Landscape-scale modeling of reference period forest conditions and fire behavior on heavily logged lands

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Abstract. Forest conditions prior to extensive land clearing are often used as a point-of-reference by ecologists and resource managers for characterizing the historical range of variability in forest conditions shaped by intact disturbance regimes. Quantitative data on forest reference conditions can be developed from forest surveys and reconstructions using dendroecology; however, these methods lack the spatial resolution needed for landscape management. In this paper, we combine predictive vegetation mapping methods with reference forest conditions inferred from early forest surveys, dendroecology, and fire simulation models to develop landscape-scale reference conditions for forest structure, forest fuels, fire frequency, and fire behavior using the Lake Tahoe Basin, California as an example.

The dendroecological reconstruction method used for the Lake Tahoe Basin forests was not sensitive to variation in decomposition rates suggesting that our method provided robust estimates of reference period forest characteristics. The cluster analysis procedure identified five forest structure types (white fir, Jeffrey pine, red fir, lodgepole pine, and subalpine) and 15 subtypes. Each forest type had a characteristic composition, density, and basal area. Our random forests approach to classifying and mapping the spatial distribution of the five dominant reference forest structure types resulted in 51.5% classification accuracy using 14 physiographic and climatic variables. The random forests model to identify subtypes within each forest group had an average percent correct classification of 47.8%. The random forests model for fire intervals explained 67% of the variance in the point fire return interval estimates from fire-scarred trees. Estimates of reference period fuels modeled from stand structure suggested moderate fuel loads for reference forests. The predicted potential fire type for forest subtypes under extreme weather was surface fire except for red fir and the lodgepole pine subtypes with potential for crown fire. By characterizing the reference forest composition, structure, and disturbance frequency with a range of variability, managers can develop a forested landscape more resilient to changes in disturbance regime and climate. Although our approach was developed for the Lake Tahoe Basin, California, it could be applied to a wide range of forest landscapes to identify forest reference conditions.

Key words: dendroecology; ecological modeling; fire behavior; forest reconstruction; fuels; historical ecology; Lake Tahoe; predictive vegetation mapping.

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INTRODUCTION

Forest conditions at the time of Euro-American settlement and prior to extensive land clearing are often used as a point of reference by ecologists and resource managers for characterizing the historical range of variability in forest conditions shaped by intact disturbance regimes (i.e., wildfire; Kaufman et al. 1994, Swanson et al. 1994, Landres et al. 1999, Swetnam et al. 1999). Reference conditions are also used as a source of information for identifying restoration goals and the types of treatment that might be used in places where contemporary forest conditions are approaching a bounded range of variation (Moritz et al. 2013) or have moved outside their historical range of variability (Morgan et al. 1994, White and Walker 1997, Moore et al. 1999, Swetnam et al. 1999, Taylor 2004, Larson and Churchill 2012, Wiens et al. 2012). Presumably, moving highly altered forests towards conditions within the historical range of variability should increase their resilience to wildfire and reduce the risk of unexpected outcomes such as vegetation type conversions caused by unusually severe wildfire related to high fuel loads from logging and or fire exclusion (Weatherspoon and Skinner 1996, Landres et al. 1999, Moore et al. 1999, Savage and Mast 2005, Odion et al. 2010). Consequently, identifying reference conditions is a key step in the ecosystem management-restoration planning process but it is a particularly challenging task in locations where most if not all of the pre-settlement forests have been removed by logging and other types of human activity (Landres et al. 1999, Swetnam et al. 1999, Scholl and Taylor 2010, Wiens et al. 2012).

Quantitative data on forest reference conditions can be developed from various sources including early land surveys and forest reconstructions using dendroecology (Fulé et al. 1997, North et al. 2007, Scholl and Taylor 2010, Collins et al. 2011). In the western USA, late-19th century General Land Office (GLO) surveys have been used to estimate forest structure before areas were logged or cleared for grazing or other uses. GLO survey data have limitations including surveyor bias in tree selection (species and size), violation of the assumption of random tree distribution, and small sample size that affect estimates of forest structure (i.e., density, basal area, and size structure; Bourdo 1956, Bouldin 2008, Hanberry et al. 2011). Despite statistical modifications (Anderson et al. 2006, Bouldin 2008, Williams and Baker 2011, Hanberry et al. 2012), GLO estimates of forest structure and species composition lack sufficient detail to guide forest restoration management because the scales of aggregation (i.e., number of survey points) used to estimate forest attributes are difficult to interpret with known degrees of confidence (Bouldin 2008, Hanberry et al. 2011, Williams and Baker 2011). For example, Williams and Baker (2011) assessed the scales of aggregation needed to estimate Ponderosa pine (Pinus ponderosa) forest density using GLO data and found that tree density was estimated well only by pooling data from widely spaced (0.8–1.6 km) point measurements of two to four trees each over an area 2.6–5.2 km². Estimates of basal area, species composition, and diameter-class distributions required pooling data across even larger areas (>7.8 km²) with the least accurate estimates for forest size structure (Williams and Baker 2011). Spatial heterogeneity in structural attributes (density, size, age, basal area), which is a hallmark of many ponderosa pine and dry mixed conifer forests (Cooper 1960, White 1985, Youngblood et al. 2004, Beaty and Taylor 2007, Scholl and Taylor 2010, Larson and Churchill 2012) occurs mainly at small spatial scales (<0.4 ha; Larson and Churchill 2012) and is not well captured by small point samples from aggregated samples (Bouldin 2008, Hanberry et al. 2011). This could lead to misguided goals and objectives for restoration of forest structural conditions typical of forests with an intact fire regime.

Quantitative data on forest structure (i.e., density, basal area, size structure, and volume) in newly established national forests were collected by the US Forest Service in 1911 (Scholl and Taylor 2010, Collins et al. 2011) and in the 1930s (Wieslander 1935, University of California-Berkeley 2006), and have been used as reference conditions in California. Comparisons of survey data with current conditions in the same locations have been used to identify forest change caused by climate change, logging, fire suppression, or other land use practices (Scholl and Taylor 2010, Collins et al. 2011, Dolanc et al. 2013). However, detailed forest survey data on presettlement forest conditions is sparse in most...
forested ecosystems. Quantitative data on stand structure and species composition can also be developed using dendroecology (Füle et al. 1997, 2002, Huffman et al. 2001, Scholl and Taylor 2010). Dendroecological techniques provide data on forest structure (i.e., species composition, density, size structure, basal area) and disturbance history (e.g., type, frequency, return interval, and severity) in plots (e.g., Mast et al. 1999) or across landscapes (e.g., Brown 2006, Scholl and Taylor 2010) but studies are generally focused on a single forest type (but see Cocke et al. 2005) over limited areas (1–2000 ha). While land and forest surveys provide broad-scale coverage of early forest conditions, they may lack detail on forest structure and disturbance regime dynamics that can be inferred from dendroecological studies.

Combining dendroecological and forest survey data with the method of predictive vegetation mapping has the potential to provide landscape-scale representations of forest reference conditions and disturbance regimes across landscapes that can be used to guide restoration management of highly altered forests. Establishing the relationship between vegetation structure, disturbance, and site conditions (e.g., moisture and temperature) is an interpretation and extension of ecological niche theory (Chase 2011) and is the basis for predictive vegetation mapping. There is a long history of interpreting how variability in forest composition and structure is related to site conditions (e.g., Bray and Curtis 1957) and environmental gradients (Whittaker 1973, Kessel 1977) in temperate forest ecosystems. Predictive vegetation mapping, in contrast, uses established relationships between vegetation, disturbance, and site conditions to predict the geographic distribution of the vegetation composition across a landscape from mapped environmental variables (Franklin 1995, De’ath and Fabricus 2000, Cutler et al. 2007). Predictive vegetation models are usually developed for current conditions and use spatially explicit data on forest vegetation (i.e., species distribution and abundance) interpreted from remote sensing imagery and site data (e.g., slope, aspect, and elevation) derived from digital elevation models to predict vegetation community type.

In this paper, we combine predictive vegetation mapping methods with reference forest conditions inferred from early forest surveys, dendroecology, and fire simulation models to develop landscape-scale reference conditions for forest structure, forest fuels, fire frequency, and fire behavior for the Lake Tahoe Basin (LTB). We chose the LTB to implement our approach because most forests in the basin were heavily logged in the late 19th century, and forest density and fire hazard have increased significantly and are the focus of restoration management (Chrisopherson et al. 1996, Taylor 2004, Raumann and Cablk 2008, Safford et al. 2009). Our specific research objectives were to: (1) dendroecologically reconstruct reference period forest types using sites in the LTB and similar forested ecosystems in the Sierra Nevada and southern Cascades; (2) develop a predictive vegetation model to distribute reference forest conditions across the landscape; (3) develop a predictive fire frequency model using dendroecologically reconstructed fire histories from sites in the LTB and similar forests in the Sierra Nevada and southern Cascades, and then (4) estimate surface fuel loads and fire behavior for reference forest conditions distributed across the landscape. Although our approach was developed for the LTB, it could be applied to a wide range of forest landscapes to identify forest reference conditions at landscape scales.

