refer to this inventory as the Lassen-Plumas site. All forest inventories were located systematically based on the public land survey system. Each inventory adopted a belt transect approach, with transects ranging from 20.1 m to 40.2 m wide and 402 m long, spanning the length of one 16.2 ha (40 ac) quarter-quarter (QQ) section. The number of transects in each QQ section varied by site, resulting in sampling intensities ranging from 3% to 40% by area. Multiple transects within a single QQ section were pooled so that our observed sampling unit was at the QQ section scale (16.2 ha). This resulted in a total of 2791 samples distributed across the Sequoia

National Forest ($n = 379$), Stanislaus National Forest ($n = 265$), El Dorado National Forest ($n = 611$), and the Lassen-Plumas ($n = 1534$).

From these samples, we calculated tree density (trees ha^{-1}) and total live basal area (m^2 ha^{-1}) by species. Total basal area is the cross-sectional area of inventoried live trees measured at diameter at breast height (DBH). Using live basal area, we estimated species-specific AGLB (Mg ha^{-1}) using established methods (Zhou and Hemstrom 2009, Knight *et al* 2020) (supplementary methods) and calculated pine fraction as the ratio of pine basal area relative to the total amount of basal area for a given QQ section. While trees <30.5 cm DBH were included in some inventories, these recordings were inconsistent within individual surveys and not tallied across all sites. To maintain consistency between datasets, we established a minimum DBH cut-off of 30.5 cm in our calculations of tree density and live basal area. While this does underrepresent the contribution of smaller-sized trees, datasets that included these smaller size classes showed that they composed a relatively small fraction of the overall inventory (1%–3% of total live basal area) (Stephens *et al* 2015).

2.3. Historical and future environmental conditions

To evaluate how biophysical characteristics are related to historical forest structure, we extracted underlying climate and topographic data for our historical dataset. Climate data were acquired from raster datasets derived from the Basin Characterization Model (Flint *et al* 2013, 2014), which provides 30 year climate averages (1920–1951) that overlap with the timing of our historical forest inventories. Climate variables included mean values for maximum summer (June–August) temperature (°C), winter (December–February) precipitation (mm), annual climatic water deficit (mm), and 1 April snowpack (mm). Topographic data were acquired from LANDFIRE and included elevation (m), slope (degrees), and aspect (degrees). We converted aspect to a categorical variable with breakpoints at 0°/360°, 90°, 180°, and 270° to correspond to northeast-facing, southeast-facing, southwest-facing, and northwest-facing slopes, respectively. Since the lowest resolution of spatial data used was 270 m, we resampled datasets accordingly to 270 m.

To assess how environmental conditions shift with climate change, we used the Basin Characterization Model's 30 year averages during 2040–2069 for the same climate variables extracted for historical reconstructions. While this dataset provides downscaled projections from several global climate models, we used a subset of four models which are considered in California's Fourth Climate Change Assessment as sufficiently simulating the state's future climate (Pierce *et al* 2018) and have been used to project future carbon dynamics in the Sierra Nevada (Liang *et al* 2017a, 2017b). These models include the Geophysical Fluid Dynamics Lab coupled model (GFDL-CM3), the National Center for Atmospheric Research Community Climate System Model (CCSM4), the Centre National de Recherches Mètèorologiques Coupled Global Climate Model (CNRM-CM5), and the Model for Interdisciplinary Research on Climates (MIROC5). We averaged each climate variable across all models to create a multi-model ensemble which is the preferred approach when predicting future climates (Pierce *et al* 2009). In terms of emission scenarios, we chose to use RCP 8.5. Although this may be considered a more 'aggressive' representative concentration pathway, it matches well with carbon emissions resulting from current policies and shows highly plausible emission levels by 2100 (Schwalm *et al* 2020).

2.4. Data analysis

An initial set of all seven climate variables, elevation, slope, and aspect was considered to explain the variation in historical tree density, basal area, pine fraction, and total AGLB. Multicollinearity amongst explanatory variables was reduced by removing variables with a Pearson's correlation coefficient greater than 0.7 (supplementary figure 2). This threshold resulted in a final candidate set of six variables including slope, aspect, maximum summer temperature, annual climatic water deficit, winter precipitation, and 1 April snowpack.

We then input our reduced number of predictor variables into a random forest model using the *randomForest* package in R (Liaw and Wiener 2002, R Core Team 2020) to determine which variables were the most important in explaining historical forest structures. Random forest is a machine learning algorithm that aggregates bootstrapped estimates of multiple decision trees, which leads to greater accuracy and lower error rates relative to traditional linear regression models (Povak *et al* 2014). We created random forest models for tree density, basal area, pine fraction, and total AGLB starting with all six predictor variables. Based on the percentage increase in mean standard error, we removed the least important variable from each model and re-ran random forest. We repeated this stepwise process until only two variables remained in each model which generated five potential models for each response variable. We selected the 'best' performing model based on the greatest percentage of variation explained and lowest root mean standard error (Povak *et al* 2014, Collins *et al* 2021) for the five models for each response variable (supplementary figure 3). The variables contained within these models were used as inputs in a regression tree analysis using the *rpart* package in R (Therneau and Atkinson 2019) to identify thresholds in the environmental conditions associated with historical forest conditions. We used an ANOVA method for splitting variables and a complexity parameter of

0.035 (the increase in R^2 value at each split that must occur for the split to be accepted). To avoid an overly complex regression tree, we increased the complexity parameter to 0.05 when predicting AGLB.

To evaluate how underlying environmental conditions associated with historical forest structures shift with climate change, we used the same thresholds identified by regression tree analyses and applied them to future climate variables. We then calculated the number of sites that could exist within that environmental space. We estimated historical and future tree density, basal area, pine fraction, and total AGLB at a landscape scale by applying the best random forest model to a 270 m resolution raster dataset containing each model's associated climatic and topographic variables. To determine how shifts in underlying environmental conditions manifest as changes in forest structure at the landscape scale, we subtracted the historical predictions of tree density, basal area, pine fraction, and total AGLB from the predictions generated using future climate conditions. To avoid extrapolating beyond the natural range of variation in the sampled environmental space, the region where we extrapolated our predictions was filtered for ecological system codes designated by LANDFIRE that matched our QQ dataset. Ecological systems are a classification scheme that describe the natural range of variation in plant communities based on regional distribution, vegetation physiognomy and composition, environment, and disturbance (Comer *et al* 2003). Similar to previous studies, we also excluded any topographic or climatic values that were not within the environmental space of the historical dataset (Stephens *et al* 2018b). This resulted in our predictions of landscape-scale forest structures being constrained only to areas that are representative of the site characteristics and disturbance history where our QQ sections were located (supplementary figure 4).

