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Novel characterization of landscape-level variability in historical vegetation structure

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Abstract. We analyzed historical timber inventory data collected systematically across a large mixed-conifer-dominated landscape to gain insight into the interaction between disturbances and vegetation structure and composition prior to 20th century land management practices. Using records from over 20 000 trees, we quantified historical vegetation structure and composition for nine distinct vegetation groups. Our findings highlight some key aspects of forest structure under an intact disturbance regime: (1) forests were low density, with mean live basal area and tree density ranging from 8–30 m^2 /ha and 25–79 trees/ha, respectively; (2) understory and overstory structure and composition varied considerably across the landscape; and (3) elevational gradients largely explained variability in forest structure over the landscape. Furthermore, the presence of large trees across most of the surveyed area suggests that extensive stand-replacing disturbances were rare in these forests. The vegetation structure and composition characteristics we quantified, along with evidence of largely elevational control on these characteristics, can provide guidance for restoration efforts in similar forests.

Key words: central Sierra Nevada, California, USA; fire severity; forest restoration; historical range of variability (HRV); mixed-conifer forest; timber inventories; vegetation classification; Yosemite National Park.

Introduction

Ecological restoration is one of the primary land management goals for public lands throughout the western and southern United States (USDA-FS 2012). The rationale behind this is that many ecosystems are presently degraded, and as a result, are not resilient to contemporary and expected future disturbances and stressors (Fulé 2008, Stephens et al. 2013). Dry forest types that historically experienced frequent, low- to moderate-severity fire are receiving considerable attention for prioritizing restoration efforts (Franklin and Johnson 2012). This is due to the widely documented forest change at both the stand (i.e., tree densification, shifts in species composition) and landscape scale (i.e., loss of heterogeneity) relative to pre-Euro-American conditions (Fulé et al. 1997, Hessburg et al. 2005, Brown et al. 2008, Scholl and Taylor 2010, Hagmann et al. 2013, 2014). In the Sierra Nevada it is a common assertion that this forest change, in conjunction with increasing incidence of high to extreme fire weather (Collins 2014), is leading to uncharacteristically large stand-replacing fire patches (Mallek et al. 2013).

Accurate historical characterizations are paramount to our understanding contemporary forest degradation, and thus the need for restoration (Swetnam et al. 1999, Safford et al. 2012). The problem is that historical data sets are often incomplete and/or highly localized (<100 ha), resulting in imperfect characterizations of forest conditions prior to the dominant change agents (i.e., widespread timber harvesting and fire suppression/exclusion). This is particularly true for larger landscapes (>10 000 ha), and as a result our understanding of landscape-scale variability in forest conditions is limited. In this study we address this knowledge gap by using a unique historical data set on