**Methods**

**Study area**

Euro-Americans first traveled through the Lake Tahoe region in 1844 but large numbers of Euro-Americans did not settle in the basin until the 1860s. The discovery of the Comstock Lode silver ore deposit in 1859 initiated intense logging in the basin to provide timber for mining operations (Strong 1984). Logging is estimated to have reduced the area of forest present in the mid-19th century by 67%, and old growth stands are currently very rare in low and middle elevation forests (Manley et al. 2000, Barbour et al. 2002). The climate is Mediterranean with cool, wet winters and warm, dry summers. Most precipitation (80%) falls as snow in the winter. A temperature and precipitation gradient exists in the LTB going from west to east across the lake. Mean monthly temperatures at Tahoe City, California on the west shore of Lake Tahoe range.
from −1.4°C in January to 15.9°C in August, and mean annual precipitation is 83.8 cm. On the east shore of Lake Tahoe, mean monthly temperatures at Glenbrook, Nevada range from 0.5°C in January to 17.8°C in August, and mean annual precipitation is 45.7 cm.

**Reference period forest reconstruction**

Because the LTB was so thoroughly logged in the late 19th century, published studies of old growth forest are geographically and topographically limited. We chose to supplement the local data with data from completed studies of more extensive old growth forests in Lassen Volcanic National Park (LAVO) and Yosemite National Park (YNP) in order to better represent variation in forest structure associated with different site characteristics (e.g., slope, aspect, and elevation). LAVO and YNP are found on the western slope of the Sierra Nevada (Fig. 1) and receive somewhat more precipitation than the LTB, but the same species dominate forests in the three locations. For the LTB, plot and stand-level data (400-m² plots and 300-m transects with 10 sampling points; N = 185 plots or transects) on reference period forest structure were obtained for studies summarized in Taylor (2000b, 2004), Barbour et al. (2002), Nagel and Taylor (2005), Scholl and Taylor (2006), Beaty and Taylor (2007, 2008), and Taylor et al. (2014). For reference period conditions in Lassen Volcanic National Park (LAVO), plot and stand-level data (200–5000-m² plots; N = 203 plots) were gathered from previous studies including those in Taylor (1990, 2000a). For Yosemite National Park (YNP), plot and stand-level data (800-m² plots; N = 399) were gathered from the Vegetation Type Mapping Project conducted by A. E. Wieslander in the 1930s (Wieslander 1935; http://vtm.berkeley.edu/). We eliminated Wieslander plots with trees species not represented in the LTB (e.g., *Quercus* spp.) and plots outside the elevation range of the LTB (<1,891 m and >3,318 m). Wieslander recorded stems by species in 30 cm size-classes (i.e., 10–30, 31–60, 61–90, and 90+ cm), necessitating the aggregation of the LTB and LAVO datasets into 30 cm size-classes for classification and modeling purposes.

For the LTB and LAVO datasets, forest conditions for the reference period were reconstructed for plots in uncut forests using dendroecological methods (Fulé et al. 1997). The reference dates for the forest reconstructions varied by location and date of the last widespread fire. Few fires were recorded after 1880 in fire scar samples from forests on the west or east shore of Lake Tahoe (Taylor 2004, Nagel and Taylor 2005, Beaty and Taylor 2007, 2008). In LAVO, the reference period (representing the pre-fire suppression period for our study) ended in 1904 (Taylor 2000b). Reconstructing forest conditions for earlier dates in the LTB and LAVO would be less precise because woody material in the forest would have been consumed by later fires. In YNP, the reference period continued until 1899 in some mixed conifer stands in the park (Scholl and Taylor 2010). Three decades later, Wieslander (1935) surveyed the forest vegetation in the park and found some evidence of recent fires. Even if fire was not widespread on the landscape, it is unlikely that regeneration from 1900 to 1930s would have grown into the 10–30 cm size class at the time of Wieslander’s surveys. Consequently, we used Wieslander’s 1935 plot data in YNP as a representation of reference forest structure and they were not reconstructed further back in time.

Forest conditions for the reference period in the LTB were reconstructed using measurements of the contemporary forest and the following reconstruction procedure modified from Fulé et al. (1997, 2002): (1) for complete tree cores, the diameter of live trees in 1880 was determined by subtracting the radial growth from 1880 to the contemporary sampling date; (2) for incomplete tree cores, the diameter of live trees in 1880 was determined by subtracting species-specific average annual radial growth, estimated from cored trees >100 years old (n = 1509), from the measured diameter for each year from 1880 to the contemporary sampling date; (3) the death date for dead and down trees was estimated using tree decay class (Maser et al. 1979) and cumulative species-specific decomposition rates calculated from diameter-dependent equations (Thomas 1979, Rogers 1984); (4) decomposition rates for each species were calculated for slow (25th percentile), median (50th percentile), and fast (75th percentile) decomposition to evaluate the sensitivity of estimated death date and forest structure to decomposition rates for individual trees; and (5) the diameter of dead and down
trees that were alive in 1880 was estimated by subtracting species-specific average annual radial growth from the measured diameter for each year from 1880 to the estimated death date, and then adjusting diameters for bark loss. The same methodology was used to reconstruct reference conditions with the LAVO dataset except the target year of reconstruction was 1904 and only the 50th percentile was used because less detailed decay classes were recorded during data collection.

Reference period forest structure types

Groups of plots (N = 745) with similar reference period forest structure and composition were identified using cluster analysis. First, a
matrix was developed using the density (no./ha\(^{-1}\)) of each tree species in 30-cm size classes for each plot. Species included white fir (\textit{Abies concolor}), red fir (\textit{Abies magnifica}), Jeffrey pine (\textit{Pinus jeffreyi}) or ponderosa pine (\textit{Pinus ponderosa}), sugar pine (\textit{Pinus lambertiana}), lodgepole pine (\textit{Pinus contorta var. murrayana}), western white pine (\textit{Pinus monticola}), incense cedar (\textit{Calocedrus decurrens}), and mountain hemlock (\textit{Tsuga mertensiana}) (nomenclature follows Hickman 1993). While other tree species are locally abundant in the LTB such as quaking aspen (\textit{Populus tremuloides}) and whitebark pine (\textit{Pinus albicaulis}), we were not able to locate suitable old-growth sites for reconstruction, necessitating removal of plots with these species for modeling purposes. Next, we used Ward’s method and relative Euclidean distance to cluster plots and identify forest structure types (McCune et al. 2002). A multi-response permutation procedure was used to assess the group discrimination of the cluster analysis (MRPP; McCune et al. 2002). Evaluation of the MRPP resulted in five forest structure types. The clustering and MRPP procedure was then repeated for plots within each structure group to identify 15 forest structure subtypes.

Then, we compared our results to the GLO survey of the LTB conducted from 1861 to 1897. The GLO data include approximately 2600 measurements of trees collected at the corners and quarter-corners as witness trees during land surveys of the \~80,000 ha of land area in the watershed. While the data are coarse and have well-known limitations (Bourdo 1956, Williams and Baker 2011), they provide broad estimates of forest density and basal area near the time of initial Euro-American settlement in the LTB. We calculated basin wide forest density (stems·ha\(^{-1}\)) and basal area (m\(^2\)·ha\(^{-1}\)) using the median distance (rather than mean distance) to tree measurement data and a point-quarter method (Cottman and Curtis 1956). This approach may be more appropriate because the distribution of distances to trees was not normally distributed (Shapiro-Wilk test, \(W = 0.72, p < 0.0001\)) making the median a more accurate measure of central tendency.

**Spatial model of forest reference conditions**

The distribution of the five forest structure types and 15 forest structure subtypes across the LTB landscape was determined using topographic and climatic variables associated with each of the 745 source plots and their designated forest structure type and subtype, and a random forests model. Random forests models are an extension of classification and regression trees (CART); however, rather than building a single CART model, random forests models build hundreds of CART models using randomized subsets of plots and their associated explanatory variables (Cutler et al. 2007). Each CART is a bootstrapped sample representing \~63% of the dataset, with a remaining portion (out-of-bag observations) used to test the percent correct classification of the CART model. Then, the predictions for each of the many CART models are combined to identify the strongest explanatory variables for the random forests model. Further explanation of CART and random forests is available in De’ath and Fabricus (2000) and Cutler et al. (2007), respectively.