3. Results

Historical forest inventories revealed that median tree density across our study sites ranged from 34 to 75 trees ha^{-1}, live basal area varied between 14.5 and 39.5 m^2 ha^{-1}, while median AGLB spanned 19.9–59.1 Mg ha^{-1} (supplementary table 2). In half of our inventoried sites (Stanislaus and Lassen-Plumas), pine was the dominant component of the landscape (pine fraction ∼0.60–0.63), while the other locations (Sequoia and El Dorado) showed that forest overstory was mainly mixed-conifer with shared dominance among several species (pine fraction ∼0.33–0.43). For all forest structure metrics, our top random forest models included a combination of climatic and topographic variables, specifically: maximum summer temperature, winter precipitation, annual climatic water deficit, 1 April snowpack, slope, and aspect. Since predictions of historical and future live basal area closely resembled results for AGLB ($r^2 = 0.97$ for both historical and future), we report results for AGLB only and provide results for live basal area in the supplementary materials to avoid redundancy (supplementary figures 6 and 7).

Regression tree analysis showed that maximum summer temperature and winter precipitation were the main drivers of historical tree density (figure 1). Maximum summer temperature had the strongest influence on historical tree density, with 92% of sites exhibiting hotter conditions (maximum summer temperature ⩾24 °C). Depending on winter precipitation, sites that were hotter and drier (winter precipitation < 229 mm) were associated with ∼47 trees ha^{-1}, while wetter sites (winter precipitation ⩾229 mm) were associated with ∼69 trees ha^{-1}. While cooler sites (maximum summer temperature <24 °C) were associated with higher tree densities, they were still limited to ∼78 trees ha^{-1}. Break points established by regression tree analysis suggested that 99% of future landscapes are characterized by hotter conditions that were historically associated with lower tree densities (figure 1). In fact, the percentage of sites historically characterized by lower summer temperatures (maximum summer temperature < 24 °C) substantially decreased from 5% to <1% under future climate conditions.

Applying our top random forest model to interpolate historical tree density across the Sierra Nevada/southern Cascade study region revealed noticeable gradients (figure 2(a)). Tree density was the lowest in the western portion of the region at lower elevations, where summer temperatures were higher. Density generally increased eastward towards higher elevations as temperature decreased. However, a majority (85%) of the historical landscape was composed of forests with <75 trees ha^{-1}. Hotter conditions became more prevalent across future landscapes, resulting in 99% of the entire region having projected tree densities <75 trees ha^{-1} by 2069 (figure 2(b)). While 5% of the future landscape still aligned with historical tree densities (±1 tree ha^{-1}), our results showed that 78% of the region was predicted to support lower tree densities than what was present historically (figure 2(c)). Historically cool environments were the most vulnerable to change, where shifts in climatic conditions aligned with forests that contained as much as 168 trees ha^{-1} less than historical conditions.

A combination of climate and topography influenced historical species composition (figure 3), with 80% of sites exhibiting trends towards pine dominance (pine fraction > 0.50). Maximum summer temperature had the strongest influence on species composition, with very cold environments (<25th percentile) limiting pine fraction to 0.28 when maximum summer temperature fell below 24 °C. Warmer sites (>24 °C) had higher pine dominance, especially when terrain was relatively flat (slope <11°)

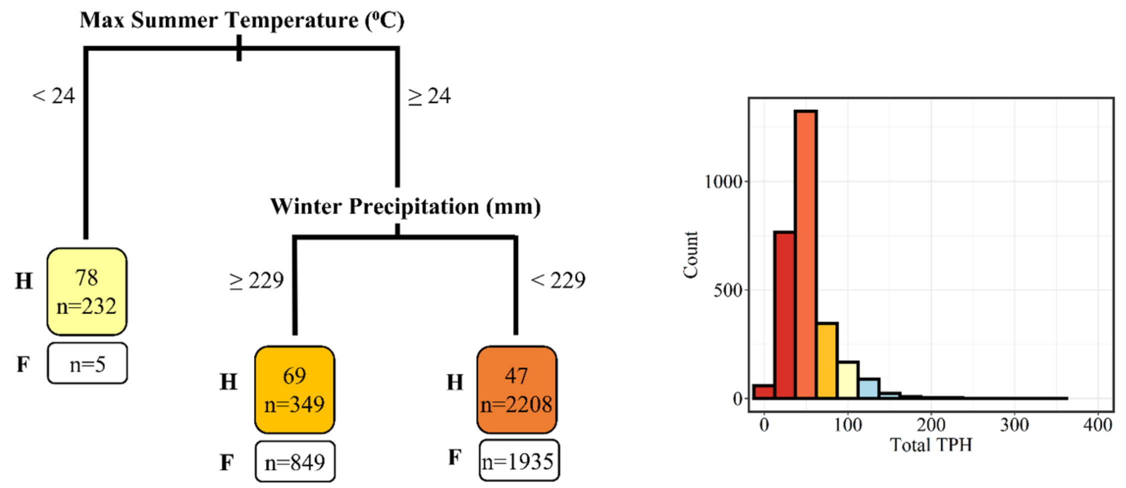

Figure 1. Regression tree output explaining the influence of biophysical variables on tree density (trees ha^{-1}). Colored boxes at the ends of the regression tree branches contain mean trees ha^{-1} (TPH) and number of quarter-quarter (QQ) sections (n) in each resulting group, for the historical (H) inventory and how the inventories would be distributed given future (2040–2069; F) climate conditions. The colors in the histogram correspond with different historical TPH values observed.