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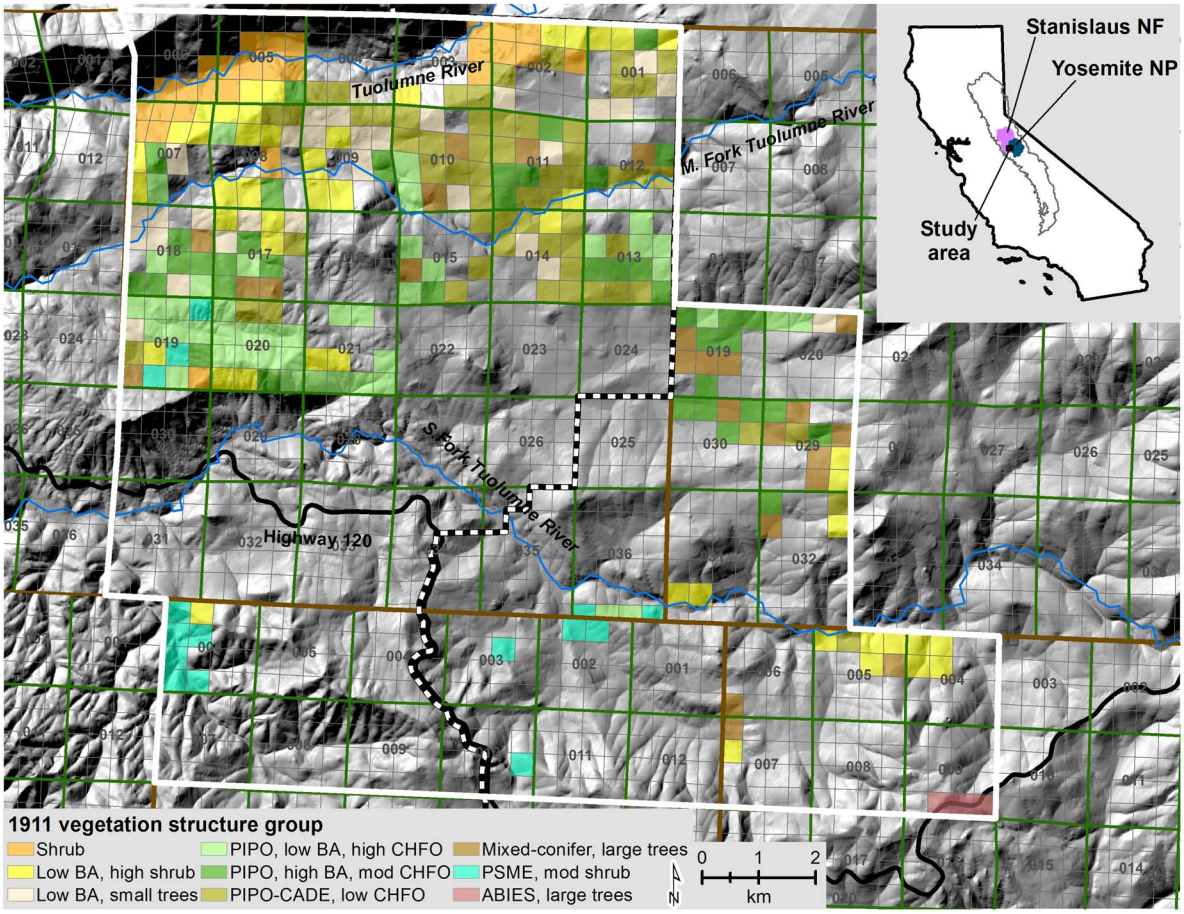

FIG. 1. Quarter-quarter sections (16.2 ha each) with archived data from a systematic timber inventory conducted in 1911. This inventory spanned portions of the Stanislaus National Forest (NF) and Yosemite National Park (NP) located in the central Sierra Nevada, California, United States (shown in inset; the boundary between Stanislaus NF and Yosemite NP within the study area is delineated by the black and white dashed line). The heavy white outline depicts the study area boundary. Colors correspond with vegetation structure groups that were identified by a cluster analysis using the tree and understory vegetation inventory (see *Methods*). Vegetation group abbreviations are as follows: Basal area, BA; *Abies concolor* + *Abies magnifica*, ABIES; *Pinus ponderosa*, PIPO; *Chamaebatia foliolosa*, CHFO; *Calocedrus decurrens*, CADE; *Pseudotsuga menziesii*, PSME.

vegetation structure across a large, predominantly forested landscape. The data are from systematic timber inventories conducted by the U.S. Forest Service in 1911.

In an earlier effort we used a portion of this historical data set to investigate change driven primarily by 20th century fire exclusion and use policies (Collins et al. 2011). Here, we were able to obtain additional historical data in the same format for a much larger area. This additional data allowed for investigation into the controls on variability in historical vegetation structure and composition across a large landscape (16 800 ha). We had two primary objectives: (1) identify relatively distinct vegetation groups based on historical forest overstory and understory structure and composition, and (2) explore the extent to which topographic characteristics explain the distribution of vegetation groups over the landscape. Given the detailed nature of the historical data (20 700 individual tree observations) and its overall extent, we believe this work can provide insight into the interaction between disturbance and vegetation structure and composition prior to 20th century land management practices.