Fourteen topographic and climate variables were determined for each plot including 11 variables generated from 100-m (1-ha resolution) digital elevation models (DEM; Appendix: Tables A2 and A3). We used a 1-ha resolution because it represents a unit of scale useful for forest management and maintains variability in topography that may influence forest structure and composition in a mountainous landscape. DEM-derived variables included elevation (m), slope (\(^{\circ}\)), northness and eastness (a measure of aspect that ranges from -1 [south or west] to +1 [north or east]), average daily solar radiation computed over a year (kWh·m\(^{-2}\)), total seasonal solar radiation (winter, spring, summer, and fall; kWh·m\(^{-2}\)), topographic wetness index (TWI; a measure of moisture availability derived from topography), and topographic position index (TPI; location on the landscape relative to the surrounding pixels). We also extracted average maximum and minimum temperature and average annual precipitation (1971–2000; 800-m resolution) for the location of each plot from the PRISM Climate Group (2011). Climate variables were scaled to a 1-ha resolution by assigning the value of the 800-m PRISM pixel to the centroids of the 100-m pixels included in the larger grid. While this method of downscaling is crude, our primary objective was to capture the strong
precipitation and temperature gradient from west to east across the LTB that would affect site and forest conditions. We also note that 30-year normals for the contemporary period do not represent the absolute values of reference period climate.

We considered additional variables including soil characteristics and vegetation indices derived from remote sensing products but changes in land use (i.e., logging) have altered soil properties and vegetation from their reference, rendering these variables unsuitable for the random forests model. We removed non-vegetated (i.e., barren or rock) locations and areas dominated by shrubs by clipping areas of these cover types >10 ha from the reference period forest structural type maps. We identified non-vegetated areas >10 ha from the Tahoe Basin Existing Vegetation Map layer (v. 4.1; Greenberg et al. 2006) in a GIS. It is assumed that some non-vegetated and shrub dominated areas existed in the reference period. For these locations <10 ha, our maps represent the potential forest structure type on that site.

Finally, we developed a map of forest types using the GLO data to compare with the reference forest structure types. Each GLO tree was classified into a forest type matching one of the main forest structure types that were identified by our model. This classification was conducted by assigning a witness tree to the dominant forest structure type that it represented. We allowed higher elevation forest types to be plotted on top of lower elevation forest types in a GIS for visual comparison to the mapped reference forest. Then, we quantified the classification error of the random forests model by asking if the assigned GLO forest type at each witness tree point matched the modeled forest structure type for the cell overlapping that same point.

**Reference period fire frequency, fuels, and fire behavior**

Data on reference period fire regimes and topography were compiled from the location of wood samples with crossdated fire scars from studies in the LTB (n = 134) and LAVO (n = 92) (Taylor 2000b, Nagel and Taylor 2005, Taylor and Beaty 2005, Scholl and Taylor 2006, Beaty and Taylor 2007, 2008). These samples provided data on reference period point fire return interval (PFRI) and season of fire in lower (i.e., Jeffrey pine and Jeffrey pine/white fir) and upper (i.e., red fir/western white pine) montane forests. Samples represented a broad range of elevation (1901–2460 m), slope (2–64°), and aspect (0–360°).

The distribution of reference PFRI across the landscape was also determined using a random forests model with seven DEM-derived explanatory variables (i.e., elevation, slope, TPI, TWI, average daily solar radiation, and northness/eastness) for each fire scar sample. The random forests model of PFRI differed from the random forests model of forest structure types and subtypes because PFRI is a continuous variable and goodness of fit statistics ($r^2$) on the out-of-bag samples are reported rather than percent correct classification.

The Fire and Fuels Extension of the Forest Vegetation Simulator (FFE-FVS; Western Sierra Variant) was used to estimate fuel loads from the list of trees (species and diameter) for each subtype. Surface fuel estimates were output by time-lag size class (i.e., 1-hr, 10-hr, and 100-hr). The surface fuel estimates were then used to identify the most similar standard surface fuel model (i.e., Anderson 1982, Scott and Burgan 2005) for each subtype using FFE-FVS. FFE-FVS was then used to estimate canopy fuel variables (i.e., canopy bulk density, canopy base height, and stand height) for each subtype.

We used FFE-FVS and standard fuel models to estimate potential fire behavior for each subtype. Standard surface fuel models were used, rather than custom models, because the standard models have been calibrated with observed fire behavior under conditions similar to those simulated in the model runs (Rothermel and Rinehart 1983, Burgan and Rothermel 1984). To more accurately evaluate potential crown fire behavior for each subtype, we added seedlings and saplings to each subtype tree list based on estimates from previous research (Parker 1989, Taylor 2004, Stephens and Gill 2005, Scholl and Taylor 2006, Beaty and Taylor 2007).

Fire behavior is strongly influenced by fire weather conditions and fuel moisture (Reinhardt and Crookston 2003). We were interested in simulated fire behavior under the most extreme fire weather conditions. Consequently, we used 98th percentile weather conditions for our simulations of potential fire behavior. FireFamily Plus
Table 1. Reconstructed mean diameter, basal area, and density for the reference forest in the LTB estimated using three decomposition condition models (25th percentile, 50th percentile, 75th percentile).

| Characteristic | 25th | 50th | 75th |
|---------------|------|------|------|
| Diameter (cm) | 36.8 | 37.1 | 36.3 |
| Basal area (m²·ha⁻¹) | 40.5 | 37.5 | 35.7 |
| Density (stems·ha⁻¹) | 235.1 | 217.5 | 212.4 |

Notes: Values are for trees >10 cm dbh. Decomposition classes were not significantly different for the three variables (p < 0.05, ANOVA).

Table 2. Reference forest structure type characteristics including percent area coverage of the LTB determined from the spatial reconstruction model, median density (lower and upper quartile), median basal area (lower and upper quartile), and relative abundance (%) of each species.

| Forest type     | Area (%) | Wilcox means comp† | Median density (stems·ha⁻¹) | Median basal area (m²·ha⁻¹) | Relative abundance (%)‡ |
|-----------------|----------|---------------------|----------------------------|-----------------------------|--------------------------|
| White fir       | 24.9     | A                   | 200 (125, 92)              | 41.1 (23.9, 70.9)           | G1 17.0 14 6.0 9.6 0.7 0.4 0.0 |
| Jeffrey pine    | 20.4     | B                   | 113 (70, 189)              | 29.6 (14.3, 44.9)           | G1 21.4 69.9 2.8 1.9 3.6 0.2 0.1 0.0 |
| Red fir         | 47.6     | C                   | 228 (150, 351)             | 54.8 (32.3, 83.8)           | G1 4.1 3.2 0.6 1.3 71.9 3.1 14.9 0.9 |
| Lodgepole pine  | 5.9      | D                   | 289 (160, 420)             | 45.1 (18.1, 69.2)           | G1 1.6 1.5 0.0 0.0 8.8 82.0 3.0 3.0 |
| Subalpine pine  | 1.1      | E                   | 330 (260, 527)             | 50.7 (30.9, 76.5)           | G1 0.0 0.0 0.0 0.0 6.2 16.5 11.0 65.8 |

† Forest types with the same letter for the Wilcox means comparison test do not have significantly different mean total densities (p < 0.05).
‡ WF = white fir (Abies concolor); JP = Jeffrey pine (Pinus jeffreyi); IC = incense cedar (Calocedrus decurrens); SP = sugar pine (Pinus lambertiana); RF = red fir (Abies magnifica); LP = lodgepole pine (Pinus contorta); WP = western white pine (Pinus monticola); MH = mountain hemlock (Tsuga heterophylla).
The upper montane forest types, RF and LP, had more basal area and were denser than lower elevation JP and WF forests. High elevation SA forests were the densest with high basal area, and they were dominated by mountain hemlock. The overall GLO basin density and basal area was 147 stems/ha and 52.4 m²/ha, respectively, falling within the range of values calculated for the reference forest structure types.

The clustering and MRPP procedure used on plots in each forest group yielded 15 forest subtypes (Table 3 and Fig. 2). The JP, RF, and LP types had three subtypes, the WF group had four subtypes, and the SA group had two subtypes. Subtypes were distinguished by the dominant one or two species in the group and a “small”, “mid”, or “large” diameter descriptor for the size of the dominant species where appropriate. The “small” subtypes showed reverse J-shaped distributions for the dominant species (Fig. 2). The peak in the diameter distribution shifted to the right for the “mid” and “large” diameter types. Individual subtypes were co-dominated by varying amounts of other species highlighting the variability within main forest structure group. For example, the Small RF subtype was >80% red fir whereas the RF-WP subtype was >50% white pine. Not all subtypes were evenly distributed across the basin ranging from <1% coverage to 36.9% (Table 3).

### Spatial model of forest reference conditions

The random forests model had an overall plot-level correct classification of 51.5% for the forest structure types and a kappa of 0.37 (Table 4). However, when the WF and JP types were cross-classified to either group to account for the overlap of these species in JP and WF forests, the overall fuzzy correct classification increased to 62.7% (fuzzy correction followed Gopal and Woodcock 1994, Grossmann et al. 2010). Prior to fuzzy correction, the JF forest structure type was classified as WF 45% of the time leading to possible spatial inaccuracies when mapping forest types and over-representing the historic distribution of WF. The RF group had the highest correct classification (62.3%), and the JP and WF fuzzy correct classification was 74.8% and 71.5%, respectively.