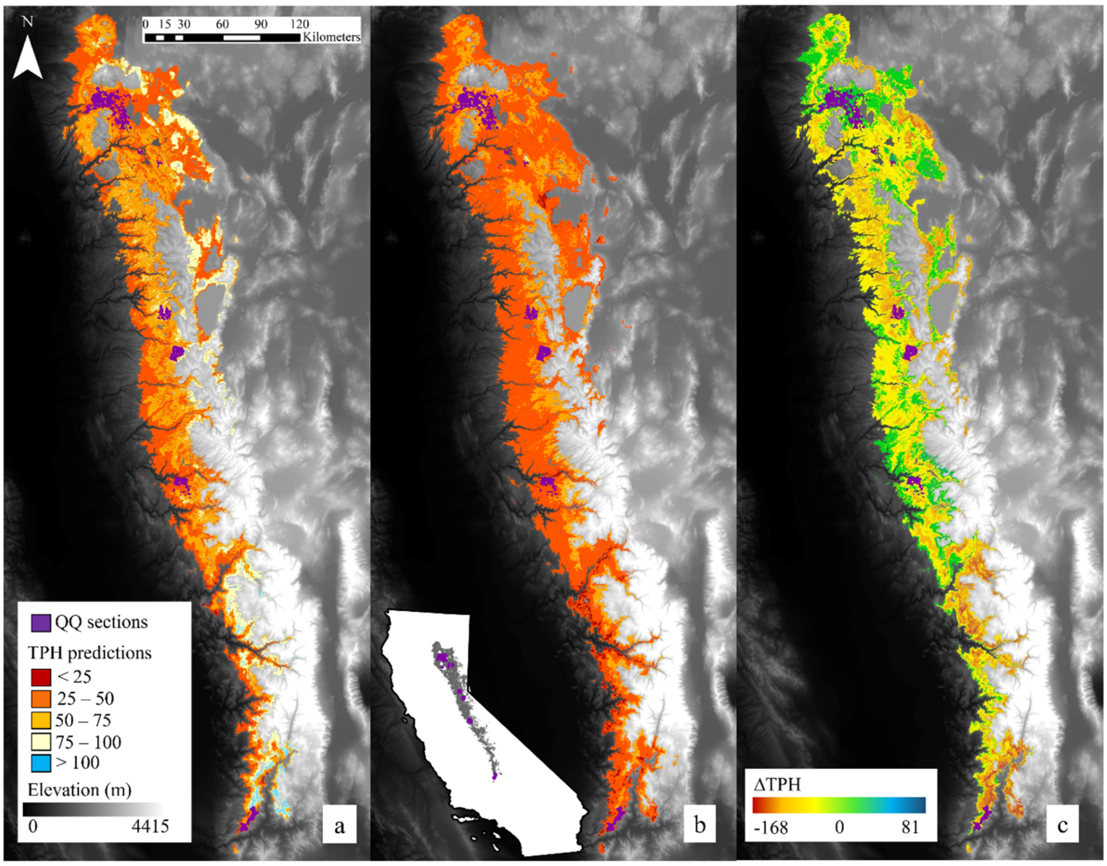

Figure 2. Comparison of landscape historical (1911–1936) and future (2040–2069) tree density (trees ha^{-1}) using model predictions of historical (a) and future (b) landscape tree density (trees ha^{-1}: TPH). Predictions were generated from the random forest model using the historical timber inventories and applied across the environmental space (supplementary figure 4) represented by those inventories. Predictors included means of maximum summer temperature, winter precipitation, 1 April snowpack, aspect, and slope. Future climate variables were averaged using a multi-model ensemble. ΔTPH (c) represents the difference between what was predicted in future TPH and what was predicted historically ($TPH_{Future} - TPH_{Historical}$).

and dry (winter precipitation <229 mm: pine fraction ~0.66). Shifts towards hotter conditions in the future suggest an increased prevalence of environments that historically facilitated pine dominance (figure 3). Cooler sites (maximum summer temperature <24 °C) where pine dominance was limited to only ~0.28 almost became non-existent (<1%) under future climate conditions.

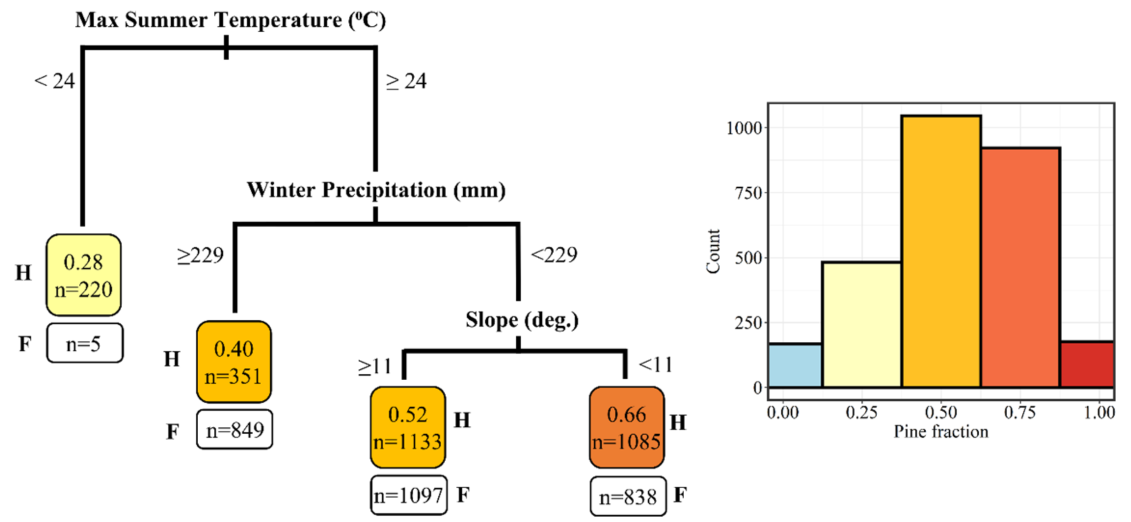

Figure 3. Regression tree output explaining the influence of biophysical variables on pine fraction. Colored boxes at the ends of the regression tree branches contain mean pine fraction and number of quarter-quarter (QQ) sections (n) in each resulting group, for the historical (H) inventory and how the inventories would be distributed given future (2040–2069; F) climate conditions. The colors in the histogram correspond with different historical pine fraction values observed.

The patterns observed in pine fraction opposed the trends observed in tree density, with higher pine fraction estimated at lower elevations where temperatures were higher and decreasing to the east as temperatures lowered (figure 4(a)). In fact, a linear regression detected a negative relationship between tree density and pine fraction ($p < 0.01$; $r^2 = 0.35$). However, 50% of the historical landscape was still composed of pine-dominated forests (pine fraction > 0.50). Hotter conditions increase under climate change resulting in a 30% increase in forests associated with pine dominance, totaling 71% of the entire region by 2069 (figure 4(b)). Although we found that 8% of forested areas still aligned with historical pine fraction (±1%), our findings also indicated that 62% of the future landscape will favor greater pine fraction than what was present historically (figure 4(c)).

Maximum summer temperature and winter precipitation were the only drivers of historical AGLB (figure 5). Maximum summer temperature had the strongest influence on AGLB, with the hottest (maximum summer temperature ⩾24 °C) and driest (winter precipitation <182 mm) environments exhibiting the lowest levels of AGLB (∼26 Mg ha^{-1}), constituting a majority (48%) of sites. Although we observed higher levels of AGLB under higher levels of precipitation (>182 mm) and cooler summer temperatures (<24 °C), AGLB was still limited to ∼39–59 Mg ha^{-1}. Sites with lower AGLB are favored in the future due to climatic shifts towards warmer and drier environments (figure 5). In fact, sites that were characterized by cooler summer temperatures (<24 °C) decreased from 9% to <1% under future climate predictions.

Spatially comprehensive predictions of AGLB followed the same trends as tree density, increasing eastward towards higher elevations as temperature decreased (figure 6(a)). However, a majority (68%) of the historical landscape was composed of forests with AGLB < 40 Mg ha^{-1}. Not only were hotter and drier conditions likely to persist under climate change, our findings indicate that sites which can only support <40 Mg ha^{-1} compose 85% of the landscape by 2069 (figure 6(b)). Although 6% of the future landscape still aligned with historical AGLB (±1 Mg ha^{-1}), we found that 76% of the region was predicted to support lower AGLB than what was present in the past (figure 6(c)). Historically cool and moist environments are the most vulnerable to change, with shifts in climatic conditions aligned with forests that contained as much as 131 Mg ha^{-1} less AGLB than historical conditions.

