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Settlement-era forest structure and composition in the Klamath Mountains: reconstructing a historical baseline

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Abstract. Historical baselines of forest conditions provide reference states to assess how forests have changed through time. In California, the Public Land Survey System (PLSS) provides tree inventory data between 1872 and 1884 at 93.2-km^2 (36 mi^2) resolution. Although these data provide a spatially extensive record of settlement-era forest conditions, reconstructions using PLSS data have been limited and controversial in western landscapes. Recent improvements in the application of plotless density estimators (PDE) have made reconstructions more accurate and robust. The purpose of this study was to use PDE to reconstruct the settlement-era forest conditions in Six Rivers National Forest—a floristically diverse temperate forest in the Klamath Mountains of northwestern California—to quantify differences with modern conditions. Records of fires and harvests were used in conjunction with the PLSS data to understand the influence of forest management during the previous century. The contemporary forest in Six Rivers contains three times more trees than in the settlement era with a comparable increase in tree basal area. Forest composition during the settlement era was predominantly Douglas-fir (34.4%), pine (24.2%), and oak (21.9%) by basal area. Contemporary forests support more Douglas-fir (45.2%) and a similar amount of pine (26.1%), while oaks have decreased by more than half (9.3%). These increases in tree abundance occurred despite extensive, mid-century timber harvesting in Six Rivers. Although large fires have burned in Six Rivers between 2000 and 2019, far fewer fires occurred during the twentieth century. Our results suggest that effective fire suppression contributed to the densification of the contemporary forests in Six Rivers.

Key words: California settlement; fire suppression; historical baselines; plotless density estimation (PDE); public land survey system (PLSS); tree density.

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Introduction

In an era of rapid climate and land-use change, quantifying the patterns and processes of past ecosystems vitally informs the stewardship of contemporary ecosystems (Beller et al. 2020). For example, global and national land management projects use natural baselines (before human modification) and historical baselines (data gathered in the recorded past) as starting points to detect the magnitude of landscape changes and to establish targets for restoration (Swetnam et al. 1999, Alagona et al. 2012, IPBES 2018). However, evidence for pre-modern natural baselines is constrained by poor spatial or temporal resolution, limited taxonomic resolution, and physical degradation (Egan and Howell 2005). Data for historical baselines, though obtainable, often represent only

a single snapshot of a community and can underestimate or overestimate the extent of change (Barak et al. 2016). The need for robust baselines is particularly acute for ecosystems with altered disturbance regimes (Higgs et al. 2014).

For many forests in the USA, management decisions implicitly rely on an understanding of ecosystem change relative to the recent past. For fire-prone, semi-arid forests in California, a common baseline is the state of the forest prior to the imposition of active fire suppression (Egan and Howell 2005, USFS 2013). A century of suppression has significantly modified the structure and composition for many of California's conifer-dominated forests (Steel et al. 2015). Most efforts to date to determine baselines have focused on the yellow pine and mixed conifer forests of the Sierra Nevada and Southern Cascade Range (e.g., Collins et al. 2011, Taylor et al. 2014, Hagmann et al. 2018). Result has largely converged on similar findings: Prior to fire suppression, these forests were open and dominated by large, drought and fire-tolerant trees. Presumably, this structure was maintained by frequent low- and moderate-severity fires. In the absence of fire, contemporary forests have increased in density and shifted species composition toward more fire-sensitive species. However, some research has argued that pre-suppression forests in the Sierra Nevada were dense, closed-canopy forests maintained by fire regimes that included historically extensive, high-severity fires (Baker 2014, Baker and Hanson 2017, Baker and Williams 2018).