Spatial variation in forest type was most strongly related to elevation followed by maximum temperature, slope, minimum temperature, and A3). The upper montane forest types, RF and LP, had more basal area and were denser than lower elevation JP and WF forests. High elevation SA forests were the densest with high basal area, and they were dominated by mountain hemlock.

The overall GLO basin density and basal area was 147 stems/ha and 52.4 m²/ha, respectively, falling within the range of values calculated for the reference forest structure types.

### Table 3. Mean elevation, percent area coverage of the LTB determined from the spatial reconstruction model, median density, basal area, and relative abundance by species for the 15 reference forest structure subtypes by forest type.

| Forest type and subtype | Mean elevation (m) | Basin coverage (%) | Median density (stems/ha⁻¹) | Median basal area (m²/ha⁻¹) | Relative abundance (%)†‡ |
|-------------------------|-------------------|-------------------|-----------------------------|-----------------------------|---------------------------|
| White fir               |                    |                   |                             |                             |                           |
| Small WF-JP             | 2058              | 23.6              | 206.5                       | 30.7                        | 78.5                      |
| WF-JP-SP                | 2093              | 0.1               | 154.0                       | 61.4                        | 45.1                      |
| WF-RF-JP                | 2107              | 1.1               | 220.0                       | 50.2                        | 48.2                      |
| Mid WF-JP               | 2157              | 0.1               | 182.5                       | 45.0                        | 67.1                      |
| Jeffrey pine            |                    |                   |                             |                             |                           |
| Small JP-WF             | 2084              | 1.2               | 150.0                       | 24.7                        | 24.0                      |
| Mid JP-WF               | 2133              | 2.9               | 93.0                        | 27.3                        | 26.2                      |
| Large JP-WF             | 2166              | 16.3              | 95.1                        | 39.8                        | 12.8                      |
| Red fir                 |                    |                   |                             |                             |                           |
| Small RF                | 2281              | 0.02              | 300.0                       | 58.9                        | 3.7                       |
| Mid-large RF            | 2349              | 36.9              | 225.0                       | 56.7                        | 4.4                       |
| RF-WP                   | 2466              | 10.7              | 178.0                       | 46.4                        | 4.2                       |
| Lodgepole pine          |                    |                   |                             |                             |                           |
| Small LP                | 2175              | 0.8               | 351.0                       | 54.2                        | 0.1                       |
| LP-RF                   | 2588              | 0.3               | 264.5                       | 59.6                        | 0.2                       |
| LP-WF                   | 2754              | 4.8               | 200.0                       | 51.5                        | 6.2                       |
| Subalpine               |                    |                   |                             |                             |                           |
| MH-RF                   | 2668              | 0.7               | 340.0                       | 66.5                        | 0.1                       |
| MH-WP                   | 2717              | 0.5               | 322.0                       | 46.1                        | 0.0                       |

† Subtypes were named by the dominant one or two species in the group and a “small”, “mid”, or “large” diameter descriptor for the size of dominant species where appropriate. ‡ See Table 2 for description of abbreviations.
Fig. 2. Relative abundance of stems in 30 cm size classes (i.e., 10–30 cm, 31–60 cm, 61–90 cm, 90+ cm) for the 15 reference forest structure subtypes. WF = white fir (Abies concolor); JP = Jeffrey pine (Pinus jeffreyi); IC = incense cedar (Calocedrus decurrens); SP = sugar pine (Pinus lambertiana); RF = red fir (Abies magnifica); LP = lodgepole pine (Pinus contorta); WP = western white pine (Pinus monticola); MH = mountain hemlock (Tsuga mertensiana).

Table 4. Plot-level accuracy statistics for the random forests model for reference forest structure types.

| Forest type   | White fir | Jeffrey pine | Red fir | Lodgepole pine | Subalpine | Row total | Percentage correct | Percentage fuzzy correct | GLO percentage correct† |
|---------------|-----------|---------------|---------|----------------|-----------|-----------|---------------------|----------------------------|--------------------------|
| White fir     | 83        | 30            | 35      | 10             | 0         | 138       | 52.5                | 71.5                       | 25.4                     |
| Jeffrey pine  | 53        | 36            | 23      | 7              | 0         | 119       | 30.3                | 74.8                       | 57.8                     |
| Red fir       | 29        | 12            | 129     | 30             | 7         | 207       | 62.3                | ...                        | 66.3                     |
| Lodgepole pine| 14        | 7             | 37      | 113            | 23        | 194       | 58.2                | ...                        | 16.7                     |
| Subalpine     | 0         | 0             | 11      | 33             | 23        | 67        | 34.3                | ...                        | 28.6                     |
| Column total  | 179       | 85            | 235     | 193            | 53        | 745       | 51.5                | 62.7                       | 50.3                     |

Kappa 0.37 0.51 0.37

Note: The diagonal values in bold italic type show correct classification.
† For the Percentage fuzzy correct, the white fir and Jeffrey pine types were considered correctly classified if either white fir or Jeffrey pine was chosen as a classification. This adjustment allowed for the overlap that is common in mixed conifer forests.
‡ GLO percentage correct is the assessment of classification error between the GLO forest structure types and the modeled reference forest structure types.
annual precipitation, and summer solar radiation (Fig. 3a; Appendix: Tables A2 and A3). The spatial distribution of forest types exhibited several distinct patterns (Fig. 4). First, the JP and WF types each covered 20–25% of the LTB and were dominant at lower elevations, but the JP (WF) group was more widespread on the east (west). Second, the RF group covered nearly half of the LTB and occupied the elevational belt above the JP and WF types, ringing the basin. Third, the LP group had a bimodal distribution and occupied high elevation sites above RF and mesic low elevation flats. Fourth, the SA group was restricted to high elevation areas above the RF and LP types. In combination, SA and LP forests only covered 7% of the LTB.

The random forests model to identify subtypes within each forest group had an average percent correct classification of 47.8% (Appendix: Table A4). The JP subtype model had the highest correct classification and the SA subtype model had the lowest. Kappa values were lower (range 0.06–0.38) for the subtypes than forest group models but the values suggest that the models provide additional understanding of the controls on spatial variability within the forest structure types.

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The spatial distribution of subtypes shows that some subtypes were more prevalent than others (Fig. 4, Table 3). In the JP group, the Large JP-WF subtype covered the largest area and occupied moister and higher elevation sites than other JP subtypes. The most widespread subtype in the WF group was Small WF-JP, occupying moister and lower elevation sites than other subtypes in this group. In the RF group, the Mid-large RF subtype was the most widespread and occupied mesic mid-elevation sites. The most widespread subtype in the LP group was LP-WF which occupied moist low elevation sites. In the SA group, the MH-RF and MH-WP subtypes were almost equally spread in the subalpine zone where they occupied lower and upper slope positions, respectively.

At the basin scale, the GLO map captures the same general features present in the reference period forest structure type map including: (1) the WF and JP forest types split on the west and east shores; (2) the RF type just above the WF and JP forest types in elevation; (3) the LP type located in the higher elevations as well as in the flat, low elevation sites; and (4) the sparse SA type at the highest elevations (Appendix: Fig. A2). We found that our model correctly classified 50.5% of the GLO survey points with the strongest and weakest classification in the RF (66.3% correct) and LP (16.7% correct) forest types, respectively (Table 4). Again, the classification of WF was problematic with only 25.4% accuracy suggesting that our model over-predicted the spatial distribution of WF.

Reference period fire frequency, fuels, and fire behavior

The random forests model for fire intervals explained 67% of the variance in the PFRI estimates from fire-scarred trees. PFRI was most strongly related to elevation followed by slope, TPI, TWI, and annual solar radiation (Fig. 3b). Modeled PFRI values ranged from 13 to 95 years.
Appendix: Fig. A3) and the random forests model demonstrated the strong relationship between PFRI and elevation in the LTB.

Estimates of surface fuels varied by reference forest subtype (Appendix: Table A5). On average, the RF subtypes had the greatest amount of surface fuels ranging from 6.1–8.2 mg ha$^{-1}$ and the LP subtypes had the least (3.3–5.7 mg ha$^{-1}$). FFE-FVS selected the TL5 model as most similar to the surface fuel estimates in all subtypes. Canopy fuel characteristics varied among forest subtypes (Appendix: Table A6). Canopy bulk density was higher for RF and LP (range 0.03–0.12 kg m$^{-3}$), and lower for JP, WF, and SA.
subtypes (range 0.02–0.07 kg m⁻³). Canopy base height was lowest in the RF subtypes (2.4 m for all RF subtypes) and greatest in the JP and LP subtypes (9.1–13.7 m). Stand heights were greatest in RF (range 34.1–37.2 m) and lowest in JP (range 22.3–29.6 m).