4. Discussion

Historical Sierra Nevada/southern Cascade mixed conifer forests were dominated by low tree densities (∼53 trees ha^{-1}), low basal area (∼22 m^2 ha^{-1}), low AGLB (∼34 Mg ha^{-1}), and high pine dominance over a large geographic extent (36°–40° latitude). Although there was some variability in structure, which was associated with local climate, moisture, and underlying topography, it was surprising that variability in historical forest conditions was not more pronounced. Our spatially comprehensive predictions reflected these limited ranges indicating broad convergence in forest structure across this large region. This convergence is remarkable given the strong gradients in the biophysical environment throughout the lower montane zone of the Sierra Nevada and southern Cascade Range (North *et al* 2016). Frequent lightning fire and Indigenous burning throughout this region (Taylor *et al* 2016, Safford and Stevens 2017) is the most likely explanation for

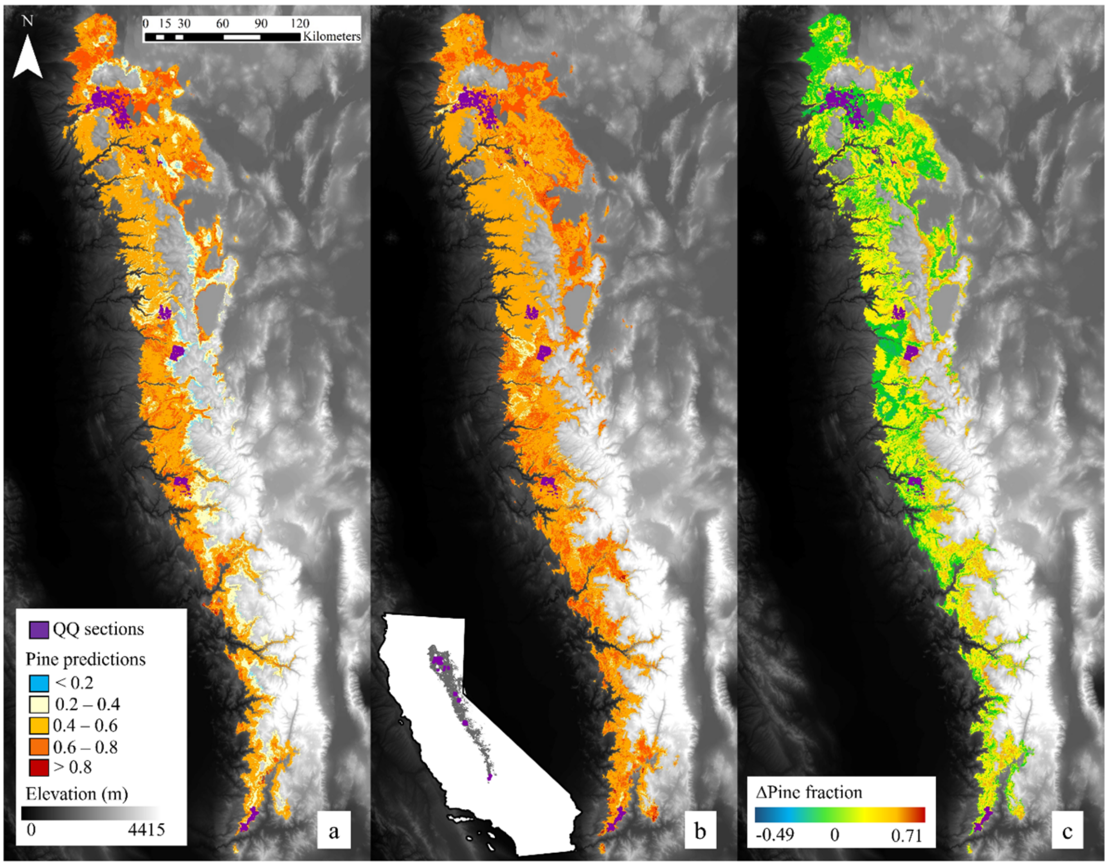

Figure 4. Comparison of landscape historical (1911–1936) and future (2040–2069) pine fraction using model predictions of historical (a) and future (b) landscape pine fraction. Predictions were generated from the random forest model using the historical timber inventories and applied across the environmental space (supplementary figure 4) represented by those inventories. Predictors included means of maximum summer temperature, winter precipitation, 1 April snowpack, aspect, and slope. Future climate variables were averaged using a multi-model ensemble. ΔPine fraction (c) represents the difference between what was predicted in the future and what was predicted historically (Pine fraction $_{\text{Future}}$ − Pine fraction $_{\text{Historical}}$).

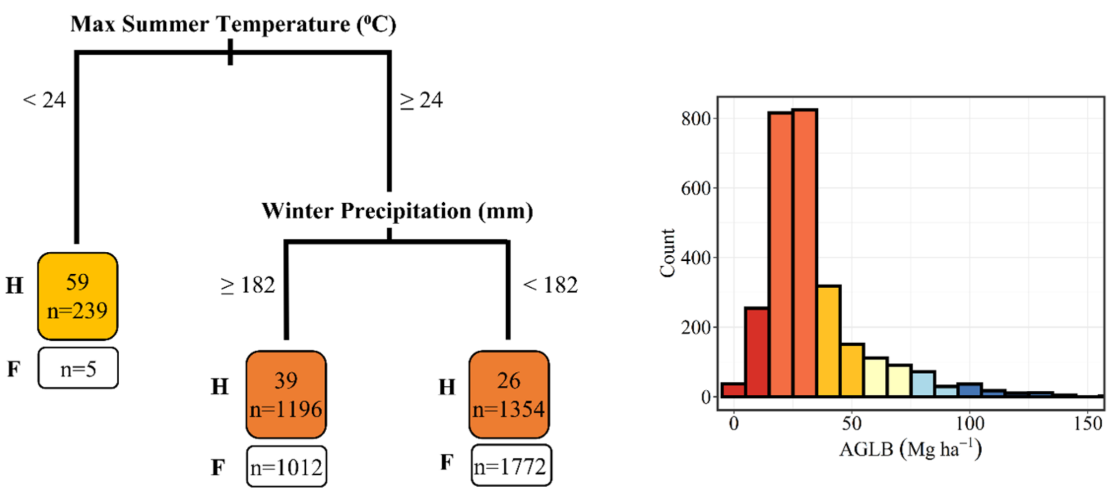

Figure 5. Regression tree output explaining the influence of biophysical variables on aboveground live tree biomass (AGLB; Mg ha^{-1}). Colored boxes at the ends of the regression tree branches contain mean aboveground live tree biomass (B) and number of quarter-quarter (QQ) sections (n) in each resulting group, for the historical (H) inventory and how the inventories would be distributed given future (2040–2069; F) climate conditions. The colors in the histogram correspond with different historical AGLB values observed.

this convergence in forest structure and composition. Our results suggest that fire may have homogenized forests, at least at the spatial resolution of our predictions (270 m), by partially masking local controls on biomass accumulation. In other words, differences in site productivity may not have been