The structure and composition of settlement-era forests in northwestern California, in contrast, are dissimilar enough to warrant their own exploration. Unlike the montane forests of the Sierra Nevada and Cascade Range, the Klamath Mountains bioregion harbors the most diverse conifer forests in North America (Cheng 2004) and exceptionally diverse hardwood forests with oak dominant woodlands (Skinner et al. 2006). The Klamath area supported a mixed-severity fire regime characterized by mostly small, low-intensity, frequent fires, and infrequent large, burns of mixed-severity (Taylor and Skinner 2003). The region's diverse patterns of topography, climate, and soils have created heterogeneous vegetation patterns (Fig. 1) more complex than those found in the Sierra Nevada or Southern Cascade Range

Fig. 1. Historical photograph from the Sawyer's Bar area shows the spatial complexity of settlement-era vegetation along the Salmon River in the Klamath National Forest, which borders Six Rivers to the east (Eldridge 1910).

(Sawyer and Thornburgh 1977, Skinner et al. 2018). Taylor and Skinner's (2003) reconstruction of the historical forest in the Hayfork study area of Shasta–Trinity National Forest suggests a similar impact of fire suppression, namely an increase in tree density and a shift toward more fire-sensitive species. However, this detailed effort was limited in spatial extent (25 km^2). Given the heterogeneity of the Klamath region, the characteristics of the pre-settlement forests and the extent of its divergence from the contemporary forests remain unclear.

Northern California forests are high priority landscapes for federal and state restoration projects (USFS 2013), particularly the Klamath Mountains bioregion. These forests are expected to undergo rapid decline in conifer dominance (Tepley et al. 2017, Serra-Diaz et al. 2018) as climate change disrupts the mechanisms that promote forest stability, namely regeneration, growth, and fire tolerance. As the forests transform, they become more at risk of increasingly large and severe fires because of dangerously high fuel loading coupled with a projected warmer climate (Westerling 2018).

In U.S. forest management planning, the determination of historical baselines most often relies on forest inventories from the settlement era (Hanberry and Dey 2019), which is defined in the western United States as the period beginning in 1848 when substantial numbers of miners settled in the region and displaced Native populations (Bright 1978, Busam 2006). In conjunction with western migration across much of the USA, the General Land Office (GLO) through the Public Land Survey System (PLSS) conducted systematic land surveys designed to demark territory, categorize resources, and aid settlement (Schulte and Mladenoff 2001). Central to the PLSS data were witness trees (or bearing trees), that is, trees for which the bearing and distance from post-markers were known (Whitney and DeCant 2001), that today provide the best record of forest composition from this time period.

PLSS records thus provide a quantitative path to understanding historic forest ecosystems in western federal landscapes (Galatowitsch 1990, Bjorkman and Vellend 2010). In southwestern Oregon, PLSS surveys have been used to reconstruct vegetation cover (Duren et al. 2012), while other research concerning western land surveys has focused on specific phenomenon in discrete forest types (e.g., fire regime reconstruction in dry forests, Hessburg et al. 2005, Baker 2012, 2015, Odion et al. 2014, Baker and Williams 2018). Summaries of PLSS data exist for some areas (e.g., the Eldorado National Forest, Fites-Kaufman 1997; Lake Tahoe Basin, Manley et al. 2000; Stanislaus, Sierra, and Sequoia National Forests, Hyde 2002). In contrast, eastern North American public land survey records have been used extensively to reconstruct forest density, biomass, and changing composition (e.g., Radeloff et al. 1999, Whitney and DeCant 2001, Rhemtulla et al. 2009, Hanberry et al. 2012*b*) and to guide land management (Friedman and Reich 2005, Goring et al. 2016, Kujawa et al. 2016).

This study uses robust methods for plotless density estimation (PDE methods) to analyze the PLSS survey data (~1880s) and characterize settlement-era forest conditions in the California portion of the Klamath Mountains' bioregion. Specifically, we determined historical baseline conditions for the forest, which we then compared to modern vegetation survey data to determine how fire suppression and timber harvests have changed this forest. We also used reconstructed basal area to estimate aboveground live biomass for the settlement era. Estimating settlement-era biomass in California is particularly important because California is one of the few jurisdictions in the world to enact greenhouse gas emissions reductions and has a legal obligation to understand, measure, and manage its forest carbon (AB-23 2006). We asked the following:

1. Have tree density, basal area, and biomass of the contemporary forest increased in comparison to settlement-era forest conditions?
2. Were oak and pine-dominated forests more common during the settlement era?
3. Do documented changes in the disturbance regime since the settlement era explain the differences in forest structure and composition?

