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Mixed-conifer forest reference conditions for privately owned timberland in the southern Cascade Range

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Abstract. The overwhelming majority of information on historical forest conditions in western North America comes from public lands, which may provide an incomplete description of historical landscapes. In this study we made use of an archive containing extensive timber survey data collected in the early 1920s from privately owned forestland. These data covered over 50,000 ha and effectively represent a 19% sample of the entire area. The historical forest conditions reconstructed from these data fit the classic model of frequent-fire forests: large trees, low density, and pine-dominated. However, unlike other large-scale forest reconstructions, our study area exhibited relatively low overall variability in forest structure and composition across the historical landscape. Despite having low variability, our analyses revealed evidence of biophysical controls on tree density and pine fraction. Annual climatic variables most strongly explained the range in historical tree densities, whereas historical pine fraction was explained by a combination of topographic and climatic variables. Contemporary forest inventory data collected from both public and private lands within the same general area, albeit not a direct remeasurement, revealed substantial increases in tree density and greatly reduced pine fractions relative to historical conditions. Contemporary forests exhibited a far greater range in these conditions than what existed historically. These findings suggest that private forestland managed with multiaged silviculture may be similar to public forestland with respect to departure in forest structure and compositions from that of historical forests. However, there may be differences between management objectives that favor timber production, more typical on private lands, vs. those that favor restoration, increasingly supported on public lands.

Key words: environmental controls; forest reconstruction; historical ecology.

Introduction

Historical ecological information is essential for understanding the dynamics of ecosystems that are substantially departed from their "natural" states (Swetnam et al. 1999). The availability of robust and extensive historical ecological data is limited for many ecosystem types because of the lack of either preserved remnant material or archived observations. Forests of western North America are an exception in that there is a relative abundance of preserved material (e.g., sedimentary charcoal and pollen, tree rings) and archived data (e.g., timber inventories, aerial photographs). The historical ecological information gleaned from these sources has been used to help guide forest restoration efforts (Long et al. 2014, Stine et al. 2014, Spies et al. 2018).

The overwhelming majority of information on historical forest conditions in western North America comes from public lands (Romme 1982, Fulé et al. 1997, Larsen 1997, Taylor 2000, Moore et al. 2004, Brown et al. 2008, Hagmann et al. 2019). The reasons for this include access to publicly available historical data, funding from public land management agencies, and access to study sites. Although public forest lands likely span wide ecological and environmental gradients, it is unclear if the existing reconstructions cover the range of conditions that may have existed historically on private forest land. One could surmise that the acquisition of private forestland was not based on random selection; rather it was

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likely based on forest and landform characteristics that were more favorable for timber management. As an example, Collins et al. (2015) noted that areas surveyed by the U.S. Forest Service in 1911 within a central Sierra Nevada mixed-conifer forest tended to have lower elevations than areas not surveyed but within the same study-area boundary. A majority of these unsurveyed areas had land patents on them, which are often a precursor to private acquisition of public land (Collins et al. 2016). Higher elevations corresponded with greater densities of large trees, which presumably would be preferred for private timberland acquisition (Collins et al. 2015). The upshot is that our representation of historical landscapes may be incomplete because of the lack of historical data from private forestlands.

Early timber inventories have been used to describe historical forest conditions in a number of independent study sites in California and Oregon (Hagmann et al. 2013, 2014, Collins et al. 2015, Stephens et al. 2015, 2018). The inventories were largely conducted prior to the major structural and compositional changes associated with later 20th-century land use practices including widespread grazing, logging, and fire suppression (Safford and Stevens 2017), supporting their use as reference conditions for forest restoration. The large spatial coverage (10,000–50,000-ha landscapes) and quantitative detail (i.e., individual tree sizes, species) of these inventories allowed these studies to characterize the range of forest conditions that existed historically robustly (Hagmann et al. 2018). Furthermore, because the inventories were tied to the Public Land Survey System, the spatial locations of individual plots are known, which allows for analyses of potential edaphic and climatic influences on variability in forest conditions across large landscapes (Collins et al. 2015, Stephens et al. 2018). However, the historical inventory data are not without limitations. Given the timber focus of the surveys, there were inconsistencies among survey areas on how nonmerchantable attributes were recorded. Specifically, dead trees and noncommercial tree species may have been ignored, and the minimum tree size considered to be merchantable was variable. These inconsistencies are difficult to reconcile because it is impossible to know whether these attributes were present at the time of the survey but omitted, or they were largely absent from these historical landscapes. Some early transect-based forest inventories from the Sierra Nevada included trees >15 cm diameter at breast height (DBH) (Collins et al. 2015, Stephens et al. 2018), and found that the number of trees in this smaller size class was similar to that in the immediate larger size class. Another method to reconstruct forest structure uses General Land Office (GLO) density estimators and has the advantage of including oaks but has a problem of undefined minimum tree diameters (Knight et al. 2020). Unfortunately, these same attributes (dead, noncommercial species, and small trees) may also be underrepresented in dendrochronology-based forest reconstructions because such materials could have decomposed long ago. Even with these limitations, these early forest inventories can provide important information for managers and scientists interested in understanding variability in landscape-scale forest structure before logging and fire suppression.

In this study we make use of another recently "discovered" archive containing extensive information from a timber survey conducted in the southern Cascade Range of California. This historical timber survey is unique from those used in previous studies for several reasons. First, it is the only large-spatial-extent (>10,000 ha) survey that we are aware of for this region. Second, it is based on a highly intensive sampling effort for such a large-scale survey. Ritchie (2016) presented historical information from an intensive forest survey also in the southern Cascade Range, but the spatial scale was limited to approximately 4,000 ha. Lastly, the survey from which we analyzed data was conducted almost entirely on privately owned forestland, much of which remains in private holding to this day. Our specific objectives with this study were (1) to describe the range of historical forest conditions across the survey area and compare that to contemporary forest conditions, (2) to investigate the influence of biophysical factors on observed variability in historical and contemporary forest conditions, and (3) to predict historical forest conditions across a large spatial domain using modeled relationships with biophysical variables. Our broader goal through these objectives is to leverage this spatially detailed and highly quantitative historical data set to inform large-scale forest restoration efforts across ownerships.

Methods

Study area

The historical timber inventory data span the upper portions of three eight-digit Hydrologic Unit Code watersheds in northern California (Fig. 1). Most of this inventory was conducted in the southern Cascade Range, with a small portion extending into the northern Sierra Nevada. Mean elevation for inventoried areas is 1,557 m and mean annual precipitation is 1,240 mm. Based on climate data from 1981 to 2010, mean minimum January temperature was −3.9°C, and mean maximum July temperature was 27.3°C (Flint et al. 2013). The majority of the inventoried area is lower montane mixed-conifer forest which is dominated by the following tree species: ponderosa pine (*Pinus ponderosa*), sugar pine (*P. lambertiana*), white fir (*Abies concolor*), incense-cedar (*Calocedrus decurrens*), and Douglas fir (*Pseudotsuga menziesii*) (North et al. 2016). Red fir (*A. magnifica*), generally considered an upper montane species, made up approximately 2% of the historical species composition. Prior to 1905 low- to moderate-severity fire was common in this area, with median fire return intervals of 12–14 yr (Skinner and Taylor 2018).