Potential fire behavior under the 98th percentile fire weather conditions was lower for reference fuel conditions in JP subtypes than in other forests as evidenced by the less extreme torching and crowning indices and prediction on surface fires only (Table 5). The rate of spread and probability of torching in the JP subtypes suggest that the surface fires will be quick
moving but only torch individual trees or small patches. Although there was variability in flame length, rate of spread, crowning index, and torching index among subtypes in the other forest types, only the RF subtypes experienced passive crown fire under the heaviest fuel loadings (i.e., FB10). The LP-RF subtype also showed potential for conditional crown fire with a crowning index exceeding 20-ft windspeed but a torching index below the threshold, suggesting that sufficient canopy fuels exist to carry a crown fire under any fuel model conditions. Fire type for all other subtypes was classified as surface. Nevertheless, all subtypes showed potential for torching with fuel models characteristic of higher fuel loads (i.e., TL5 and FB10).

**DISCUSSION**

**Reference period forest reconstruction**

Our reconstruction of reference period forest composition and structure for the LTB and LAVO combined with early survey data from YNP provides a robust estimation of stand-level forest conditions prior to major Euro-American settlement in the northern Sierra Nevada and southern Cascade region. However, the dendroecological methods we used were dependent on the presence of live and dead trees at each sampling location. Fire, logging, and decay can eliminate the evidence required for reconstruction (Speer 2010). Selection of sampling sites that ceased burning in the late 19th and early 20th century made it unlikely that woody material was consumed over the past century or more. Additionally, the majority of the sites consisted of uncut old-growth forest or well-preserved stumps that provided an anthropogenically undisturbed data source.

The decay of dead trees can only be addressed by understanding species-specific decay rates and assessing the sensitivity of decay rates on reference period forest structure. The slow, median, and fast decomposition models were used to provide a range of variability in the estimated death date by changing the speed at which a dead tree moves from one decay class to another. Tree decay is controlled by site conditions, species type, and tree size. The Mediterranean climate persistent across our sampling region slows the decay process with warm, dry summers and the majority of precipitation falling as snow during the winter months. Even in a dry climate, some species types are more resistant to decay than others because of the greater concentration of resins or pitch in the wood that inhibit fungal growth (Phillips and Croteau 1999). However, in California forests, decay rates between Abies and Pinus spp. have been found to be similar (Harmon et al. 1987). The earliest death date estimate for trees in our stands using the slow decomposition model was ~1933 for both Pinus and Abies species. This suggests that trees that died between 1880 and ~1933 may be unaccounted for in our reconstruction because of complete decomposition. The decay of small stems following the last known fire would result in an underestimation of the frequency and basal area of small stems (Fule´ et al. 1997, Scholl and Taylor 2010, Taylor et al. 2014). Our forest reconstruction did not reconstruct understory stems <10 cm and is likely to underestimate density and basal area because it is difficult to reconstruct small diameter stems (Fule´ et al. 1997). However, the contribution of large diameter stems to the total basal area would be less affected unless tree death and complete decomposition occurred within the first several decades following fire secession (Taylor et al. 2014).

We assessed the sensitivity of our reconstruction to variation in decay rates and their effect on stand density and basal area but found no statistical difference between the mean stand conditions for low, median, and high rates. Similarly, a sensitivity analyses for mixed conifer stands in YNP demonstrated that estimates of reference period density, basal area, and diameter were not strongly influenced by the decomposition conditions used to estimate tree death date (Scholl and Taylor 2010). Moreover, Scholl and Taylor (2010) found that the reconstructed density and basal area for the reference year 1899 was statistically similar to values from a 1911 forest survey in the same location. This indicates the reconstruction method used in our study provides robust estimates of reference period forest characteristics.

**Reference period forest structure types**

One way to evaluate the efficacy of the predicted reference forest characteristics is to compare modeled density and basal area esti-
mates to stand-scale reference period estimates for forests in the LTB and elsewhere in the Sierra Nevada (Table 6). Our estimates of density are somewhat greater than suggested by previous research but our basal area is broadly similar to previous estimates. In the mixed conifer (MC) forest types (including WF and JP), reference WF forests had a median density of 200 trees ha\(^{-1}\) and 41.1 m\(^2\) ha\(^{-1}\) basal area, while the reference JP forests had a median density of 113 trees ha\(^{-1}\) and 29.6 m\(^2\) ha\(^{-1}\) basal area. Our reference density estimates were greater than previous reconstructions of MC and JP forest types in the LTB reporting 132 trees ha\(^{-1}\) and 68 trees ha\(^{-1}\), respectively (Taylor et al. 2014). Basal area estimates were also higher in the reference WF and JP forests than previous LTB estimates (29.4 and 25.5 m\(^2\) ha\(^{-1}\) for MC and JP; Taylor et al. 2014). However, there is some overlap between the JP and MC types for both density and basal area suggesting that our reconstructed estimates are comparable to previous LTB reconstructions. Elsewhere in the Sierra Nevada, reference MC (including WF and JP) densities from reconstructed and early survey data ranged from 63 to 204 trees ha\(^{-1}\) and basal area ranged from 24.3 to 51.5 m\(^2\) ha\(^{-1}\) (Sudworth 1900, North et al. 2007, Scholl and Taylor 2010, Van de Water and North 2011). Our estimates of density and basal area for WF and JP fall within the range of these estimates for MC stands. Additionally, a survey of old-growth MC, WF, and JP stands in the LTB showed densities and basal areas (for trees >40 cm) similar to our reference estimates for these forest types (Barbour et al. 2002). For RF and LP in the LTB, we estimated reference stand densities of 228 and 289 trees ha\(^{-1}\) and 54.8 and 45.1 m\(^2\) ha\(^{-1}\) of basal area, respectively. A previous reconstruction estimated 162 trees ha\(^{-1}\) for RF and 186 trees ha\(^{-1}\) for LP (Taylor et al. 2014), much lower than the current study. However, our basal area estimates were comparable to the previous estimates of 55.8 m\(^2\) ha\(^{-1}\) and 59.7 m\(^2\) ha\(^{-1}\) for RF and LP in the LTB (Taylor et al.

| Stand structure     | White fir | Jeffrey pine | Red fir | Lodgepole pine | Subalpine | Mixed conifer† | Central tendency‡ |
|---------------------|-----------|--------------|---------|----------------|-----------|---------------|-----------------|
| This study          | 200       | 113          | 229     | 289            | 330       | ...           | 218             |
| Basal area          | 41.1      | 29.6         | 54.8    | 45.1           | 50.7      | ...           | 44              |
| Reconstructed Taylor et al. (2014) | ... | 68          | 162     | 186            | ...       | 132           | 137             |
| Density             | ...       | 25.5         | 55.8    | 59.7           | ...       | 29.4          | 42.6            |
| Basal area          | ...       | ...          | ...     | ...            | ...       | 204           | 204             |
| Van de Water and North (2011) | ... | ... | ... | ... | ...       | 25.0         | 25              |
| Density             | ...       | ...          | ...     | ...            | ...       | 67            | 67              |
| Basal area          | ...       | ...          | ...     | ...            | ...       | 51.5          | 51.5            |
| North et al. (2007) | ...       | ...          | ...     | ...            | ...       | 120           | 120             |
| Density             | ...       | ...          | ...     | ...            | ...       | 24.3          | 24.3            |
| Basal area          | ...       | ...          | ...     | ...            | ...       | 25.5          | 25.5            |
| Scholl and Taylor (2010) | ... | ... | ... | ... | ...       | 51.5         | 51.5            |
| Density             | ...       | ...          | ...     | ...            | ...       | 120           | 120             |
| Basal area          | ...       | ...          | ...     | ...            | ...       | 52.4          | 52.4            |
| Sudworth (1900)§    | 228       | 178          | 346     | 306            | ...       | 178           | 178             |
| Density             | 36.1      | 33           | 44.8    | 26.1           | ...       | 34.5          | 35.3            |
| Basal area          | ...       | ...          | ...     | ...            | ...       | 51.5          | 51.5            |
| General Land Office | ...       | ...          | ...     | ...            | ...       | 147           | 147             |
| Density             | ...       | ...          | ...     | ...            | ...       | 52.4          | 52.4            |
| Barbour (2002)      | 108       | 63           | 107     | ...            | ...       | 67            | 107             |
| Density             | 41        | 27           | 53      | ...            | ...       | 40            | 54              |
| Basal area          | ...       | ...          | ...     | ...            | ...       | 54.8          | 54.8            |
| Contemporary Taylor et al. (2014) | ... | 343          | 538     | 617            | ...       | 403           | 475             |
| Density             | ...       | 46.4         | 48.5    | 47.8           | ...       | 57.2          | 50              |

Note: Please see the text for a description of calculations.
† The mixed conifer forest type was associated with stands with no clear dominance by a species.
‡ The Modeled, General Land Office, and Sudworth datasets were calculated using the median while the Barbour and Taylor Reference and Contemporary datasets used the mean as a measure of central tendency.
§ We chose a subset of the Sudworth data representing forest types present in the LTB.
There are no studies for comparison that explicitly estimated reference period conditions for the SA forests. From a landscape perspective of forest density and basal area in the LTB, the overall GLO estimates (not forest type specific) of these characteristics (147 trees ha$^{-1}$ and 52.4 m$^2$ha$^{-1}$) fell within the range of previous reconstructions and were similar to the overall reference estimates in the current study (Table 6).