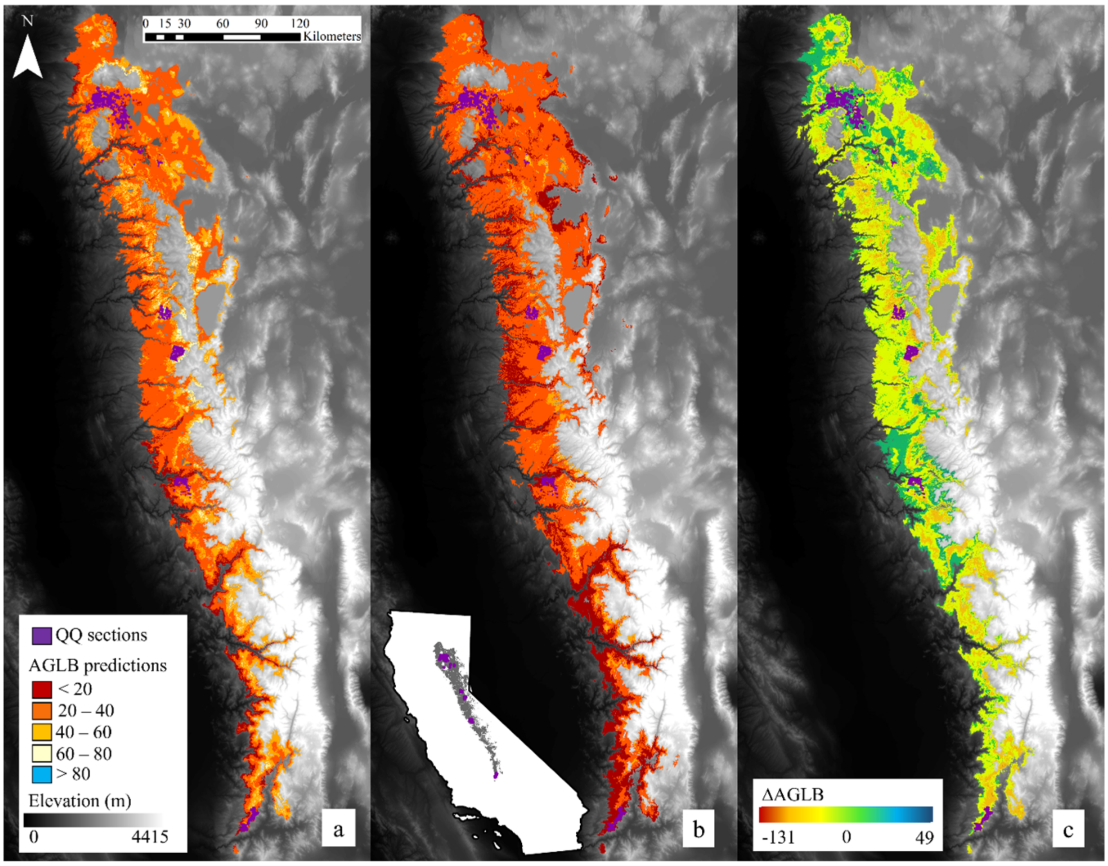

Figure 6. Comparison of landscape historical (1911–1936) and future (2040–2069) aboveground live tree biomass (Mg ha^{-1}) using model predictions of historical (a) and future (b) landscape aboveground live tree biomass (AGLB). Predictions were generated from the random forest model using the historical inventories and applied across the environmental space (supplementary figure 4) represented by those inventories. Predictors included means of maximum summer temperature, winter precipitation, 1 April snowpack, aspect, and slope. Future climate variables were averaged using a multi-model ensemble. ΔAGLB (c) represents the difference between what was predicted in future AGLB and what was predicted historically ($AGLB_{Future} - AGLB_{Historical}$).

allowed to be fully expressed because frequent fire selected for a low density, generally pine-dominated forest condition with low fire hazards.

Despite the broad scale pattern of convergence in forest structure and composition, our findings indicated local (270 m) maximum summer temperature and winter precipitation were most strongly associated with variability in forest structure and composition (figures 1, 3 and 5). Slope gradient was also associated with variability, but to a lesser extent. Historically cooler and moister sites were associated with greater tree density, AGLB, and fir species dominance, which is consistent with findings from contemporary reference areas (Lydersen and North 2012, Lydersen and Collins 2018). However, based on our projections using near-term future climate, environmental conditions associated with these characteristics largely disappear from the region by 2069 (figures 2, 4, 6 and supplementary figure 7). A vast majority of the study region aligned with more xeric future conditions, demonstrating that forests likely to persist under climate change should be composed of lower tree density, basal area, AGLB, and more pines. We submit that since our projections are based on forest conditions that persisted for several hundred years throughout the region (Safford and Stevens 2017) and they integrate future climate, the projections offer a reasonable approximation of future resilient forests.

Given the challenges that forests face over the next century, we must be realistic about how we can meet societal needs while ensuring that forested ecosystems can be sustained. In anticipation of novel ecosystems under climate change, some argue for more proactive approaches that focus less on returning to past conditions and focus more on creating desirable states for the future (Seastedt *et al* 2008). This strategy stems from the idea that climate change may produce interactions between vegetation and disturbances that have no historical analog (Wurtzebach and Schultz 2016). If this is the case, strict adherence to historical forest conditions to guide restoration treatments may not be entirely effective for adapting forests to future conditions. Long-term forest conservation may require integrating the lower range of historical variation in tree density, basal area, and AGLB to adapt to novel ecological conditions. While this approach may converge with forest conservation and fire hazard reduction goals (Stephens *et al* 2020a), it will require adjusting expectations regarding the contribution of forests toward greenhouse gas reduction goals. We found that the Sierra Nevada/ southern Cascade region may be unable to support AGLB >40 Mg ha^{-1} by 2069, a value approximately 25% of current AGLB stocks (supplementary table 3). While AGLB is only part of the total carbon stored by forest ecosystems, it is the dominant vegetation pool (California Air Resources Board 2018) and a robust indicator of total stored carbon (supplementary figure 8).

In California, initial expectations regarding the carbon sequestration potential of forests were based on conditions in 1990 (AB 32). Yet the climate has warmed about 0.5 °C per decade between 1990 and 2020 in the study region (Goss *et al* 2020). Current expectations regarding greenhouse gas reductions in the natural and working lands (NWL) sector are for 15–20 MMT CO_2e by 2030 (California Air Resources Board 2017). Forest currently account for more the 95% of the carbon stored in NWL (CARB 2018). Yet the impacts of a warming climate and increased burn area and severity may lead to an overall reduction in carbon storage from type conversion (Coop *et al* 2020). Based on the relationship between AGLB and total biomass (supplementary figure 8), these forests store a total of 1,167 MMT CO_2e. We project that the median AGLB in 2069 will be no more than 40 Mg ha^{-1}, which translates to 307 MMT CO_2e stored in the total biomass pool. These extrapolations suggest that this region could emit 860 MMT CO_2e over the next 50 years (2019–2069). Liang *et al* (2017a) projected the Sierra Nevada's carbon carrying capacity under climate-wildfire interactions through the late 21st century and found that the region could lose as much as 78% of current aboveground carbon stocks, which aligns with our projections of climate-resilient forests supporting <25% of current AGLB. Clearly the transition of the forest to future climate will have major implications for California's effort to reduce greenhouse gas emissions and this should be accounted for when exploring the trade-offs between carbon storage and restoration treatments.