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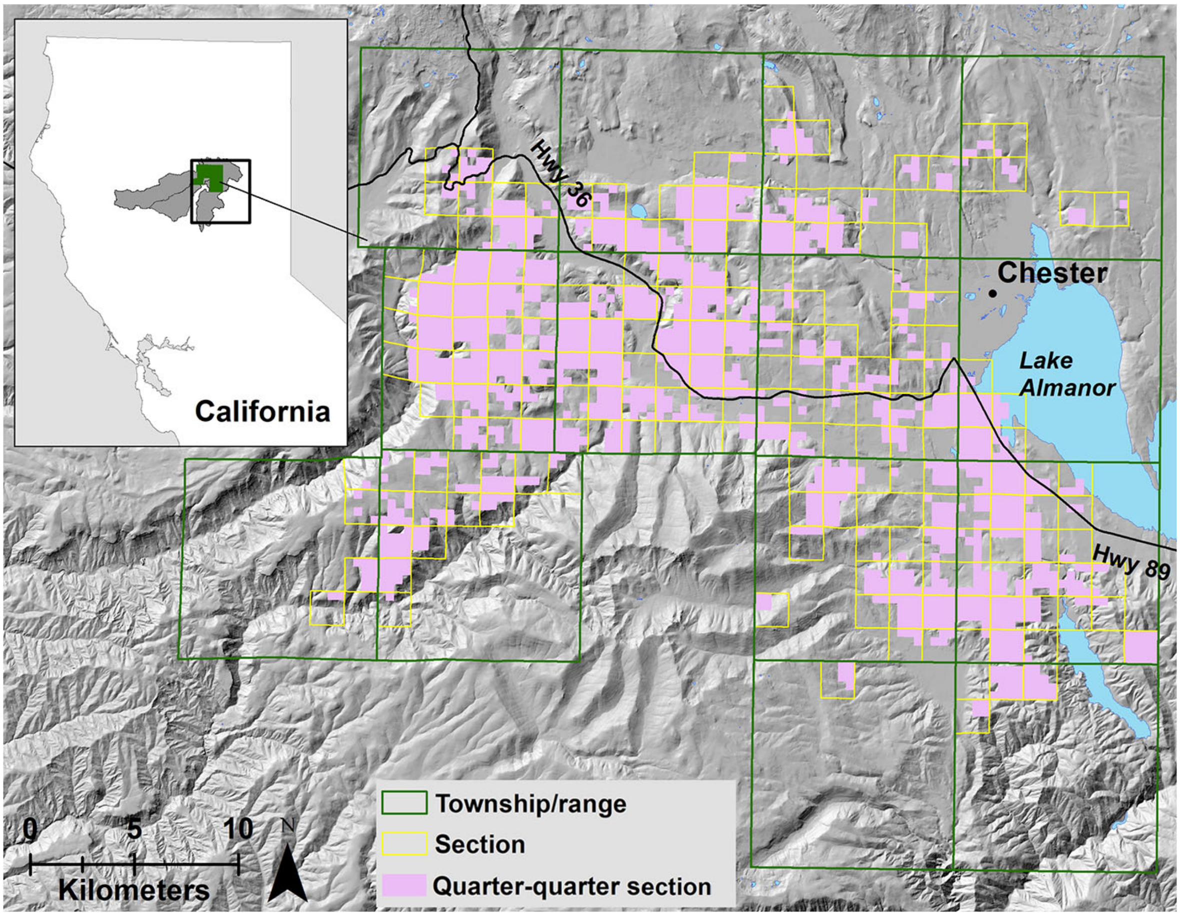

FIG. 1. Locations and overall extent of a historical timber inventory conducted in 1924. This inventory was based on the Public Land Survey System, with individual quarter-quarter sections (pink) being the observational unit for sampling. The inset shows broader region with eight-digit Hydrologic Unit Code watersheds (gray) and the search extent from which contemporary inventory data were gathered (black square outline).

Historical inventory data

The historical forest inventory within our study area was conducted in 1924 (Fig. 2) and was located systematically based on the Public Land Survey System (PLSS). It is worth noting that there likely was a lag between the timing of this survey and the last fire recorded in tree ring-based fire history reconstructions. However, we submit this lag did not have a strong influence on the data given the minimum diameter of trees included and the time it would take for trees to reach that diameter (Lydersen et al. 2013). Except for a small portion that was censused (<1%), the inventory consisted of individual samples containing four parallel belt transects, 40.2 m wide by 402 m long, run through quarter-quarter sections (QQs; 16.2 ha or 40 acre survey units). Cumulatively these transects covered 40% of each surveyed QQ. Although not explicitly stated in the accompanying documentation, the survey appears to have been limited to trees >30.5 cm (12 in.) DBH, presumably the merchantability threshold at the time. This general method for locating transects and inventorying trees is consistent with other historical timber surveys that used the PLSS for sample locations and belt transects to sample individual trees (e.g., Hagmann et al. [2013], Collins et al. [2015], Stephens et al. [2015]), although some surveys had a smaller minimum DBH for recorded trees. Similarly, the lack of hardwood tree species, primarily California black oak (*Quercus kelloggii*) in the study area, suggests that this survey was limited to conifers, which is also consistent with other historical timber surveys. Dead trees were recorded, but only if they appeared to have merchantable volume. The specific criteria guiding this determination of what was merchantable was not provided; hence our analyses only focused on live trees.

The archived data sheets from this survey were included in a report prepared by Brown and Brown, Inc. for Curtis, Collins & Holbrook Company, owner of the surveyed timberland in 1924. The report was made

Fig. 2. Photographs taken as part of historical timber inventory conducted in 1924. These photographs were from a report prepared by Brown and Brown, Inc. for Curtis, Collins & Holbrook Company, owner of the surveyed timberland. The captions accompanying these photographs in the report were: Left—"An example of small tapering clean-bodied old growth [ponderosa] pine. Clean-bodied or free from limbs for 90 feet." Right—"Fine quality [s]ugar pine 77 inches in diameter in the bark. White fir in the background." Note people standing in front of large trees in both photos. Images reproduced with permission from Collins Pine Company.

available to us by Collins Pine Company, current owner of the surveyed timberland, via high-resolution scanned images. Introductory material in the report indicated that no prior logging had occurred in the surveyed areas. The data sheets contain summaries of the transect tallies by species, for a given QQ (Appendix S1: Fig. S1). Additionally, the data sheets contain written descriptions of the timber quality for each species present, along with general site characteristics. The report contained inventory data for 1,552 QQs, which were largely concentrated in the 14 contiguous PLSS townships (Fig. 1). However, there were 71 QQs scattered across seven additional townships further south, which were not adjacent to the main group of townships. Given the much lower proportion of sampled QQs in these southern townships and the fact that they were geographically disjunct, we opted to remove those 71 QQs from the analyses, leaving 1,481 QQs in our historical data set. These 1,481 QQs make up 23,992 ha of sampled area within a larger study area (defined by a convex hull polygon) of 52,206 ha. Because the sampled area within an individual QQ was 40% of the QQ, there was an effective sampling proportion across the larger study area of 19%.