METHODS

The historical timber inventory data used here spans portions of the Stanislaus National Forest and Yosemite National Park in the central Sierra Nevada (Fig. 1 inset). Elevation for inventoried areas ranges from 776–2140 m, with the forest area characterized as west-slope Sierra Nevada pine–mixed-conifer forest consisting of sugar pine (*Pinus lambertiana*), ponderosa pine (*Pinus ponderosa*), white fir (*Abies concolor*), red fir (*Abies magnifica*), incense-cedar (*Calocedrus decurrens*), and Douglas-fir (*Pseudotsuga menziesii*). The climate is

mediterranean, with cool, wet winters and hot, dry summers. Annual precipitation, primarily as snow, averages just over 100 cm/yr. Mean monthly temperatures range from 4°C in January to 20°C in July (Crane Flat Remote Automated Weather Station, 1992–2014). Prior to 1900 low- to moderate-severity fire was common in this area, with a mean point fire return interval of 12 years (Scholl and Taylor 2010). This was based on reconstruction with extensive fire scar and age structure data in an area that overlapped the Yosemite portion of our study area (Fig. 1).

All of the historical forest inventories within our study area were conducted in 1911, and consisted of belt transects located systematically based on the Public Land Survey System. Transects spanned the mid-line of quarter-quarter sections (16.2-ha or 40-acre survey units; QQs) in a 40.2×402 m area (1.6 ha) and were a 10% sample of each surveyed QQs (USFS 1911, Collins et al. 2011). Due to the large amount of QQs within the overall study area with no historical inventory data available (~70% of QQs) our data actually represent a 3% sample of the entire study area (Fig. 1). All trees >15.2 cm diameter at breast height (dbh, 1.37 m) were tallied by species within belt transects. Trees 15.2–30.5 cm dbh were tallied as "poles" and trees >30.5 cm dbh were tallied into 5.1 cm dbh and 4.9 m height classes. Records specific to the timber surveys in this area indicate that all trees were tallied (USFS 1911), but the lack of California black oak (*Quercus kelloggii*) suggests that the inventories may have been limited to all conifers. In addition to inventorying trees, shrub cover was recorded by species for each transect. Datasheets also contained written descriptions of site characteristics, including noting previous logging. Based on these descriptions there was no logging in any of the 1911 inventoried areas.

We generated the following forest structure and composition variables for each transect ($n = 294$ transects): total basal area, basal area proportion by tree species, total tree density, tree density by dbh class (15.2–30.4 cm, 30.5–61.0 cm, 61.1–91.4 cm, >91.4 cm), and shrub cover (%). We also included cover of a low-stature shrub, bear clover (*Chamaebatia foliolosa*), which was recorded separately from the shrub cover estimate. These structure and composition variables were used in a *k*-means cluster analysis to identify distinct vegetation groups. Input variables were *z*-score standardized prior to clustering to account for differences in scale. We followed standard practices by choosing the number of clusters that corresponded with an abrupt flattening of the curve depicting within-group sum-of-squares-error as a function of the number of clusters.

For each transect with historical data we generated the following topographic and moisture availability variables: elevation, aspect (reclassified), slope gradient, topographic position index (TPI), topographic relative moisture index (TRMI), actual evapotranspiration (AET), and annual climatic water deficit. Topographic variables were derived in ArcGIS 10.2 using a digital elevation model obtained from the National Elevation Dataset (Gesch et al. 2002). We reclassified aspect so that values ranged from 0 (xeric) to 20 (mesic) using the approach outlined in Parker (1982). We identified four topographic position index (TPI) classes (valley bottom, gentle slope, steep slope, and ridgetop) using the CorridorDesigner toolbox (Majka et al. 2007), with a neighborhood size of 200 m. The cutoff point for gentle vs. steep slope was 6° (10.5% grade). We calculated TRMI using TPI, reclassified aspect, slope, and curvature following the method of Parker (1982). We calculated AET and annual climatic water deficit using soil water holding potential, temperature, and precipitation (Churchill et al. 2013). We used the soil water holding capacity in the top 150 cm of the soil (USDA-NRCS 2014), and weather data from the period 1901–1910 that was obtained from Climate WNA (Wang et al. 2011). AET and water deficit were calculated at a 30 m resolution, and other topographic variables were calculated at a 10 m resolution. Mean values for topographic variables within a transect area were extracted using zonal statistics, and a TPI class was assigned to each transect based on the majority area in each class. Mean values and ranges for these variables are presented in the Appendix: Table A1.