Although our results are limited to projections from four climate models (GFDL, CNRM, CCSM, and MIROC), each driven by the RCP 8.5 scenario, these models showed fidelity over the historical period when evaluated for California's Fourth Climate Change Assessment and bracketed a range of possible future climate conditions (Bedsworth *et al* 2018). However, the interpretation of our results should be tempered by understanding a couple key assumptions underlying our analytical approach. Applying an established relationship between historical climate/moisture availability and forest structure/composition to project future forest conditions assumes that we not only captured the appropriate controls on forest conditions, but these controls will exert a similar influence into the future as well. The known influence of extreme events on forest conditions (Millar and Stephenson 2015) challenges both assumptions. Specifically, our historical climate/moisture data may not include the extreme events that influenced extant forest structure and composition at the time of the inventories. As a result, our future projections may be missing these important influences. Additionally, there may be some novel climatic and moisture availability controls that will be expressed in the future that fundamentally shift the composition and structure of these forests. For example, uncertainties associated with precipitation in climate models that best represent California means that precipitation could increase with climate change. If temperature also goes up, then snowlines could increase in elevation (Hatchett *et al* 2017), which can increase how much AGLB a site can support. We found evidence of this in the increased levels of tree density and AGLB in some regions when we predicted landscape forest structure under future climates (figures 2 and 6). However, higher temperatures and reduced snowpack described in California's Fourth climate Change Assessment are associated with a greater frequency of large wildfires (Westerling 2018) that will ultimately accelerate carbon losses in the region we analyzed (Liang *et al* 2017a, 2017b). Even if forests could support higher AGLB than what our results are suggesting, reducing current tree density and promoting pine-dominated forests back to the historical range of variation can help increase resiliency to large-scale disturbances like drought and wildfires (North *et al* 2021). While we admit that our findings do not provide hard rules for forest management, and that a range of future forest conditions can vary slightly across individual climate models (supplementary figures 9–12), we believe that they still provide useful guidelines for re-evaluating expectations for aboveground carbon storage in a majority of the Sierra Nevada/southern Cascade region where fires are likely to occur.

It is worth noting that forested ecosystems are not fragile, and that historical vegetation characteristics could still be resilient to climate change. Theoretical frameworks that describe resiliency highlight the importance of contextualizing ecosystem integrity across a range of conditions (i.e. alternative stable states) that could persist under climate change (Hessburg *et al* 2019), including those that existed historically. We found that 2%–4% of the region analyzed showed only a 1% difference between historical forest conditions and what could exist under climate change. This range increases to 14%–34% of the region when increasing the threshold to a 10% difference between historical and future forest conditions. Estimating the threshold of change that could occur before resiliency is compromised is beyond the scope of our analyses, but the stability of reference conditions found in other studies suggest that historical conditions are still an improvement over fire-suppressed conditions for promoting resiliency. Contemporary reference forests where fire remained active or was re-introduced support this assertion. These forests, which have similar structures to historical forests (Jeronimo *et al* 2019), demonstrated low vulnerability to severe wildfire effects despite increasing trends in burn severity across larger regions (Collins *et al* 2009, Collins and Stephens 2010, Rivera-Huerta *et al* 2016, Stephens *et al* 2021). In addition, restoration treatments at the stand scale mitigated tree mortality (Knapp *et al* 2021) despite experiencing California's most severe drought in the last 1200 years (Griffin and Anchukaitis 2014). Not only do these findings demonstrate how forests with characteristics analogous to historical structures persist under current conditions, but also reveal that restoring historical conditions can serve as one of the pathways available for adapting forests to climate change.

Ultimately, the decision to apply restoration treatments should be guided by management objectives and whether meeting those objectives is possible under climate change. Our comprehensive assessment of how biophysical thresholds can manifest landscape forest changes provide guidance on prioritizing and implementing forest restoration treatments in areas where they are most likely to be needed and effective. However, our study also highlights the inherent conflict between restoration goals and greenhouse gas reduction targets and suggests a re-examination of the role of frequent-fire forests in California's carbon policies.

Data availability statement

The data that support the findings of this study are available upon reasonable request from the authors.

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Author contributions

Alexis A Bernal: methodology, formal analysis, writing original draft. Scott L Stephens: conceptualization, funding acquisition, writing original draft. Brandon M Collins: conceptualization, funding acquisition, writing original draft. John J Battles: methodology, formal analysis, writing original draft.

Conflict of interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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References

Allen C D, Breshears D D and McDowell N G 2015 On underestimation of global vulnerability to tree mortality and forest die-off from hotter drought in the anthropocene *Ecosphere* **6** 1–55

Bedsworth L, Cayan D, Guido F, Fisher L and Ziaja S 2018 Statewide Summary Report. California's fourth climate change assessment. Publication number: SUM-CCCA4-2018-013 p 133 (available at: https://www.energy.ca.gov/sites/default/files/2019-11/Statewide_Reports-SUM-CCCA4-2018-013_Statewide_Summary_Report_ADA.pdf)

Beller E E, McClenachan L, Zavaleta E S and Larsen L G 2020 Past forward: recommendations from historical ecology for ecosystem management *Glob. Ecol. Conserv.* **21** e00836

California Air Resources Board 2017 California's 2017 climate change scoping plan p 132 (available at: ww3.arb.ca.gov/cc/scopingplan/scoping_plan_2017.pdf)

California Air Resources Board 2018 An inventory of ecosystem carbon in California's natural & working lands p 63 (available at: ww3.arb.ca.gov/cc/inventory/pubs/nwl_inventory.pdf)

California and United States Department of Agriculture, Forest Service P S R 2020 Agreement for shared stewardship of Califonira's forest and rangelands between the state of California and the USDA, forest service pacific southwest region p 9 (available at: www.gov.ca.gov/wp-content/uploads/2020/08/8.12.20-CA-Shared-Stewardship-MOU.pdf)

Caprio A and Swetnam T W 1993 Historic fire regimes along an elevational gradient on the West Slope of the Sierra Nevada, California *Proc. Symp. Fire Wilderness Park Management: Past Lessons and Future Opportunities* Gen. Tech. Rep. - Intermountain Res. Station. USDA For. Serv. INT-GTR-320 (*Missoula, MT*) vol 5 pp 173–9

Christensen G A, Gray A N, Kuegler O, Tase N A, Rosenberg M and Groom J 2019 AB 1504 California forest ecosystem and harvested wood product carbon inventory: 2017 reporting period *Final Report* p 455 (available at: https://bof.fire.ca.gov/media/beddx5bp/6-final_forest_ecosys_hwp_c_2019_feb2021_all_ada.pdf)