Our analyses were based on two key attributes reported in the historical datasheets, number of trees and average tree diameter (Appendix S1: Fig. S1). These were reported by species for each QQ, and the number of trees was scaled to represent the total for the entire QQ ($\sim$16.2 ha). We converted this to trees per hectare (TPH) based on the reported area of each QQ (Appendix S1: Fig. S1). Average tree diameter was reported as stump diameter, which we adjusted to DBH using the taper equations from Wensel and Olson (1995).

Contemporary forest inventory data

The bounding area for which we assessed contemporary forest conditions is approximately 788,000 ha centered primarily on western Plumas County (Fig. 1). This is considerably larger than the historical timber survey area, but it was necessary given the much lower sampling density in our contemporary data set. We used plot-level data from Forest Inventory and Analysis program (FIA) to characterize contemporary forest conditions. Because FIA inventories are conducted on 10-yr rotations, we identified FIA plots that were surveyed between 2011

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and 2018 that fell within the bounding area (n = 274). We then conducted a series of filtering exercises, following the methods of Stephens et al. (2018), to select plots that would serve as an appropriate comparison to our historical data. This included selecting plots within the elevation range of the historical data (1,113–1,923 m; n = 204) and removing plots where the reported elevation was markedly different than what was extracted from a digital elevation model based on publicly available plot coordinates, which are "fuzzed" within approximately 0.8 km of the true plot location (Woudenberg et al. 2010). To account for this fuzzing of coordinates, we only retained plots that were within 150 m of elevation discrepancy (n = 182). We then selected plots recorded with one "condition" only, indicating that the entirety of the plot could be described as having similar ages, species composition, and disturbance history (n = 110). We also removed an additional 29 plots because of a history of recent fire activity (n = 81), and 1 plot where stand age was recorded as zero (only seedlings present; n = 80). Because the historical timber survey data did not contain hardwoods, we also excluded three plots where the dominant vegetation was categorized as California black oak, and one plot categorized as tanoak (*Notholithocarpus densiflorus*; n = 76). We also excluded hardwoods from all estimates of tree density and basal area. We further removed plots with <9-m^2/ha basal area, which may be considered nonforested by FIA for a variety of reasons, for example, recent timber harvest or other severe disturbance, which follows the approach from Stephens et al. (2018). This filtering approach left us with 71 plots in our final contemporary data set for analyses.

To make historical and contemporary data sets comparable, we excluded QQs that also contained <9 m^2/ha basal area (n = 102), totaling 1379 QQs in our final historical data set. Although this may bias our results against historical conditions that facilitated low basal area, we wanted to be consistent with the plot characteristics we used to filter our FIA data. We also only counted trees at least 30.5 cm DBH in our estimates to match the assumed DBH cut-off for historical inventories. Because our sampled FIA plots covered a wider geographic range than our historical data, we extracted ecological system codes from LANDFIRE's biophysical settings data set (LANDFIRE 2020) to assess whether the variability in locations would bias the forest conditions we estimated. Ecological systems are part of a classification scheme that incorporates regional distribution, vegetation physiognomy and composition, and environmental setting to describe the natural range of variation in plant communities (Comer et al. 2003). Based on extracted data, we found that both data sets exhibited the same ecological systems and had similar distributions in their representation across sites regardless of location (Appendix S1: Table S1). This suggests that the FIA plots we selected serve as appropriate comparison to our QQ data, despite the disparity in sample size.

For both the 1,379 lots in the final historical data set and the 71 plots in the final modern FIA data set, we extracted underlying climate and topographic data. A digital elevation model was acquired from the U.S. Geological Survey National Elevation Data Set[7] at 1/3 arc-second (8 × 10 m) resolution and converted to corresponding slope and aspect layers using QGIS. We converted aspect to a categorical variable with breakpoints at 135° and 315° to correspond to northeast-facing and southwest-facing slopes. Climate data were acquired from the Basin Characterization Model data set (Flint et al. 2013) for the same geographic footprint at 270-m resolution. Climate variables included 30-yr mean values from 1981 to 2010 for maximum temperature (annual and June), climatic water deficit (annual and June), actual evapotranspiration, April 1 snowpack, and annual precipitation. For spatial predictive models, all data were scaled and aligned at 270-m resolution.

Data analysis

An initial set of all seven climatic variables, elevation, slope, and aspect was considered to explain the variation in historical forest conditions including TPH and pine fraction (calculated as the live basal area of *Pinus* spp. divided by the total live basal area of a given plot). We calculated basal area by multiplying TPH by the adjusted average stump diameter (explained previously). This calculation of basal area is only possible if we assume the reported average diameter is actually the quadratic mean diameter, which we do assume given its relationship with the reported volumes. Given the indirect nature of the basal area estimate, along with its high correlation with TPH (Pearson's r = 0.84) we opted not to analyze it statistically. Multicollinearity amongst explanatory variables was reduced by removing variables with a Pearson's correlation coefficient >0.7 (Appendix S1: Fig. S2). This threshold resulted in a final candidate set of five variables, including maximum annual temperature, slope, aspect, annual climatic water deficit, and annual precipitation. Although we also evaluated higher and lower thresholds of correlation to test the number of parameters included in our models, we did not find any substantial improvements to our final models.

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 Development Core Team 2020) to predict which variables were the most important in explaining historical forest conditions. 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). Similar to methods established by Povak et al. (2014), we started with all five predictor variables in the same random forest model for each

[7] https://viewer.nationalmap.gov/

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forest condition. 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 process until only two variables remained in each model. We selected the best-performing model predicting each forest condition based on the greatest percentage of variation explained and lowest root mean standard error (Appendix S1: Fig. S3). 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 important thresholds in those variables that are associated with the different mean values of historical forest conditions. We used an ANOVA method for splitting variables and a complexity parameter of 0.02 (the increase in R^2 value at each split that must occur for the split to be accepted). For the pine fraction response variable, we used a complexity parameter of 0.03 to avoid an overly complex regression tree.