To investigate potential bias in the historical timber survey data we calculated mean elevation and AET for all QQs within the study area (Fig. 1), then compared them for QQs with and without historical data. Given that we had a census of the study area for elevation and AET, i.e., one value for every QQs in the study area, we used randomization tests to identify whether group means of the two variables were statistically different ($P < 0.05$) from those that would be expected by chance. Randomization tests generated distributions for each group by reshuffling the data and randomly assigning observations to groups using all of the observations, as opposed to re-sampling, and then assessing where actual group means lie on the distributions to determine P values. The tests do not rely on assumptions of normality and homoscedasticity (Manly 2007). These tests were performed using the "coin" package (Hothorn et al. 2006*a*) in the statistical program R (R Development Core Team 2014).

We used a conditional inference tree analysis with the topographic variables as predictors to explain the distribution of the identified vegetation groups across the landscape. This analysis was performed using the "ctree" function in the "party" package (Hothorn et al. 2006*b*) in R. This technique identifies influential explanatory variables using a partitioning algorithm that is based on the lowest statistically significant P value derived from Monte Carlo simulations, which avoids overfitting and biased selection among covariates

TABLE 1. Average structural characteristics for the nine historical vegetation groups identified from the *k*-means cluster analysis.

Characteristic	Shrub	Low BA, high shrub	Low BA, small trees	PIPO, low BA, high CHFO
n	27	48	31	44
Understory cover (%)				
CHFO	2.4	25	32.5	79.5
Shrub	84.1	54.3	21.6	10.6
BA, by species (m^2/ha)				
ABCO	0	0.9	0.1	0
ABMA	0	0	0	0
CADE	0	2	4	3.4
PILA	0	1.2	0.5	1.8
PIPO	0	3.5	4.9	7.9
PSME	0	0.5	0.4	0.8
Total live BA (m^2/ha)	0.1 (0–2)	8.1 (2–19)	9.9 (2–16)	13.9 (6–22)
Live tree density (no./ha) by dbh				
15–30 cm	0.1	6.3	23.7	7.8
30–61 cm	0.1	9.6	14.2	12.1
61–91 cm	0.1	4.9	6	9.6
>91 cm	0	4.2	4.9	8.2
Total live tree density (no./ha)	0.3 (0–5)	25.0 (6–47)	48.9 (31–93)	37.7 (11–54)

Notes: Ranges are reported in parentheses next to averages for total live basal area (BA) and tree density. Species codes are as follows: *Chamaebatia foliolosa*, CHFO; *Abies concolor*, ABCO; *Abies magnifica*, ABMA; *Abies concolor* and *Abies magnifica*, ABIES; *Calocedrus decurrens*, CADE; *Pinus lambertiana*, PILA; *Pinus ponderosa*, PIPO; and *Pseudotsuga menziesii*, PSME.

† Does not include the shrub group in the reported averages.

(Hothorn et al. 2006*b*). A significance level of 0.05 was used in assessing all splits.