Differences between individual modeled forest types and previous studies can be attributed to several factors. First, previous studies were restricted in the number of sampling plots, limiting the range of variation possible in density and basal area. Our reconstruction used 745 plots with an average of 149 plots (67–207 range) per forest type to estimate stand characteristics. Second, a smaller range of environmental variation (e.g., slope, aspect, elevation) was used in previous research than provided by the current study’s sampling methodology. We collected data for forest types across the range of environmental conditions experienced within each type, creating more robust estimations of stand characteristics that would result from site quality. Third, identification of forest types may have caused differences in stand density and basal area estimates. For example, following reconstruction we used cluster analysis to identify forest types rather than relying on a priori assumptions (e.g., Van de Water and North 2011, Taylor et al. 2014) that assigned individual stands to a forest type. Our cluster analysis resulted in two MC forest types, WF and JP, that parsed more subtle differences in species composition and stand characteristics.

Contemporary forests in the LTB are different than the reference forests and all forest types have increased in density and basal area (with the exception of RF) over the past 130 years since logging and fire suppression (Taylor 2004, Beaty and Taylor 2007, 2008, Taylor et al. 2014). Using Taylor et al. (2014) as representative of unlogged and fire-suppressed contemporary forest conditions in the LTB, forest density has increased by 118% and basal area by 14%. Forest density changes were greatest in the JP forests (200% increase) but all forest types at least doubled in trees per ha. While all forest types have seen increases in density, not all forest types have seen proportional increases in basal area. Increases in basal area were greatest in the lower elevation MC (39% in WF and 57% in JP forests, but the RF and LP forest types had basal areas greater than or equal to the contemporary period. The changes in basal area over time are reflected in the diameter distributions of dominant species within each forest type. All forests shifted from larger diameter trees in the reference forests to smaller diameter trees in the contemporary unlogged forests. The left skew in the reference diameter distribution has also been observed for MC forests in YNP (Scholl and Taylor 2010, Collins et al. 2011). The diameter shift is most pronounced in the RF and LP forests with few contemporary trees >60 cm suggesting that the increase in basal area in contemporary high elevation forests are the result of ingrowth rather than growth of dominant large diameter trees.

Increases in tree density and basal area from the reference period to present in the LTB are also accompanied by changes in species composition (Taylor and Beaty 2005, Beaty and Taylor 2007, 2008, Taylor et al. 2014). The WF and JP forests have shifted in species composition from fire tolerant Jeffrey pine- to white fir-dominated forests that are less tolerant of frequent surface fires (Beaty and Taylor 2007). Throughout the Sierra Nevada, changes in species composition from shade-intolerant pine to shade-tolerant fir have been driven by the exclusion of fire (Taylor 2000b, Taylor and Skinner 2003, Mast and Wolf 2004, Van de Water and North 2010, Collins et al. 2011). While reference WF forests were present in the LTB, fires burned less frequently allowing some white fir trees to grow large enough to gain some fire resistance (Taylor 2004).

In contemporary RF forests, the exclusion of fire was likely less important than the influence of logging on contemporary species composition because fires burned less frequently than in lower elevation JP and MC forests (Taylor 2004, Taylor and Beaty 2005, Beaty and Taylor 2007, Taylor et al. 2014). Logging in RF forests favored the rapid ingrowth of small diameter lodgepole pine trees causing a shift away from red fir dominated stands. High-elevation reference LP forests do not appear to be shifting in composition but are becoming denser with more stems in smaller diameter classes. Low elevation LP forests (i.e., LP-WF subtype) co-dominated by white fir trees might also experience a shift to shade-tolerant
Our reconstruction represents a snapshot in time for reference forest types growing under an active fire regime. Within each reference forest type, forests were likely at varying stages of forest succession. However, changes in forest structure appear to be more likely than changes in species composition because site variables largely control forest type in western conifer forests. Then, fire interacts with the forest type. We cannot predict successional stage with our landscape-scale model but we do provide a range of values for forest density by species and size class to account for the variability in forest successional stage within forest type. The comparison of the reference forests to the contemporary forests highlights the successional process in the absence of fire.

Spatial model of forest reference conditions

Predictive vegetation mapping from ecological survey data is commonly conducted at the species level rather than the community level (Franklin 1995, Guisan and Zimmermann 2000, Guisan and Thuiller 2005, Ferrier and Guisan 2006). Few community level studies attempt to predict forest composition and structure and those that do rely on remote sensing imagery as the primary predictive landscape variables (Ohmann and Gregory 2002, Ferrier and Guisan 2006). Spatially explicit modeling of presettlement or reference forest structure types on a landscape scale has not been previously attempted with the exception of coarse-resolution methods using GLO data (Williams and Baker 2011, 2012). Our random forests approach to classifying and mapping the five dominant reference forest structure types in the LTB resulted in 51.5% classification accuracy of plot-level data using 14 physiographic and climatic variables. In comparison, the prediction accuracy of a similar landscape-scale model of contemporary forest types in coastal Oregon resulted in 45% overall classification accuracy using 10 vegetation classes and 34 predictor variables (Ohmann and Gregory 2002). In western and central Oregon, mapping of contemporary community types (composition only) resulted in 41–57% correct classification (Grossmann et al. 2010, Ohmann et al. 2011). Modeling methodologies varied across studies but the primary difference between our work and previous models was the use of remotely-sensed data to predict vegetation type. Modeling of reference forest types is necessarily limited in the types of predictors available. Obviously, remote sensing was not available and soils were likely to change following widespread logging of the LTB. Despite these limitations, our model performed as well as models classifying contemporary forest types.

Our random forests model also signals that forest structure types in the LTB are strongly controlled by a few physiographic variables. The model identified elevation as the strongest predictor of forest classification with maximum temperature and slope also strong predictors of forest structure type. This is consistent with the current distribution of forest types in the LTB (Manley et al. 2000, Taylor 2004, Greenberg et al. 2006) and throughout the Sierra Nevada (Parker 1989, 1995, Taylor 1990, Beatty and Taylor 2001, Bekker and Taylor 2001). The GLO data provided an independent validation of the random forests model and showed that the model is consistent in its overall classification accuracy of main forest structure types; though, there were some notable differences in classification accuracy among forest types (Table 4). For example, the WF forest structure type appears more dominant in the southern portion of the LTB than expected from the GLO survey data. Spatial inaccuracies were likely the result of sourcing white fir plots from somewhat moister sites on the western portion of the Sierra Nevada and the general overlap of mixed conifer forests in the region. Finally, the visual analysis of the GLO and random forests generated maps confirms the strength of elevation, maximum temperature, and slope as controlling variables in forest distribution.

Reference period fuels and fire behavior

Estimates of reference period fuels modeled from stand structure suggest moderate fuel loads (i.e., TL5) for reference forests based on similarity of time-lag values to standard fuel models. Similar Timber Group (FB) or Timber Litter (TL) surface fuel models (i.e., TL4, TL7, FB08, FB10) were suggested in a previous reconstruction of surface fuels for old-growth stands in the
LTB (Taylor et al. 2014). However, in a direct comparison of time-lag size class fuel loads, the current study values fell within the range of values for one previous reconstruction in the LTB (Taylor et al. 2014) but were lower than a second surface fuel reconstruction in the Sierra Nevada (Van de Water and North 2011). Differences in surface fuel estimates might be a function of the amount of variation captured in the plot-level data collection. In the current study, we captured current and reference forest conditions across a range of conditions in 745 plots versus 32 (Taylor et al. 2014) or 36 (Van de Water and North 2011) plots in previous studies.