To compare how TPH and pine fraction may differ between historical and modern forests given the same environmental conditions, we used the breakpoints identified by the regression tree analysis of our historical data and aggregated the modern FIA data set according to those thresholds. We then estimated the mean values of each forest structure variable within that environmental space. Finally, we estimated historical TPH and pine fraction at a landscape scale by applying the best random forest model predicting each structure to a 270-m resolution raster data set containing each model's associated climatic and topographic variables. To avoid extrapolating beyond the range of the sampled environmental space, we excluded any topographic or climatic values that were not within the environmental envelope of the historical data set, as was done by Stephens et al. (2018).

Results

Mean historical density of trees >30-cm DBH in this study area was 44.6 trees/ha and mean basal area was 16.5 m^2/ha (Table 1). For all historical forest structure metrics, mean annual maximum temperature, slope, mean annual climatic water deficit, and mean annual precipitation were predictor variables in the top random forest models. Regression tree analysis of TPH in 1924 suggests a strong influence of mean annual maximum temperature, mean annual precipitation, and mean annual climatic water deficit (Fig. 3). Temperature was the primary driver of density. Sites with annual maximum temperatures warmer than 15°C had higher average densities (42–51 trees/ha) than colder sites (37 trees/ha). Among warmer sites, the driest sites (annual precipitation < 1,019 mm) limited average tree density to 42 trees/ha. Although we observed greater average TPH in wetter sites (precipitation > 1,019 mm), tree density was also limited ($\sim$44 trees/ha) on the wettest sites when annual precipitation was >1,179 mm and climatic water deficit was <517 mm. The highest densities ($\sim$49–51 trees/ha) were observed within intermediate levels of wetness when precipitation was >1,179 mm and climatic water deficit was >517 mm or precipitation was between 1,019 and 1,179 mm.

Table 1. Summary of mean (interquartile range) historical and contemporary forest structure and environmental data used in random forest modeling and regression tree analysis.

Forest structure and data	1924	2011–2018
Trees/ha	44.6 (36.7–52.0)	160 (109–209)
Live basal area (m^2/ha)	16.5 (13.7–18.9)	34.7 (18.1–47.0)
Pine fraction	0.64 (0.53–0.75)	0.33 (0.09–0.47)
Elevation (m)	1,557 (1,459–1,654)	1,603 (1,447–1,756)
Max annual temperature (°C)	15.4 (14.8–16.0)	15.6 (14.4–16.6)
Annual climatic water deficit (mm)	499 (470–534)	527 (485–586)
Annual precipitation (mm)	1,240 (1,034–1,440)	1,382 (972–1,878)
Slope (%)	11.1 (6.2–15.5)	12.4 (5.8–17.3)

Note: Environmental data were averaged using long-term values from 1981 to 2010.

Based on breakpoints established in the regression tree analysis of historical TPH, modern forests had approximately 350% higher average TPH than historical forests across all environmental conditions (Table 1, Fig. 3). Unlike the historical data set, colder (annual maximum temperature <15°C) and wetter (annual precipitation >1,179 mm and annual climatic water deficit <517 mm) sites had the highest modern tree densities, $\sim$170 and $\sim$181 trees/ha, respectively. Although the driest sites (annual precipitation <1,019 mm) generally had lower modern tree density ($\sim$141 trees/ha), unlike the historical data set, they did not contain the lowest densities among the warmer sites. Rather, sites that had greater precipitation combined with greater climatic water deficit showed the lowest densities ($\sim$136 trees/ha). Other sites with intermediate levels of wetness (precipitation between 1,019 and 1,179 mm) showed intermediate levels of tree density ($\sim$166 trees/ha).

The historical forest condition was strongly characterized as pine-dominated forests (average pine fraction = 0.64; Table 1). Regression tree analysis demonstrated that regardless of environmental condition, historical pine fraction was ≥0.53 (Fig. 4). Unlike the other regression tree analyses, all variables were shown as strong drivers of historical pine fraction. In sites where slope was low (<10%), drier sites with precipitation <1,497 mm had 23% higher pine fraction ($\sim$0.71) than sites where precipitation was >1,497 mm ($\sim$0.55). When slope was steeper (>10%), pine fraction was comparable on warmer (maximum temperature >15°C) sites and colder (<15°C), less drought-stressed (climatic water deficit <476 mm) sites, $\sim$0.53 vs. $\sim$0.56, respectively.

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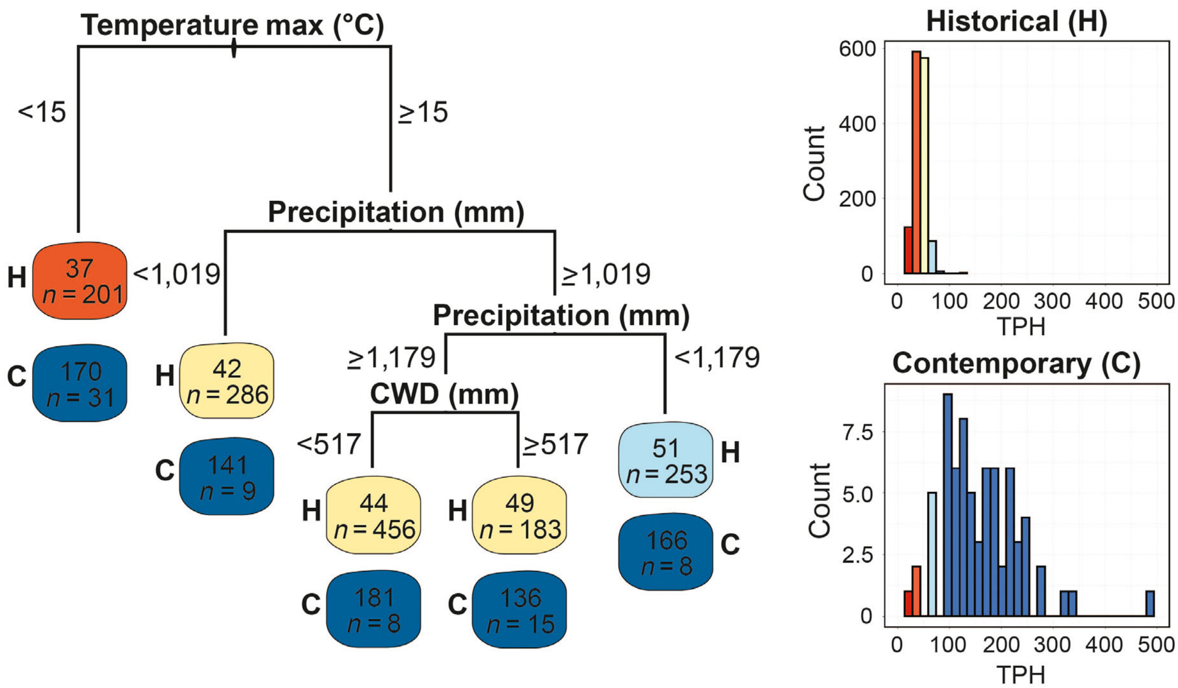

Fig. 3. Regression tree output explaining the influence of biophysical variables on tree density (trees per hectare [TPH] >30.5-cm diameter at breast height). Colored boxes at the ends of the regression tree branches contain mean TPH and number of observations in each resulting group, for the historical (H) and contemporary (C) inventory data sets. The colors correspond to different TPH values in the respective histograms. CWD = climatic water deficit.