Study site

Established in 1947 and named for the Smith, Klamath, Trinity, Mad, Eel, and Van Duzen rivers (USFS 2013), the Six Rivers National Forest (hereafter, Six Rivers) encompasses 394,420 ha

(957,590 acres) across northwestern California. The predominant forest type across Six Rivers is Douglas Fir at 46% (Fig. 2). As part of the Klamath Mountains, this management area is characterized by exceptional floristic and geologic diversity (Whittaker 1960). Pre-settlement forest assemblages of the Klamath Mountains bioregion were well established 2000 yr BP, according to Holocene-length pollen records (Mohr et al. 2000, Wanket 2002, Briles et al. 2008, Skinner et al. 2018). Over the past century, however, woodlands have become closed-forest systems with more fire-sensitive species (Crawford 2012). Currently, low-elevation forests are dominated by *Pseudotsuga menziesii* (Douglas-fir) and multiple *Pinus* (pine) species, with a broadleaf component of *Quercus kelloggii* (California black oak), *Notholithocarpus densiflorus* (tanoak), and *Arbutus menziesii* (Pacific madrone). Higher-elevation montane forests (above ~1200 m) are dominated by *Abies concolor* (white fir) and *Abies magnifica* (red fir; Sawyer and Thornburg 1977), whereas sub-alpine (above ~1700 m) zones include *Tsuga mertensiana* (mountain hemlock) and *Picea breweriana* (Brewer spruce; Sawyer and Thornburg 1977, Briles et al. 2011). On areas of ultramafic soils derived from serpentinite and peridotite bedrock, *Pinus jeffreyi* (Jeffrey pine), *Pinus monticola* (western white pine), and *Calocedrus decurrens* (incense cedar) are the dominant forest taxa (Whittaker 1960; nomenclature follows Hickman 1993).

Fire history.—Prior to twentieth-century fire suppression, the landscape had a mixed-severity