RESULTS

The *k*-means analysis resulted in nine distinct vegetation structure groups. The groups tended to separate based on three main characteristics: understory cover and composition, tree basal area (BA), and dominant tree species composition (Table 1). The shrub group was dominated by shrubs with almost no trees. This group occurred primarily in a steep river canyon in the northern part of the study area, and accounted for 9% of the historical inventory transects (Fig. 1). Two groups had low tree BA (8.1 and 9.9 m^2/ha), but differed considerably in shrub cover and small tree density: low BA, high shrub; low BA, small trees. These two groups comprised 27% of the inventoried transects. There were three groups dominated by ponderosa pine (PIPO), differing in BA (13.1, 16.8, and 21.5 m^2/ha), co-dominance with incense-cedar (CADE; 25–40% of BA), and bear clover (CHFO) cover (18, 55, and 80%): PIPO, low BA, high CHFO; PIPO, high BA, mod CHFO; PIPO-CADE, low CHFO. These three groups accounted for nearly half of the historical inventory transects and were widely distributed across the landscape (Fig. 1). The last three groups differed in tree species composition and large tree density, and collectively accounted for 15% of the historical inventory area. One group was dominated by ponderosa pine and incense-cedar, but also included sugar pine and white fir, and had the highest density of large trees (20 trees/ha, dbh > 91 cm): mixed-conifer, large trees. Another group was dominated by Douglas-fir (PSME; 50% by BA), with lesser proportions of sugar pine, incense cedar, and ponderosa pine, and had moderately high shrub cover: PSME, mod shrub. The final group was dominated by white and red fir and had the second highest density of large trees (18 trees/ha, dbh > 91 cm): ABIES, large trees. Estimated mean canopy cover, based on tree lists, ranged from 9–28%, for all tree-dominated groups (not including the shrub group; Appendix: Table A2).

Randomization tests indicated that QQs with historical survey data available had similar AET values, but tended to occur in lower elevations relative to QQs without survey data (Appendix: Table A3). Conditional inference tree results indicated strong elevational control on the distribution of vegetation structure groups across the landscape (Fig. 2). Moisture availability, as captured by AET, also exhibited some control on vegetation group distribution. The shrub group predominantly occurred at the lowest elevations (<1048 m). The two low BA groups were divided between a mid-elevation band (1277–1562 m), and either a lower elevation band (1048–1277) low BA, small trees, or low AET (<391 mm) low BA, high shrub. The three PIPO-dominated groups and the PSME, mod shrub occurred primarily at the mid-elevation band (1277–1562 m). This elevation band contained 60% of the historical inventory transects, with no further differentiation by the conditional inference tree. The mixed-conifer, large trees group was mostly split between the mid-elevation band (1277–1562 m) and the upper-mid-elevation band (1563–1840 m). The ABIES, large trees group that accounted for

TABLE 1. Extended.

PIPO, high BA, mod CHFO	PIPO-CADE, low CHFO	Mixed-conifer, large trees	PSME, mod shrub	ABIES, large trees	Average†
41	60	24	16	3	267
54.9	17.5	42.6	25.5	0	39.1
20.9	17.4	25.4	35.7	21.7	25.8
0.2	0.2	4.1	0	14.6	0.8
0	0	0	0	13.6	0.2
6.4	6.7	9.1	3.2	0	4.9
0.8	1.1	4.7	3.6	0.8	1.6
13.8	8.4	11.9	2.7	0.7	7.7
0.3	0.3	0.4	9.4	0	1
21.5 (13–31)	16.8 (9–23)	30.2 (23–39)	18.9 (11–28)	29.7 (25–33)	16.1 (2–39)
16.8	10.6	16.6	9.7	22.4	12.5
27.9	15.5	19.4	12.7	26.6	15.9
18.6	10.9	16.3	8.5	12.4	10.6
9.4	10.3	20	12.4	17.7	9.2
72.7 (53–107)	47.2 (28–73)	72.3 (53–121)	43.4 (22–70)	79.1 (59–111)	48.1 (3–121)