Colder sites with temperature <15°C had a higher pine fraction (~0.70) when coupled with higher drought stress (climatic water deficit >476 mm).

Pine dominance shifted dramatically in modern forests, with our regression tree analysis on FIA data indicating that pine fraction diminished even under the same environmental conditions as our historical data set (Fig. 4). Unlike the historical data set, low slopes were not pine dominated, with wetter sites (precipitation >1,497 mm) showing the lowest levels of pine fraction (~0.13). Drier sites with precipitation <1,497 mm had higher pine fraction (~0.38), but were still 46% lower than historical pine fraction under the same conditions. This trend was consistent in sites with steeper slopes (>10%). Although the warmest sites where maximum temperature was >15°C were similar to historical forests in that they showed lower pine fraction (~0.20) relative to the other environmental conditions, these sites were still 62% lower than historical forests. Although colder (maximum temperature <15°C) and less drought-stressed (climatic water deficit <476 mm) sites showed higher levels of pine fraction (~0.46), the highest levels of pine fraction (~0.56) were apparent in colder sites with higher drought stress (climatic water deficit >467 mm).

Based on maps generated from our best-fit random forest models predicting tree density (Fig. 5) and pine fraction (Fig. 6), there were considerable patterns in forest structure across the historical landscape. Higher tree densities appeared to concentrate at the southern portion of the study area, and lower tree densities were more apparent in the northern portion, where maximum high temperatures were more likely to be below 15°C, including several higher plateaus and ranges southeast of Lassen Volcanic National Park (data not shown). Our maps showed that pines dominated the historical landscape, with the highest portions concentrated in the northern region of our study area. The spatial distribution of pine also aligned with the distribution of tree density, with a linear regression detecting a negative relationship between tree density and pine fraction (Appendix S1: Fig. S4; $P < 0.001$).

Discussion

Past management and climate change are impacting forests across western North America with increasing high-severity fire, possibly leading to conversion to non-forest vegetation (Coop et al. 2020). Such fundamental changes to forests will impact their carbon sequestration, wildlife habitat, ascetics, and hydrology. Forests adapted to infrequent, high-severity fire regimes are more susceptible to climate-induced changes because there are few management actions that can be undertaken to conserve these forests (Westerling et al. 2011, Stephens et al. 2014). However, forests adapted to frequent, low–

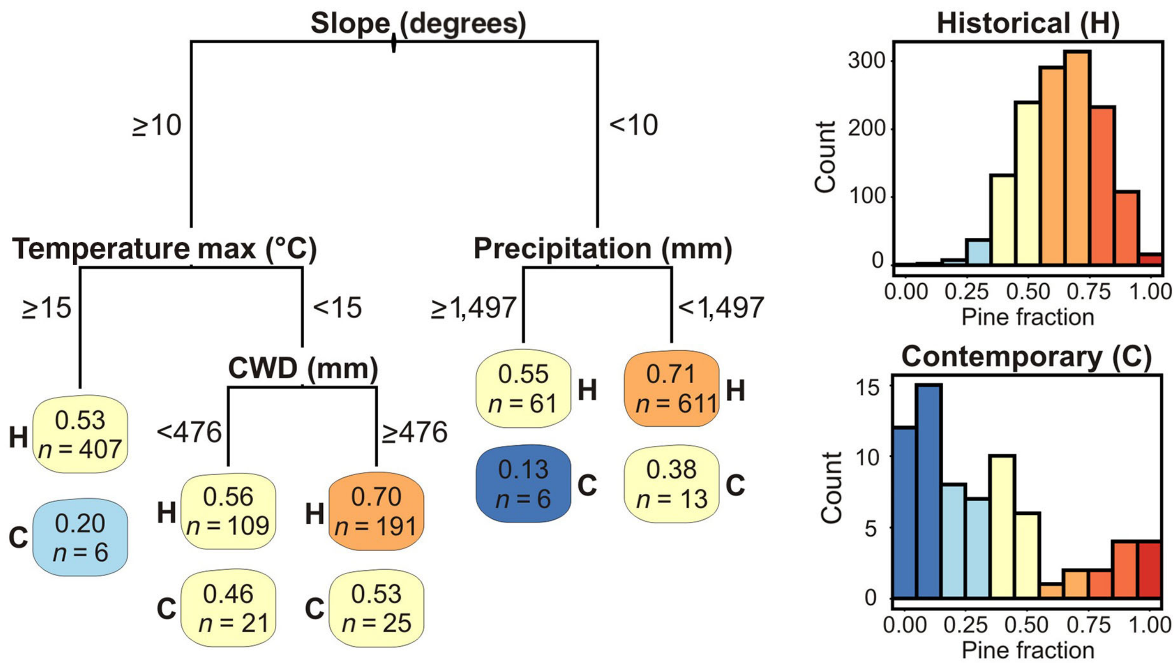

FIG. 4. Regression tree output explaining the influence of biophysical variables on pine fraction (basal area of *Pinus* spp. divided by total live basal area of a given plot). Colored boxes at the ends of the regression tree branches contain mean pine fraction and number of observations in each resulting group, for the historical (H) and contemporary (C) inventory data sets. The colors correspond with different pine fraction values in the respective histograms. CWD = climatic water deficit.

moderate intensity fire regimes can be managed to increase their resiliency (Hurteau et al. 2016, Liang et al. 2018), but a key challenge is identifying conditions that confer landscape-level resilience.

The historical landscape-level forest condition in the privately owned portion of the southern Cascade Range we studied fit the classic model of frequent-fire forests: large trees (mean pine DBH 76 cm), low mean density (44.6 trees/ha; 16.5 m^2/ha basal area), and pine-dominated (Table 1, Fig. 2). Among comparable studies with historical timber survey data, our overall average tree density and basal area estimates fell within the range of averages reported for other pine-dominated mixed-conifer forests in the southern Sierra Nevada (35.7 trees/ha, 16.1 m^2/ha from Collins et al. [2015; adjusted to only trees >30.5 cm DBH]; 54.5 trees/ha, 21.9 m^2/ha from Stephens et al. [2015]). Our overall average basal area estimate, for which lower tree DBH cutoffs would have much less influence, was also similar to those reported further north in the Cascade Range (14–21 m^2/ha [Hagmann et al. 2013, 2014, 2017, Ritchie 2016]). However, despite having similar average forest structural characteristics, our large historical landscape may be unique in that it exhibited much lower overall variability in forest structure relative to these other studies. This is evident in the narrow interquartile ranges for historical tree density and pine fraction (Table 1), which almost mirror the range in group means resulting from the regression trees explaining both variables (Figs. 3, 4). The relatively low overall variability is somewhat surprising, given the large overall extent and depth of the timber inventory data (52,206 ha sampled at 19%; Fig. 1), but may be partly attributable to less topographic relief (and associated climatic variability) in this region compared to other areas of the Sierra Nevada.