The use of custom fuel models that take direct estimations of surface fuel loads may not be prudent because custom fuel models are difficult to calibrate to known surface and crown fire behavior (Scott and Reinhardt 2001, Scott and Burgan 2005). Potential fire behavior would change with a different fuel model or fire weather condition. Our emphasis was on possible differences in potential fire types (i.e., surface, passive crown, active crown, or conditional crown) among forest subtypes under severe fire weather conditions (98th percentile). We were better able to assess potential fire behavior by using a gradient of fuel models that represent fuel loadings likely to have been present on a heterogeneous reference landscape. In a landscape with a functioning fire regime, surface fuel loads would be more spatially heterogeneous because fires consume surface fuels and influence the spatial patterns of subsequent burns until fuel loads are sufficient to carry the next fire (Miller and Urban 2000, Collins et al. 2009, Scholl and Taylor 2010). Despite moderate or even high surface fuel load estimates, the predicted potential fire type for forest subtypes under extreme weather was surface fire except for RF subtypes (potential for passive crown fire) and the LP subtypes (potential for conditional crown fire). Similarly, Taylor et al. (2014) found the potential for passive crown fire in reference mixed conifer stands with heavy surface fuels (i.e., FB10).

It is possible that more passive or even active crown fire may have been predicted with better estimates of seedling, sapling, and understory tree density for the reference period. These forest strata influence estimates of canopy fuel variables particularly canopy base height which influence torching and crowning. However, it is difficult to reconstruct the density and size of these understory strata using dendroecological techniques. In reference stands with high canopy base height (e.g., JP), torching and crowning may require windspeeds exceeding 100 km hr$^{-1}$. Our torching and crowning indices are similar to previous estimates for reference fire behavior in the LTB (Van de Water and North 2011, Taylor et al. 2014), indicating that surface fires were common in reference forests. The probability of torching variable was estimated independent of the stand canopy base height to assess the potential for single trees or small groups of trees to torch without crown fire occurring. The increased probability of torching in all reference forest types with moderate to heavy fuel loadings further evidenced the heterogeneous nature of reference surface fuels and fire behavior. While the probability of torching is less in previous research, some torching in reference forest types was likely to occur (Taylor et al. 2014). Despite the limitations in understory forest structure estimates, high severity fire was likely part of the disturbance regime in at least RF and LP forest types during the reference period with other forest types experiencing torching under moderate to heavy fuel loads.

The potential for passive and conditional crown fires, as well as higher probabilities of torching in some reference forest types, supports the presence of montane chaparral stands in the landscape that are related to high severity fire (Nagel and Taylor 2005). In the LTB (Nagel and Taylor 2005, Beaty and Taylor 2008) and greater Sierra Nevada (Beaty and Taylor 2001, Bekker and Taylor 2001), chaparral established during the reference period when fires were severe resulting in a mosaic of forest stands and open shrub fields. In comparison to modern fuel loads and the potential for extreme fire behavior in contemporary stands (Taylor et al. 2014), the threat for passive and active crown fires in reference forests was substantially smaller but present. Contemporary fire behavior modeling in the LTB suggests that all forest types could support passive or active fires under moderate and heavy fuel loads (e.g., TL5 and FB10; Taylor et al. 2014). Severe fire behavior in contemporary stands in the LTB was observed in 2007 when the Angora Fire became an active crown fire burning...
1200 ha of MC forest (Safford et al. 2009). In some locations, the Angora Fire became a surface fire after burning into areas with fuel reduction treatments suggesting that lighter reference surface fuel loads were more resilient to catastrophic wildfire (Safford et al. 2009). It is likely that high severity burning in some locations will lead to shrub field development. In a comparison of fire severity between pre-settlement and modern periods, little to no departure was found in mean annual area of high severity burning in low- to moderate-elevation forests (Mallek et al. 2013). This suggests that basinwide shrub field area may be stable over time in some forest types but field development would vary by location and fuel loadings.

**Conclusion**

We used a novel combination of dendroecological reconstruction, predictive vegetation mapping, and fire behavior modeling to develop spatially explicit reference forest composition, structure, fire frequency, fuels, and fire behavior at the landscape scale. Our approach provides a robust and repeatable approximation of reference conditions across the LTB landscape given the severity of 19th century logging and the inherent limitations of dendroecological methods to estimate past forest characteristics. By identifying reference conditions and characterizing forest composition, structure, and disturbance frequency with a range of variability, resource managers can develop targets for restoration and create a forested landscape more resilient to changes in disturbance regime and climate (Swetnam et al. 1999). In the LTB, forest management utilizes forest reference conditions to develop targets for ecological restoration including forest thinning and prescribed burning to decrease fuel loads, increase forest heterogeneity, and improve forest habitat for wildlife (Christopherson et al. 1996, USDA Forest Service 2013). Previous research has identified reference conditions using a plot-level approach that is helpful for identifying past conditions within a historic range of variability (Taylor et al. 2014) but might not fully represent the range of past forest conditions because of a more limited sampling approach. Our method of reconstruction not only utilizes plot-level information but creates a landscape representation of the heterogeneous forest conditions represented prior to major Euro-American alteration. For managers, our spatial reconstruction can be used to identify locations that are outside the historic range of variability in species composition, forest structure, fuel loads, and fire frequency, and implement a landscape-scale approach to management. Then, on the stand level, composition and structure targets for forest types can be identified from our dendroecological reconstructions and statistical modeling using data from a larger range of site locations than past research. Other methods of landscape-scale forest reconstruction (e.g., Williams and Baker 2011, 2012) do not provide a similar level of structural detail and plot-based estimates of disturbance frequency, fuels, and fire behavior. We do caution that managers must understand that the spatial accuracy of the reconstruction is not absolute and they must combine their expert knowledge of forest site conditions with our model of past conditions to adaptively manage the landscape.

Our focus was on forest composition, structure, and disturbance but the method could be adopted to estimate past forest productivity and carbon sequestration. There is considerable interest in understanding how forest carbon stocks have changed since the alteration of reference period disturbance regimes (e.g., Mladenoff and Baker 1999, Keane et al. 2002, Mladenoff 2004, Scheller et al. 2007). Our method could be used to estimate carbon storage for past forested environments on a landscape scale to better determine the effect of past and present environmental and climatic changes on carbon sequestration by providing more accurate estimates of initial conditions on a landscape scale. Large and detailed landscape-scale reconstructions can also be used to drive ecosystem models (e.g., LANDIS) and create more accurate simulations of forest succession, disturbance, and response to climate change. There is great value in being able to take plot-level data and then model forest structural characteristics over wide areas that have been altered by human activity to provide managers with some indication of what initial conditions were, how much things have changed, and which locations might need the most attention. The methodology is broadly applicable to not only the Sierra Nevada but also to regions in which reference period data are available across a range of site conditions.
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Table A1. Upper 98th percentile weather conditions for weather and fuel moisture used for fire behavior simulations for reference forest conditions in the Lake Tahoe Basin, USA.

| Climate variable                        | 98th percentile |
|-----------------------------------------|-----------------|
| Dry bulb temperature (°C)               | 30.6            |
| Low relative humidity (%)               | 2               |
| High relative humidity (%)              | 100             |
| Wind speed (km h⁻¹)                     | 32              |
| Fuel moisture                           |                 |
| 1-h (%)                                 | 2               |
| 10-h (%)                                | 3               |
| 100-h (%)                               | 5               |
| Live woody (%)                          | 70              |
| Foliar moisture content (%)             | 80              |

Notes: Data are from the Truckee, California remote automated weather station May–October 1961–2006. Foliar moisture was assumed to be 80% under 98th percentile conditions weather conditions (Agee et al. 2002).

Table A2. Summary of physiographic variables used in the random forest models by forest structure types.

| Forest type | Elevation (m) | Eastness | Northness | Slope (°) | TPI | TWI | Min temp (°C) | Max temp (°C) | Precip (cm) | Avg daily sol rad (kWh m⁻²) |
|-------------|---------------|----------|-----------|-----------|-----|-----|---------------|---------------|-------------|-----------------------------|
| White fir   | 2089          | 0.00     | –0.05     | 21        | –8.7| 6.2 | –0.3          | 13.1          | 113.1       | 1562                        |
| Jeffrey pine| 2355          | 0.00     | 0.03      | 17        | 3.8 | 4.6 | –1.1          | 11.9          | 126.7       | 1597                        |
| Red fir     | 2515          | –0.06    | –0.03     | 11        | –0.7| 4.2 | –2.6          | 11.1          | 125.3       | 1663                        |
| Lodgepole pine | 2123       | 0.02     | 0.07      | 22        | –0.4| 5.5 | –0.6          | 12.8          | 110.6       | 1606                        |
| Subalpine   | 2715          | –0.10    | 0.00      | 14        | 2.1 | 3.1 | –3.5          | 9.8           | 153.5       | 1614                        |

WF = white fir (Abies concolor); JP = Jeffrey pine (Pinus jeffreyi); IC = incense cedar (Calocedrus decurrens); SP = sugar pine (Pinus lambertiana); RF = red fir (Abies magnifica); WP = western white pine (Pinus monticola); MH = mountain hemlock (Tsuga mertensiana).