Collins B M, Bernal A, York R A, Stevens J T, Juska A and Stephens S L 2021 Mixed-conifer forest reference conditions for privately owned timberland in the southern Cascade Range *Ecol. Appl.* **31** 1–14

Collins B M, Lydersen J M, Everett R G, Fry D L and Stephens S L 2015 Novel characterization of landscape-level variability in historical vegetation structure *Ecol. Appl.* **25** 1167–74

Collins B M, Lydersen J M, Fry D L, Wilkin K, Moody T and Stephens S L 2016 Variability in vegetation and surface fuels across mixed-conifer-dominated landscapes with over 40 years of natural fire *For. Ecol. Manage.* **381** 74–83

Collins B M, Miller J D, Thode A E, Kelly M, Van Wagtendonk J W and Stephens S L 2009 Interactions among wildland fires in a long-established Sierra Nevada natural fire area *Ecosystems* **12** 114–28

Collins B M and Stephens S L 2010 Stand-replacing patches within a 'mixed severity' fire regime: quantitative characterization using recent fires in a long-established natural fire area *Landsc. Ecol.* **25** 927–39

Comer P *et al* 2003 Ecological systems of the United States: a working classification of U.S. terrestrial systems p 75 (available at: www.natureserve.org/publications/usEcologicalsystems.jsp)

Coop J D *et al* 2020 Wildfire-driven forest conversion in Western North American landscapes *Bioscience* **70** 659–73

Fettig C J, Mortenson L A, Bulaon B M and Foulk P B 2019 Tree mortality following drought in the central and southern Sierra Nevada, California, U.S *For. Ecol. Manage.* **432** 164–78

Flint L E, Flint A L, Thorne J H and Boynton R 2013 Fine-scale hydrologic modeling for regional landscape applications: the California basin characterization model development and performance *Ecol. Process.* **2** 1–21

Flint L E, Flint A L, Thorne J H and Boynton R 2014 2014 California BCM (basin characterization model) downscaled climate and hydrology—30-year summaries (available at: http://climate.calcommons.org/dataset/2014-CA-BCM)

Forest Climate Action Team 2018 California forest carbon plan: managing our forest landscapes in a changing climate p 186 (available at: https://resources.ca.gov/CNRALegacyFiles/wp-content/uploads/2018/05/California-Forest-Carbon-Plan-Final-Draft-for-Public-Release-May-2018.pdf)

Franklin J F, Mitchell R J and Palik B J 2007 Natural disturbance and stand development principles for ecological forestry *Gen. Tech. Rep. NRS*-19 vol 19 (Newtown Square: US Department of Agriculture, Forest Service, Northern Research Station) p 44 (available at: www.fs.usda.gov/treesearch/pubs/13293)

Fulé P Z 2008 Does it make sense to restore wildland fire in changing climate? *Restor. Ecol.* **16** 526–31

Goss M, Swain D L, Abatzoglou J T, Sarhadi A, Kolden C A, Williams A P and Diffenbaugh N S 2020 Climate change is increasing the likelihood of extreme autumn wildfire conditions across California *Environ. Res. Lett.* **15** 094016

Griffin D and Anchukaitis K J 2014 How unusual is the 2012–2014 California drought? *Geophys. Res. Lett.* **41** 9017–23

Hagmann R K *et al* 2018 Improving the use of early timber inventories in reconstructing historical dry forests and fire in the western United States: comment *Ecosphere* **9** e02232

Hagmann R K *et al* 2021 Evidence for widespread changes in the structure, composition, and fire regimes of western North American forests *Ecol. Appl.* **31** e02431

Hagmann R K, Franklin J F and Johnson K N 2013 Historical structure and composition of ponderosa pine and mixed-conifer forests in south-central oregon *For. Ecol. Manage.* **304** 492–504

Hagmann R K, Franklin J F and Johnson K N 2014 Historical conditions in mixed-conifer forests on the eastern slopes of the northern oregon cascade range, USA *For. Ecol. Manage.* **330** 158–70

Hatchett B J, Daudert B, Garner C B, Oakley N S, Putnam A E and White A B 2017 Winter snow level rise in the Northern Sierra Nevada from 2008 to 2017 *Water* **9** 1–14

Hessburg P F *et al* 2019 Climate, environment, and disturbance history govern resilience of Western North American forests *Front. Ecol. Evol.* **7** 1–27

Hessburg P F, Prichard S J, Hagmann R K, Povak N A and Lake F K 2021 Wildfire and climate change adaptation of western North American forests: a case for intentional management *Ecol. Appl.* **31** e02432

Higgs E, Falk D A, Guerrini A, Hall M, Harris J, Hobbs R J, Jackson S T, Rhemtulla J M and Throop W 2014 The changing role of history in restoration ecology *Front. Ecol. Environ.* **12** 499–506

Jeronimo S M A, Kane V R, Churchill D J, Lutz J A, North M P, Asner G P and Franklin J F 2019 Forest structure and pattern vary by climate and landform across active-fire landscapes in the montane Sierra Nevada *For. Ecol. Manage.* **437** 70–86

Jones G M *et al* 2020 Habitat selection by spotted owls after a megafire reflects their adaptation to historical frequent-fire regimes *Landsc. Ecol.* **35** 1199–213

Kilgore B M and Taylor D 1979 Fire history of a sequoia-mixed conifer forest *Ecology* **60** 129–42

Knapp E E, Bernal A A, Kane J M, Fettig C J and North M P 2021 Variable thinning and prescribed fire influence tree mortality and growth during and after a severe drought *For. Ecol. Manage.* **479** 118595

Knapp E E, Lydersen J M, North M P and Collins B M 2017 Efficacy of variable density thinning and prescribed fire for restoring forest heterogeneity to mixed-conifer forest in the central Sierra Nevada, CA *For. Ecol. Manage.* **406** 228–41

Knight C A, Cogbill C V, Potts M D, Wanket J A and Battles J J 2020 Settlement-era forest structure and composition in the Klamath Mountains: reconstructing a historical baseline *Ecosphere* **11** e03250

Kolb T E, Fettig C J, Ayres M P, Bentz B J, Hicke J A, Mathiasen R, Stewart J E and Weed A S 2016 Observed and anticipated impacts of drought on forest insects and diseases in the United States *For. Ecol. Manage.* **380** 321–34

Liang S, Hurteau M D and Westerling A L R 2017b Response of Sierra Nevada forests to projected climate–wildfire interactions *Glob. Change Biol.* **23** 2016–30

Liang S, Hurteau M D and Westerling A L 2017a Potential decline in carbon carrying capacity under projected climate-wildfire interactions in the Sierra Nevada *Sci. Rep.* **7** 1–7

Liaw A and Wiener M 2002 Classification and regression by randomForest *R News* **2** 18–22

Lydersen J M and Collins B M 2018 Change in vegetation patterns over a large forested landscape based on historical and contemporary aerial photography *Ecosystems* **21** 1348–63