Despite having relatively low overall variability in historical forest structure and composition, our analyses revealed evidence of biophysical controls on tree density and pine fraction (Figs. 3, 4). Annual climatic variables most strongly explained the range in historical tree densities, whereas historical pine fraction was explained by a combination of topographic and climatic variables. These general relationships mirrored those reported in Stephens et al. (2018), which was conducted in an upper-elevation mixed-conifer forest in the north-central Sierra Nevada. However, there were some differences in the specific variables identified. For example, the highest historical tree densities from Stephens et al. (2018) occurred in areas with moderate to high precipitation but with intermediate annual snowpack, whereas the highest densities in our study occurred in areas with average or higher mean annual temperature but with moderate precipitation (Fig. 3). Similarly, the greatest pine fraction from Stephens et al. (2018) occurred in lower-elevation areas with higher annual climatic water deficit, whereas our study found that the greatest pine fraction occurred in areas with flatter slope gradients

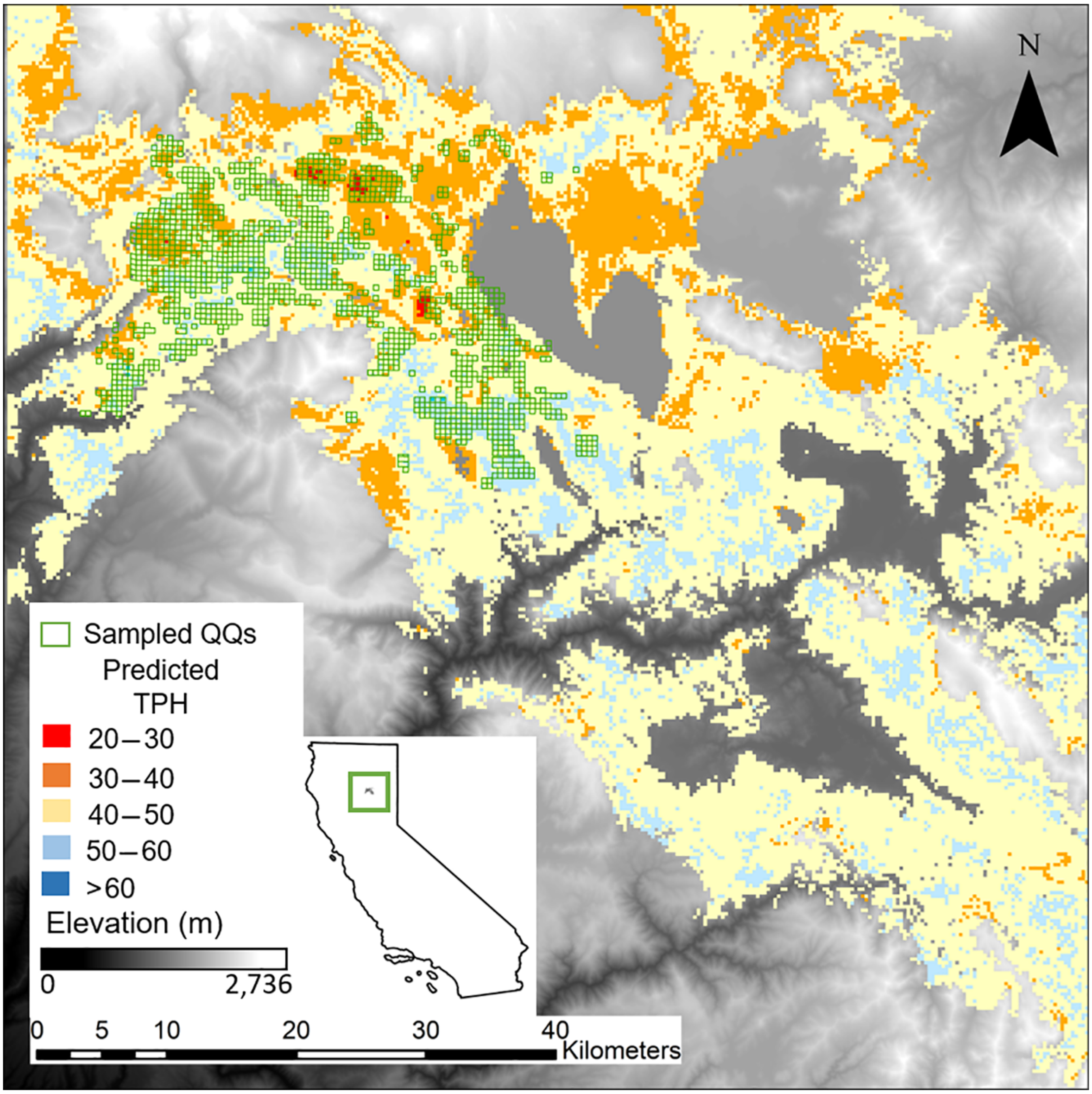

Fig. 5. Model prediction of historical landscape variation in tree density (trees per hectare [TPH] >30.5-cm diameter at breast height). Predictions were generated from best-fit random forest model using the historical data set. Predictors included means of maximum annual temperature, annual climatic water deficit, annual precipitation, and slope. Predictions were only made within the environmental envelope of the historical data set (sampled quarter-quarter sections [QQs]) and scaled to 270-m resolution.

and higher, but not extremely high, precipitation (note the 1,497-mm annual precipitation identified in Fig. 4 is greater than the 75th percentile value reported in Table 1). These discrepancies make it difficult to distill common drivers of variability across these two distinct study areas, yet clearly the biophysical environment exerted some control in both areas. Biophysical drivers of landscape-level variability in historical forest structure and composition have also been identified in other frequent fire-adapted forests (Maxwell et al. 2014, Collins et al. 2015). It is noteworthy that the expression of the biophysical environment existed despite long-term exposure to frequent fire (Hessburg et al. 2015).