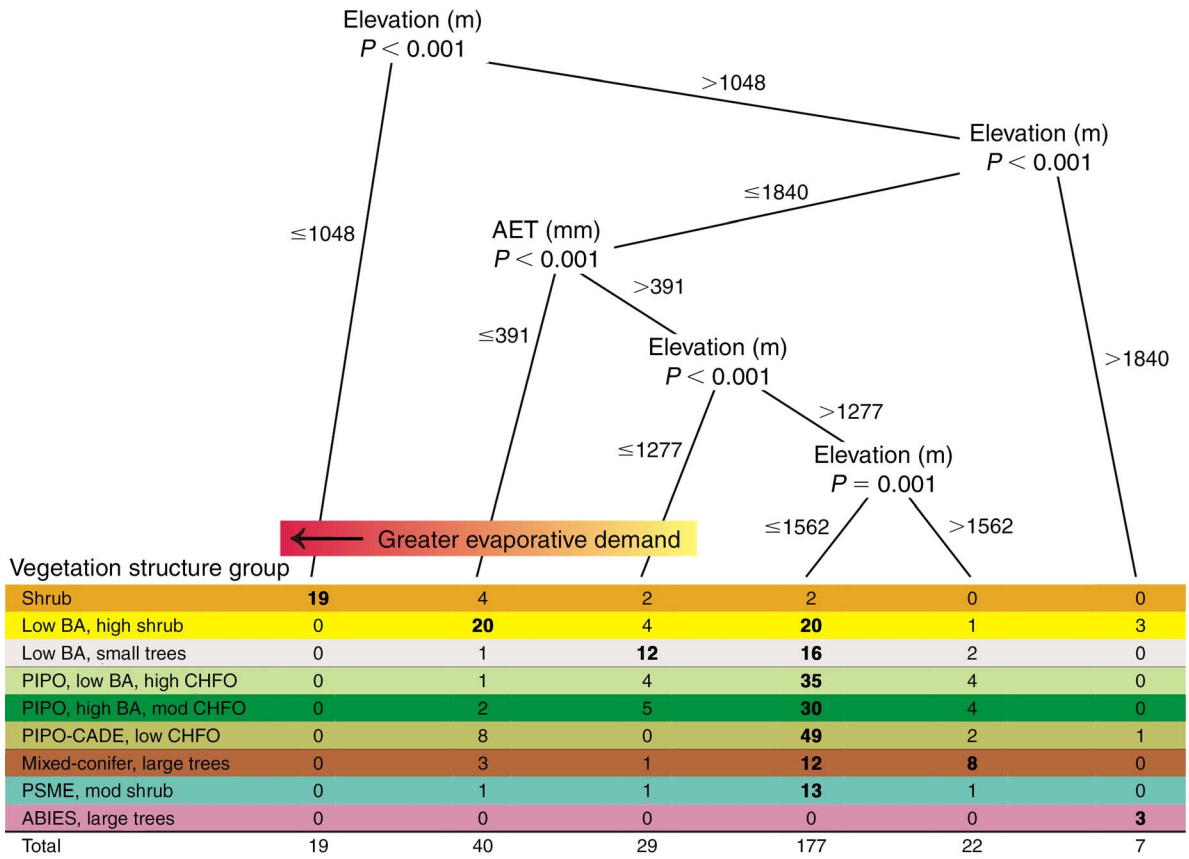

FIG. 2. Conditional inference tree output explaining the influence of elevation and actual evapotranspiration (AET) on the distribution of vegetation structure groups (abbreviations are as in Fig. 1). Numbers in the table below indicate the number of inventoried quarter-quarter sections in each terminal node, and their distribution among the nine vegetation structure groups. Numbers in bold emphasize the terminal node(s) where the majority of observations for each vegetation structure group lie.

1% of the total surveyed area, only occurred at the highest elevations (>1840 m).

Discussion

Our analyses of historical timber inventory data collected systematically across a large landscape highlight some key aspects of forest structure under an intact disturbance regime. (1) Forests were low density; mean live basal area and tree density (dbh >15.2 cm) ranged from 8–30 m^2/ha and 25–79 trees/ha, respectively, in the eight vegetation structure groups containing trees (Table 1). Furthermore, individual transect live basal areas did not exceed 39 m^2/ha (Table 1); (2) Understory and overstory structure and composition varied considerably across the landscape. This is demonstrated by the range in mean vegetation group characteristics (Table 1), as well as the distribution of vegetation groups across the study area (Fig. 1); and (3) Topographic conditions explained variability in forest structure over the landscape (Fig. 2). While these points have been demonstrated in previous studies (Brown et al. 2008, Scholl and Taylor 2010, Churchill et al. 2013, Hagmann et al. 2013), this may be the first study to provide robust quantification of both overstory and understory characteristics across a large historical landscape. These characteristics can provide guidance for restoration efforts in similar forests.