Lydersen J M, North M P, Knapp E E and Collins B M 2013 Quantifying spatial patterns of tree groups and gaps in mixed-conifer forests: reference conditions and long-term changes following fire suppression and logging *For. Ecol. Manage.* **304** 370–82

Lydersen J and North M 2012 Topographic variation in structure of mixed-conifer forests under an active-fire regime *Ecosystems* **15** 1134–46

Millar C I and Stephenson N L 2015 Temperate forest health in an era of emerging megadisturbance *Science* **349** 823-6

North M P, Collins B M, Safford H D and Stephenson N L 2016 *Ecosystems of California: Montane Forests* ed H Mooney and E S Zavaleta (Berkeley: University of California Press) ch 27

North M, Tompkins R E, Bernal A A, Collins B M, Stephens S L and York R A 2021 Operational resilience in western us frequent-fire forests *For. Ecol. Manage.* **507** 120004

Pierce D W, Barnett T P, Santer B D and Gleckler P J 2009 Selecting global climate models for regional climate change studies *Proc. Natl Acad. Sci. USA* **106** 8441–6

Pierce D W, Kalansky J F and Cayan D R 2018 *Climate, Drought, and Sea Level Rise Scenarios for California's Fourth Climate Change Assessment* p 78 (available at: www.energy.ca.gov/sites/default/files/2019-11/Projections_CCCA4-CEC-2018-006_ADA.pdf)

Povak N A, Hessburg P F, McDonnell T C, Reynolds K M, Sullivan T J, Salter R B and Cosby B J 2014 Machine learning and linear regression models to predict catchment-level base cation weathering rates across the southern Appalachian Mountain region, USA *Water Resour. Res.* **50** 2798–814

Rivera-Huerta H, Safford H D and Miller J D 2016 Patterns and trends in burned area and fire severity from 1984 to 2010 in the Sierra de San Pedro Mártir, Baja California, Mexico *Fire Ecol.* **12** 52–72

Safford H D and Stevens J T 2017 Natural range of variation for yellow pine and mixed-conifer forests in the Sierra Nevada, southern cascades, and Modoc and Inyo National forests, California, USA *Gen. Tech. Rep.—Pacific Southwest Res. Station. USDA For. Serv. PSW-GTR*-256 p 229

Scholl A E and Taylor A H 2010 Fire regimes, forest change, and self-organization in an old-growth mixed-conifer forest, Yosemite National Park, USA *Ecol. Appl.* **20** 362–80

Schwalm C R, Glendon S and Duffy P B 2020 RCP8.5 tracks cumulative CO_2 emissions *Proc. Natl Acad. Sci. USA* **117** 19656–7

Seastedt T R, Hobbs R J and Suding K N 2008 Management of novel ecosystems: are novel approaches required? *Front. Ecol. Environ.* **6** 547–53

Singleton M P, Thode A E, Sánchez Meador A J and Iniguez J M 2019 Increasing trends in high-severity fire in the southwestern USA from 1984 to 2015 *For. Ecol. Manage.* **433** 709–19

Skinner C N and Taylor A H 2018 Southern Cascade bioregion *Fire in California's Ecosystems* ed J van Wagtendonk, J W Sugihara, N G Stephens, S L Thode, A E Shaffer and K E Frites (Berkeley: University of California Press) pp 195–218

Stephens S L *et al* 2009 Fire treatment effects on vegetation structure, fuels, and potential fire severity in western U.S. forests *Ecol. Appl.* **19** 305–20

Stephens S L *et al* 2020a Forest restoration and fuels reduction: convergent or divergent? *Bioscience* **71** 85–101

Stephens S L, Agee J K, Fulé P Z, North M P, Romme W H, Swetnam T W and Turner M G 2013 Managing forests and fire in changing climates *Science* **342** 41–42

Stephens S L and Collins B M 2004 Fire regimes of mixed conifer forests in the north-Central Sierra Nevada at multiple spatial scales *Northwest Sci.* **78** 12–23 (available at: https://nature.berkeley.edu/stephenslab/wp-content/uploads/2018/01/Stephens-Collins-2004_NWSci-781-pp12-23.pdf)

Stephens S L, Collins B M, Fettig C J, Finney M A, Hoffman C M, Knapp E E, North M P, Safford H and Wayman R B 2018a Drought, tree mortality, and wildfire in forests adapted to frequent fire *Bioscience* **68** 77–88

Stephens S L, Lydersen J M, Collins B M, Fry D L and Meyer M D 2015 Historical and current landscape-scale ponderosa pine and mixed conifer forest structure in the southern Sierra Nevada *Ecosphere* **6** 1–63

Stephens S L, Martin R E and Clinton N E 2007 Prehistoric fire area and emissions from California's forests, woodlands, shrublands, and grasslands *For. Ecol. Manage.* **251** 205–16

Stephens S L, Stevens J T, Collins B M, York R A and Lydersen J M 2018b Historical and modern landscape forest structure in fir (Abies)-dominated mixed conifer forests in the northern Sierra Nevada, USA *Fire Ecol.* **14** 1–14

Stephens S L, Thompson S, Boisramé G, Collins B M, Ponisio L C, Rakhmatulina E, Steel Z L, Stevens J T, van Wagtendonk J W and Wilkin K 2021 Fire, water, and biodiversity in the Sierra Nevada: a possible triple win *Environ. Res. Commun.* **3** 081004

Stephens S L, Westerling A L R, Hurteau M D, Peery M Z, Schultz C A and Thompson S 2020b Fire and climate change: conserving seasonally dry forests is still possible *Front. Ecol. Environ.* **18** 354–60

Taylor A H, Trouet V, Skinner C N and Stephens S 2016 Socioecological transitions trigger fire regime shifts and modulate fire-climate interactions in the Sierra Nevada, USA, 1600–2015 CE *Proc. Natl Acad. Sci. USA* **113** 13684–9

R Core Team 2020 R: a language and environment for statistical computing (available at: www.r-project.org/)

Therneau T and Atkinson B 2019 rpart: recursive partitioning and regression trees (available at: https://cran.r-project.org/package=rpart)

Westerling A L 2018 Wildfire simulations for California's fourth climate change assessment: projecting changes in extreme wildfire events with a warming climate *California's Fourth Climate Change Assessment, California Energy Commission* pp 1–29 (available at: www.climateassessment.ca.gov/techreports/docs/20180827-Projections_CCCA4-CEC-2018-014.pdf)

Williams A P, Abatzoglou J T, Gershunov A, Guzman-Morales J, Bishop D A, Balch J K and Lettenmaier D P 2019 Observed impacts of anthropogenic climate change on wildfire in California *Earth's Future* **7** 892–910

Wurtzebach Z and Schultz C 2016 Measuring ecological integrity: history, practical applications, and research opportunities *Bioscience* **66** 446–57

Zhou X and Hemstrom M A 2009 Estimating aboveground tree biomass on forest land in the Pacific Northwest: a comparison of approaches *USDA For. Serv.—Res. Pap. PNW-RP-584* pp 1–18