The much higher tree densities and lower proportions of pine in contemporary forests relative to historical conditions agrees with many other investigations of forest change in frequent fire-adapted forests (e.g., Moore et al. [2004], Brown et al. [2008], Scholl and Taylor [2010], Knapp et al. [2013], Taylor et al. [2014]). These changes were evident across all biophysical divisions identified in the regression tree analysis (Figs. 3, 4). Along with these overall changes, contemporary forests

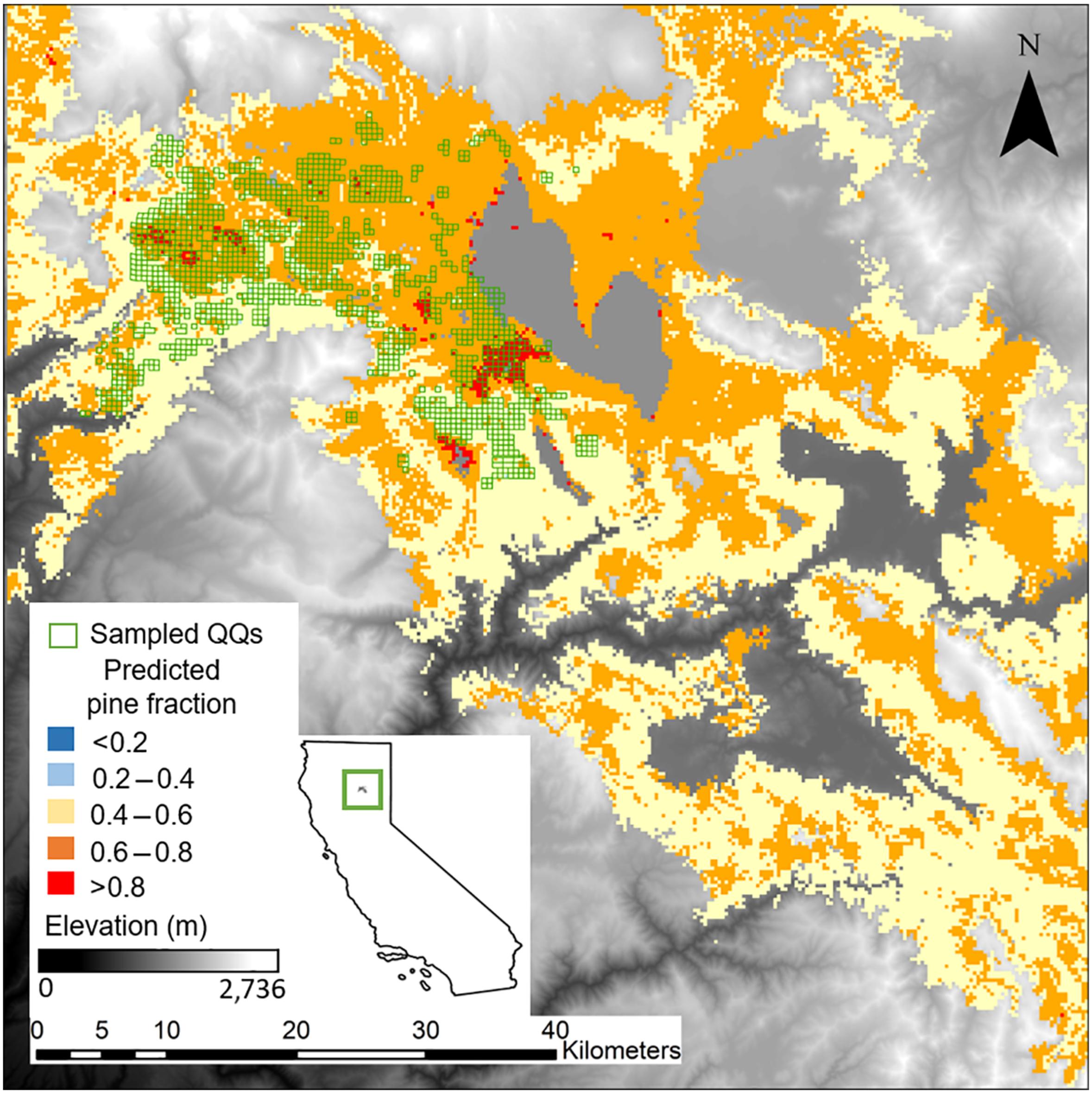

Fig. 6. Model prediction of historical landscape variation in pine fraction (calculated as the live basal area of *Pinus* spp. divided by total live basal area of the plot). Predictions were generated from best-fit random forest model using the historical data set. Predictors included means of maximum annual temperature, annual climatic water deficit, annual precipitation, and slope. Predictions were only made within the environmental envelope of the historical data set (sampled quarter-quarter sections [QQs]) and scaled to 270-m resolution.

exhibited a far greater range in conditions than what existed historically. This was apparent in the very different distributions of tree density and pine fraction depicted by the respective histograms (Figs. 3, 4). Management history undoubtedly explains some of the variation observed in the contemporary forests; in particular harvesting coupled with fire suppression and exclusion (Collins et al. 2017). Much of the study area remains in private ownership, managed for timber growth and yield with single tree selection regeneration methods in order to develop multiaged structures. Hence a complex forest structure is an intentional product of the silvicultural methods being used. Although fire suppression has typically been considered to have a homogenizing effect on forest structure in western U.S. forests (e.g., Jones et al. [2018], Ziegler et al. [2021]), decades of multiaged silviculture in this case may have restored complexity to the point that structure is more variable than it was during a period with frequent fire. Another contributing factor could be that the effect of biophysical factors, which collectively influence forest structure and composition, is muted by frequent fire. In other words, productivity gradients can be more fully expressed when fire has been removed for decades (Merschel et al. 2014). Investigating this hypothesis will likely require a more robust data set for characterizing contemporary forest conditions (i.e., remeasurement rather than FIA), as well as an ability to control for management history.

Our findings and associated inferences should be tempered by the understanding that our data sets and analyses are not without limitations. Our use of FIA plot data to quantify contemporary forest conditions makes for a fairly coarse characterization of forest change. Although a similar approach has been used in several previous studies (Hagmann et al. 2013, 2014, 2017, Stephens et al. 2015, 2017, 2018), the comparisons are imperfect. In our case we had very different sample sizes, 1,379 historical observations vs. 71 contemporary observations. This suggests that we have unequal representations of actual variability in the two time periods. However, the fact that we observed a greater range in contemporary forest conditions despite having a much smaller sample size somewhat counters this concern. Although the variability we observed may be a product of the wider geographic range of the FIA plots we sampled or slight differences in environmental conditions (Table 1), similar biophysical environments between the contemporary and historical data sets (Supplemental Material: Table S1) suggest that smaller sample of FIA plots we used were still an appropriate comparison to our historical data. However, we acknowledge utilizing FIA data to substitute for a lack of repeated measures in our QQ sites is an imperfect design and that our assessment of forest change in this area should be interpreted as general shifts in forest conditions rather than a specific quantification of change.

The depth and extent of our historical data allowed us to model variability in historical forest conditions across a large landscape, extending well beyond the sampled areas (Figs. 5, 6). Despite not projecting a large range in historical tree density or pine fraction, these models demonstrate a north–south gradient across our larger study area, with lower pine dominance and greater tree densities in southern portion (Fig. 5). Given that these model projections are based on output from our random forest analysis, these projections likely track biophysical gradients that indicate generally greater productivity in the southern half of study area. Finer-scale gradients exist as well, which are presumably tied to the interacting effects of topography and climate.