Three of the first four splits in the conditional inference tree identified factors that are generally associated with evaporative demand and overall site productivity (Fig. 2). These included two lower elevation bands, corresponding with generally hotter and drier sites having low AET, which is indicative of sites with low available moisture (Churchill et al. 2013). These areas are dominated by the shrub; low BA, high shrub; low BA, small trees vegetation groups (70% of all observations in the three terminal nodes; Fig. 2). Although the majority of the shrub group occurs in lower elevation areas (93%), only half of the historical transects in the low BA, high shrub; low BA, small trees vegetation groups occur in these areas. The other half is in the large, mid-elevation band, with no further differentiation (Fig. 2). This suggests that other mechanisms, beyond evaporative demand, are responsible for the low BA in these areas. One possible explanation is mixed-severity disturbance (e.g., fire). There are large trees present in all but one of these low BA group transects (Fig. A1), so it is unlikely that there was extensive stand-replacing fire or other disturbances, at least in the 200–400 years preceding the surveys (based on known ages of large trees in this area). What is more likely is local torching of groups of trees or small patches, or other localized disturbances such as bark beetle attacks. If indeed it was small patches of stand-replacing fire that contributed to the low BA for these two groups, the distinguishing characteristics between the groups (high shrub cover vs. high density of small trees) capture two different post-stand-replacing fire pathways: vigorous shrub response vs. abundant tree regeneration. There are a number of factors that can contribute to these two postfire pathways, but the coincident timing of favorable soil moisture conditions and tree seed availability is a critical factor for tree regeneration (Collins and Roller 2013).

Elevation was clearly a dominant factor explaining the distribution of several vegetation structure groups across our study area (Fig. 2). Elevation, via its influence on precipitation and temperature patterns, has long been noted as a driver of vegetation composition in the Sierra Nevada (Show and Kotok 1929, Barbour and Minnich 2000). The specific processes driving different vegetation assemblages are related to actual evapotranspiration and water deficit (Stephenson 1998), which in the Sierra Nevada tend to favor more pine-dominated forests in low to mid elevations and fir-dominated forests in mid to high elevations. The results from our conditional inference tree align with these observed patterns, with the ABIES, large trees group occurring exclusively in the highest elevation band, the mixed-conifer, large trees spanning the middle and upper-middle bands, and the pine-dominated groups primarily in the middle elevation band (Fig. 2). Based on results from randomization tests our historical data is shifted towards lower elevations within our study (Table A3), and hence may underrepresent vegetation groups associated with higher elevations (mixed-conifer, large trees and ABIES, large trees). However, these two groups only account for 38% of the observations in the two highest elevation bands; clearly, other vegetation groups occurred at higher elevations (Fig. 2).

Despite evidence of elevational control on the distribution of some vegetation structure groups, our conditional inference tree analysis was unable to identify factors that uniquely explained the occurrence of several vegetation groups (Fig. 2). This is most noticeable in the 1277–1562 m elevation terminal node, which included a majority of observations for six of the nine vegetation structure groups. There are two possible explanations for this. First, the scale at which we summarized vegetation structure, topography, and moisture availability may not be the optimal size or dimension to examine controls on vegetation structure and composition. This scale was dictated by the original belt transects from the timber inventory (40.2 × 402 m, or 1.6 ha). In many instances, these long and narrow transects spanned multiple aspects, slope gradients, and even slope positions, rendering the mean estimates of these variables for these transects somewhat diluted as an explanatory variable. Smaller and more regularly shaped transects or plots may have been more ideal for capturing topographic and moisture availability controls on vegetation structure, which may be better coupled at more local scales (e.g., Taylor and Skinner 2003, Lydersen and North 2012). The second possible