Table A3. Summary of physiographic variables used in the random forest models by forest structure types and subtypes.

| Forest type and subtype† | Elevation (m) | Eastness | Northness | Slope (°) | TPI | TWI | Min temp (°C) | Max temp (°C) | Precip (cm) | Avg daily sol rad (kWh m⁻²) |
|--------------------------|---------------|----------|-----------|-----------|-----|-----|---------------|---------------|-------------|-----------------------------|
| White fir                |               |          |           |           |     |     |               |               |             |                             |
| Small WF-JP              | 2058          | 0.03     | –0.05     | 21        | –7.7| 6.2 | –0.3          | 13.1          | 113.2       | 1560                        |
| WF-JP-SP                 | 2093          | –0.23    | 0.21      | 16        | 5.5 | 3.7 | 0.1           | 13.4          | 114.0       | 1580                        |
| WF-RF-JP                 | 2107          | 0.09     | –0.11     | 15        | –5.2| 5.1 | 0.1           | 13.2          | 114.7       | 1568                        |
| Mid WF-JP                | 2157          | –0.16    | –0.14     | 22        | –5.7| 4.9 | –1.2          | 12.6          | 108.1       | 1538                        |
| Jeffrey pine             |               |          |           |           |     |     |               |               |             |                             |
| Small JP-WF              | 2084          | –0.02    | 0.14      | 22        | 0.6 | 5.6 | –0.6          | 12.8          | 112.6       | 1620                        |
| Large JP-WF              | 2166          | 0.03     | 0.03      | 21        | –3.6| 5.2 | –0.7          | 12.8          | 116.5       | 1573                        |
| Mid JP-WF                | 2133          | 0.11     | 0.02      | 23        | 1.9 | 5.5 | –0.5          | 12.8          | 100.4       | 1625                        |
| Red fir                  |               |          |           |           |     |     |               |               |             |                             |
| RF-WP                    | 2466          | 0.09     | 0.08      | 22        | 3.2 | 3.9 | –1.9          | 11.2          | 124.9       | 1528                        |
| Mid-large-RF             | 2349          | –0.09    | 0.02      | 26        | 4.3 | 4.9 | –1.1          | 12            | 128.2       | 1614                        |
| Small RF                 | 2281          | 0.12     | 0.03      | 16        | 7.6 | 4.6 | –0.6          | 12.3          | 124.8       | 1615                        |
| Lodgepole pine           |               |          |           |           |     |     |               |               |             |                             |
| Small LP                 | 2175          | 0.06     | –0.06     | 12        | –2.3| 6.1 | –1.5          | 12.3          | 129.8       | 1573                        |
| LP-RF                    | 2588          | –0.12    | 0.01      | 11        | 0.1 | 3.6 | –2.6          | 11.1          | 123.2       | 1696                        |
| Subalpine                |               |          |           |           |     |     |               |               |             |                             |
| Subalpine                |               |          |           |           |     |     |               |               |             |                             |
| Subalpine                |               |          |           |           |     |     |               |               |             |                             |

†WF = white fir (Abies concolor); JP = Jeffrey pine (Pinus jeffreyi); IC = incense cedar (Calocedrus decurrens); SP = sugar pine (Pinus lambertiana); RF = red fir (Abies magnifica); WP = western white pine (Pinus monticola); MH = mountain hemlock (Tsuga mertensiana).
Table A4. Plot-level accuracy statistics for the random forests model for reference forest structure subtypes.

| Subtype model† | Kappa | Correct (%)‡ | Range (%)§ |
|----------------|-------|--------------|------------|
| White fir      | 0.10  | 44.3         | 0–68       |
| Jeffrey pine   | 0.38  | 60.3         | 25–61      |
| Red fir        | 0.14  | 44.5         | 15–73      |
| Lodgepole pine | 0.06  | 49.8         | 39–70      |
| Subalpine      | 20    | 40.3         | 21–58      |
| Mean           | 0.18  | 47.8         | 20–66      |

† Random forests models were used to distribute the subtypes within the distributions of each forest structure type.
‡ Correct is the overall percentage of correct classification.
§ Range is the range of percentage of correct classification within a forest type.

Table A5. Surface fuels (in time-lag size class) by reference forest structure type and subtype calculated using median stand conditions in Fire and Fuels Extension of the Forest Vegetation Simulator (FFE-FVS).

| Forest type and subtype | 1-hr | 10-hr | 100-hr | Total 1, 10, 100 hr | Litter | Duff |
|-------------------------|------|-------|--------|---------------------|--------|------|
| White fir               |      |       |        |                     |        |      |
| Small WF-JP             | 1.5  | 1.6   | 3.8    | 6.8                 | 1.6    | 31.8 |
| WF-JP-SP                | 1.3  | 1.3   | 4.5    | 7.0                 | 1.1    | 33.7 |
| WF-RF-JP                | 1.3  | 1.3   | 4.3    | 6.9                 | 1.2    | 30.9 |
| Mid WF-JP               | 1.4  | 1.5   | 4.7    | 7.7                 | 1.7    | 36.8 |
| Jeffrey pine            |      |       |        |                     |        |      |
| Small JP-WF             | 1.4  | 1.5   | 2.5    | 5.4                 | 0.9    | 21.9 |
| Mid JP-WF               | 1.4  | 1.6   | 2.4    | 5.4                 | 1.0    | 21.7 |
| Large JP-WF             | 1.7  | 1.8   | 2.5    | 6.0                 | 1.5    | 26.7 |
| Red fir                 |      |       |        |                     |        |      |
| Small RF                | 1.3  | 1.4   | 5.3    | 8.0                 | 1.9    | 38.6 |
| Mid-large RF            | 1.3  | 1.4   | 5.4    | 8.2                 | 2.2    | 39.4 |
| RF-WP                   | 1.6  | 1.6   | 2.9    | 6.1                 | 1.4    | 40.9 |
| Lodgepole pine          |      |       |        |                     |        |      |
| Small LP                | 0.7  | 0.7   | 1.9    | 3.3                 | 1.3    | 8.9  |
| LP-RF                   | 1.3  | 1.3   | 3.1    | 5.7                 | 3.2    | 10.4 |
| Mid-late RF             | 1.2  | 1.2   | 2.7    | 5.1                 | 2.8    | 9.8  |
| Subalpine               |      |       |        |                     |        |      |
| MH-RF                   | 1.9  | 1.9   | 4.1    | 7.9                 | 2.0    | 43.0 |
| MH-WP                   | 1.6  | 1.7   | 3.5    | 6.9                 | 2.6    | 31.3 |

Note: Fuel loads are in mg·ha⁻¹.

Table A6. Canopy fuels characteristics for reference forest structure subtypes.

| Forest type and subtype | Canopy bulk density (kg·m⁻³) | Canopy base height (m) | Stand height (m) |
|-------------------------|-------------------------------|------------------------|------------------|
| White fir               |                               |                        |                  |
| Small WF-JP             | 0.05                          | 9.1                    | 37.5             |
| WF-JP-SP                | 0.05                          | 7.9                    | 29.0             |
| WF-RF-JP                | 0.04                          | 8.2                    | 30.8             |
| Mid WF-JP               | 0.04                          | 9.4                    | 36.3             |
| Jeffrey pine            |                               |                        |                  |
| Small JP-WF             | 0.02                          | 9.1                    | 28.7             |
| Mid JP-WF               | 0.02                          | 10.4                   | 22.3             |
| Large JP-WF             | 0.02                          | 11.3                   | 29.6             |
| Red fir                 |                               |                        |                  |
| Small RF                | 0.10                          | 2.4                    | 34.1             |
| Mid-large RF            | 0.08                          | 2.4                    | 37.2             |
| RF-WP                   | 0.03                          | 2.4                    | 35.7             |
| Lodgepole pine          |                               |                        |                  |
| Small LP                | 0.03                          | 9.8                    | 25.3             |
| LP-RF                   | 0.12                          | 13.7                   | 30.2             |
| LP-WF                   | 0.08                          | 10.7                   | 29.6             |
| Subalpine               |                               |                        |                  |
| MH-RF                   | 0.05                          | 11.0                   | 37.2             |
| MH-WP                   | 0.07                          | 8.8                    | 33.5             |
Fig. A1. Relative abundance of stems in 30-cm size classes (i.e., 10–30 cm, 31–60 cm, 61–90 cm, 90+ cm) for the five reference forest structure types: WF = white fir (*Abies concolor*); JP = Jeffrey pine (*Pinus jeffreyi*); IC = incense cedar (*Calocedrus decurrens*); SP = sugar pine (*Pinus lambertiana*); RF = red fir (*Abies magnifica*); LP = lodgepole pine (*Pinus contorta*); WP = western white pine (*Pinus monticola*); MH = mountain hemlock (*Tsuga mertensiana*).
Fig. A2. Landscape representation of reference period forest structure types from the 1860s General Land Office survey in the LTB. See Methods for naming convention.
Fig. A3. Landscape representation of reference period point fire return interval (FRI) in the LTB distributed using a random forest model.