The depth and extent of the historical data set is the primary strength of this study, but these data are not without their own limitations. First, the archived records we obtained were summaries of data collected on individual transects for a given QQ. As a result, we lacked individual tree measurements, which affected our ability to generate forest structure metrics such as basal area or tree diameter distributions. Second, the lower-diameter cutoff for inclusion in our QQ summaries was 30.5 cm (12 in.) DBH. This censors our characterization of historical (and contemporary) forest conditions towards that of the mid- and overstory, which also could influence the relatively low variability we observed throughout our study area. However, Stephens et al. (2015) had the same lower DBH cutoff, yet they demonstrated fairly high variability throughout a smaller study area. Third, the lack of information on hardwood tree species, as mentioned previously, causes questions as to whether they were present, but omitted in the survey, or present, but below the 30.5-cm DBH cutoff for recording. Based on a similar data set collected 140 km away in similar forest type during a similar time period (1923), where only 17% of lots contained any individuals of the most common hardwood, California black oak (*Quercus kelloggii*), >15.2 cm DBH, and where the average fraction of plot basal area in *Q. kelloggii* was 1.7% (Stephens et al. 2018), we do not believe that the inclusion of *Q. kelloggii* (or other hardwoods) would have appreciably affected our results. Lastly, the decision not to include historical data from QQs with live basal area <9 m^2/ha, which was done to match the excluded "nonforested" areas as defined by FIA, limits our characterization of landscape-level variability. These areas with low live overstory cover can be quite important for maintaining high biodiversity (White et al. 2015). These limitations further emphasize that all historical forest reconstructions, including this one, are incomplete (e.g., Collins et al. [2018], Levine et al. [2019]). That said, these large-scale historical timber surveys are a robust source of quantitative data that require very few assumptions to generate forest structure and composition metrics (Hagmann et al. 2018).

Management Implications

The forest management regime in much of our study area for several decades has been characterized by periodic single tree selection harvests, designed to create a diversity of age and size structures for sustaining long-term timber yield. Although selective practices in this forest type risks high-grading that have led to declines in productivity (York 2015), the single-tree selection methods on these lands were designed to focus on improving growth and yield. Although large trees are periodically harvested when they show signs of productivity loss, they are not removed when reaching a predetermined diameter. Many large trees are therefore retained. Likewise, the historical fire regime also sustained a diversity of size and age structures (Safford and Stevens 2017) that retained larger trees albeit determined by fire resistance and not economic factors. Thus, although the disturbance regime of frequent fires has been replaced with a regime of frequent selection harvests, the general multiaged structure has been maintained. Uneven-aged silviculture systems would presumably be relatively well aligned with the natural disturbance regime (Seymour et al. 2002, Long 2009). However, our findings describing a past forest structure characterized by particularly low tree density, large pine fraction, large tree size, and low basal area compared to contemporary forests even

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when they are periodically harvested. Modifications to cutting cycles, stocking targets, and planting methods could be incorporated into prescriptions if an even closer alignment with historical structures is desired.

Despite periodic reductions in basal areas from harvesting, current levels of stocking are still roughly twice as high (Table 1) as when harvesting practices first started. This demonstrates that private forestland managed with multiaged silviculture may be quite similar to public forestland with respect to departure in forest structure and compositions from that of historical forests. Had harvests not occurred, basal area would likely be even higher and could still be increasing linearly where wildfire suppression was effective (Levine et al. 2016, Collins et al. 2017). Silvicultural regimes that maintain stocking levels that are higher than those maintained by frequent fire are a logical outcome of managing for timber as an objective because higher stocking, to an extent, equates to higher growth and yield. A commonality across studies that use historical ecological information is that historical basal areas are much lower than what sites are capable of when applying relative stocking indices (Long and Shaw 2012). This points to a misalignment between the objectives of managing for timber production versus maintaining low-density forests consistent with the historical condition we demonstrated. This is not a new dilemma in forests adapted to frequent fire (Show and Kotok 1924). To reduce basal areas to the levels that are suggested by this and other studies would likely compromise a timber objective. For example, harvesting to an average residual basal area level of 16.5 m^2/ha found in this study would fail to comply with the minimum stocking standards on productive private land in California (California Forest Practice Rules [CFPR] 2020). A challenge for multiaged silvicultural systems that attempt to achieve both timber and restoration objectives will be finding appropriate stocking levels that are high enough to achieve acceptable timber yield and low enough to reflect past densities, which demonstrated greater resistance and resilience to fire and drought (Safford and Stevens 2017). A further challenge will be updating forest practice regulations to accommodate lower stocking standards where restoration objectives are a goal. Future research into the implications for timber management of silviculture regimes that are even more aligned with past fire regimes is a needed area of applied study, especially considering the wealth of reconstruction studies that are now available for use in establishing postharvest structures.

The decrease in pine fraction that we found here is also in common with other studies using historical ecological information. Gap-based silviculture that reduces surface fuels (York et al. 2012) can create conditions for natural regeneration of ponderosa pine. And harvesting to create distinct canopy gaps followed by planting can allow for rapid growth of ponderosa pine that is similar to even-aged systems (York et al. 2007). Retention of large pine trees is also an important component of adapting silvicultural regimes if the objective is to restore historical structures.

Efforts to restore forest structures to conditions similar to those in place when they were influenced by frequent fires need not differ across ownerships if resilience is a management goal (Stephens et al. 2021). This is not to suggest that forest restoration objectives are uniformly desired, or that restoration prescriptions can be uniformly applied. As our results support, local factors are important in guiding forest restoration. Biophysical and management variability can both create structural heterogeneity. As an example, the lack of a larger range in tree density and pine fraction, relative to other study areas with similar historical data (e.g., Collins et al. [2015], Stephens et al. [2018], Hagmann et al. [2019]), might result in a narrower set of restoration prescriptions. Regardless of the level of historical variability in a given landscape, the maps we generated for the modeled historical densities and pine fractions could be used to "assign" different prescriptions across a project area. This would certainly introduce some complexity in implementation, but given the connection between variability and forest resilience (North et al. [2009], Koontz et al. [2020]), it may be worth pursuing.

This research, when combined with other landscape-level forest reconstructions in the Sierra Nevada (Collins et al. 2017, Stephens et al. 2015, 2018), points to much lower density forests with some differences in tree basal area. In pine mixed-conifer forests, historical basal area was one-half or lower than contemporary forests (Collins et al. 2017, Stephens et al. 2015, this work) but in areas that were fir mixed-conifer forests, basal area was largely unchanged between historical and contemporary conditions (Stephens et al. 2018). This further emphasizes that restoration programs will not be uniform, but we have the knowledge to move forward today to increase forest resilience and adaptive capacity to fire, bark beetles, and climate change.

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Supporting Information

Additional supporting information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/eap.2400/full

Open Research

Data (Bernal et al. 2021) are available from the Dryad digital repository: https://doi.org/10.5061/dryad.7d7wm37vk.

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