explanation for our inability to differentiate the occurrence of several vegetation groups is localized variability in the effects of fire or other disturbance. This variability could be a product of multiple interacting disturbances resulting in differential effects over time, or simply the effects from the most recent disturbance driven by local conditions. Under an intact fire regime, burning took place over a range of fire weather conditions, which could have influenced fine-scale patterns in vegetation, irrespective of topography (Hessburg et al. 2005). Regardless of the specific mechanisms responsible, an important point to draw from this is that variability in forest structure and composition was a salient feature in this historical landscape. With the exception of the SHRUB group in the Tuolumne River Canyon, individual vegetation groups were seldom clumped beyond four to six QQs (~60–100 ha; Fig. 1).

It is difficult to draw inference to historical disturbance regimes using forest structure data alone; multiple lines of evidence are often used (fire scars, tree establishment, death dates, etc.) to infer historical disturbance patterns (Brown et al. 2008). Despite these limitations, our historical vegetation structure and composition data indicate that extensive stand-replacing disturbances were absent this landscape. This assertion is based on the presence of large trees in the historical inventories (Table 1). For the PIPO, mixed-conifer, PSME, and ABIES groups, which accounted for 64% of the total inventory area (79% of the mid- and higher-elevation areas), mean large tree (dbh > 61 cm) densities were between 15 and 36 trees/ha (Table 1), and for individual transects large tree densities were rarely below 15 trees/ha (Appendix: Fig. A1). Open forest conditions with large trees do not rule out the possibility of fine-scale overstory tree mortality, as described previously, but they do suggest it was limited to small patches (e.g., <0.5 ha).

Our findings indicating low tree densities and our interpretations regarding historical fire effects are inconsistent with recent studies using alternate data sources to estimate historical forest conditions and fire patterns (Baker 2014, Odion et al. 2014). These studies suggest Sierran mixed-conifer forests were much denser historically, and that extensive stand-replacing fire effects were a greater component of historical fire regimes than is suggested by this work and that of others (e.g., Scholl and Taylor 2010). The large discrepancies between studies may be related to fundamental limitations of the data used by Baker (2014) and Odion et al. (2014). Beyond having the same limitation that our study has by inferring historical fire patterns from forest structure data alone, both studies have potentially biased plot and tree selections, whereas our historical data were collected systematically. Baker (2014) used witness trees of the General Land Office survey, which has been shown to be biased toward trees that were less likely to be harvested (i.e., smaller trees and/or less commercially valuable species), and hence, more likely to persist as markers for locating survey points (see Manies and Mladenoff 2000, Bouldin 2008). Odion et al. (2014) only include plot data from wilderness areas and National Parks, which in the Sierra Nevada tend to be in higher elevations. This limits the ability to make inference across the mixed-conifer zone. Additionally, Baker (2014) relied on sampling densities that consist of six to eight trees sampled per 259 ha, or 0.02–0.03 trees/ha. If historical densities were 100–200 trees/ha this sampling intensity would represent a 0.01–0.03% sample. Recall in our study we have approximately a 3% sample of the entire 16 800 ha study area.

The lack of oak species, particularly California black oak, and small trees (dbh < 15.2 cm) in our historical data indicate the inventory data we used is biased. However, other studies using independent historical data indicate that California black oak was a relatively minor component of Sierran mixed-conifer forests, representing 6–10% of total tree density (Stephens 2000, Dolanc et al. 2014) and 2% of total basal area (Stephens 2000). Based on the systematic layout of historical inventory, the depth of data collected, and the spatial scale covered, we conclude that our study is a robust reconstruction of mixed-conifer forests at the landscape scale.

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Supplemental Material

Ecological Archives

The Appendix is available online: http://dx.doi.org/10.1890/14-1797.1.sm

Data Availability

Data associated with this paper have been deposited in the USDA Forest Service Research Data Archive: http://www.fs.usda.gov/rds/archive/