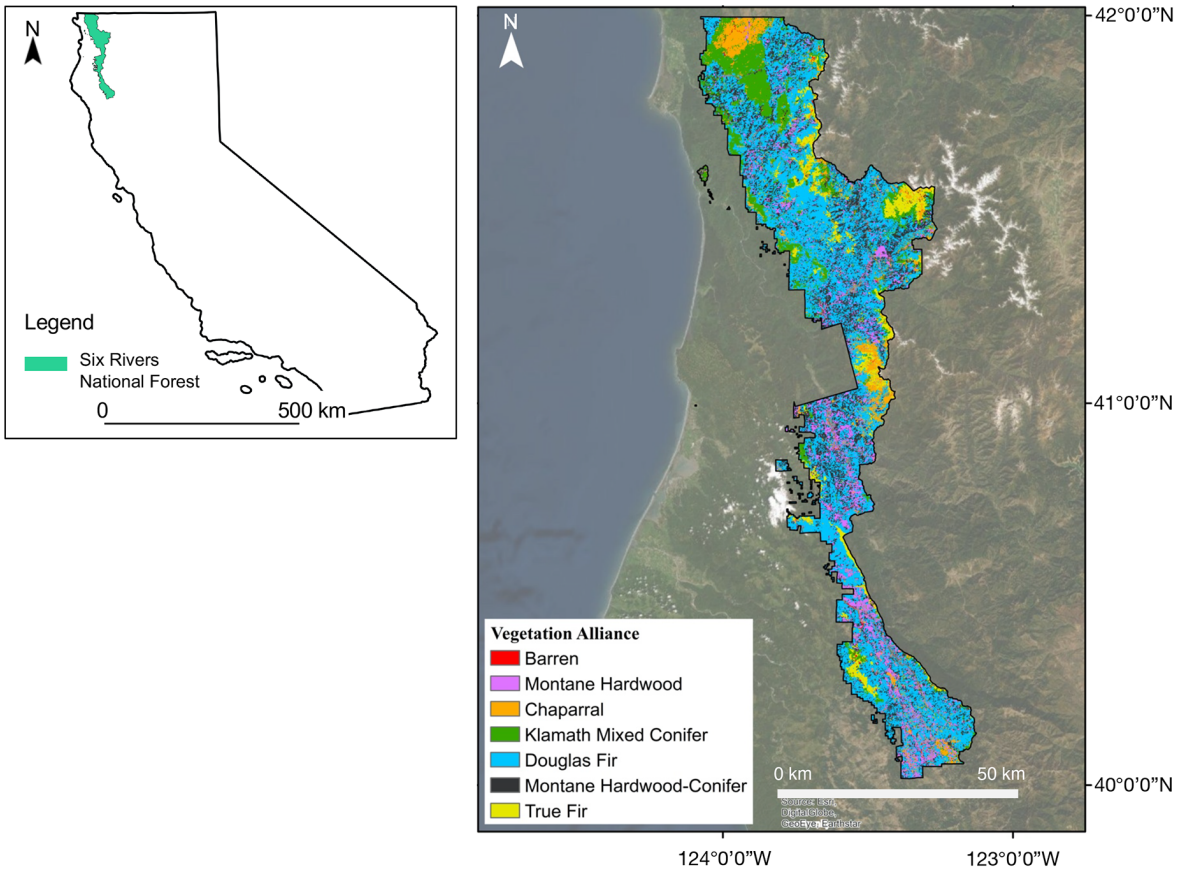

Fig. 2. Six Rivers National Forest covers nearly 400,000 ha (1 million acres) across Del Norte, Humboldt, Trinity, and Siskiyou counties (above). Vegetation alliances (right) include Montane Hardwood (purple), Chaparral (orange), Klamath Mixed Conifer (green), Douglas Fir (blue), Montane Hardwood-Conifer (black), and True Fir (yellow).

fire regime characterized by mostly small, low-intensity, frequent fires, and infrequent large, burns of mixed-severity (Taylor and Skinner 2003, Crawford et al. 2015). On average, fire rotations were short (~15–30 yr). Due to mountainous regional topography, fires burned with great spatial complexity creating openings of variable size (Taylor and Skinner 1998). At the local scale, Native burning and selective encouragement of species had significant effects on vegetation structure (Crawford et al. 2015). Native people used fire in various ways: to increase food (acorns, berries, roots) and materials (fiber for baskets), to improve hunting conditions and to facilitate religious ceremonies (Lewis 1993). Although Native ignitions appear to have been widespread, the extent of their influence on fire regimes and regional vegetation scales remains unknown (Skinner et al. 2006). The arrival of Europeans drastically disrupted and reduced Native burning practices (Busam 2006). Fire scar records and charcoal data indicate an abrupt fire-free period across the bioregion starting in the early 1900s (Agee 1991, Wills and Stuart 1994, Taylor and Skinner 1998, 2003, Stuart and Salazar 2000, Skinner 2003*a*, *b*). Fire suppression officially began in 1905 (Shrader 1965). These efforts were effective in accessible areas by the 1920s (Agee 1991, Stuart and Salazar 2000, Skinner 2003*a*, *b*, Taylor and Skinner 2003, Fry and Stephens 2006) and in remote areas after 1945 (Wills and Stuart 1994, Taylor and Skinner 1998, Stuart and Salazar 2000). The last pre-suppression fires recorded in the fire scar records for two lakes in Six Rivers occurred in 1903 and 1898 (Crawford 2012). Fire rotations increased markedly between 1900 and 1995: In the Hayfork study area, the rotation was 196 yr (Taylor and Skinner 2003) and regional fire rotations reached a high of 974 yr between 1959 and 1984 (Miller et al. 2012).

Land management.—Logging was widespread and intense throughout the Six Rivers' management area. Starting in the 1930s, the Forest Service promoted new logging developments and helped the lumber industry expand (Conners 1998). Commercial forest area was largely old-growth stands estimated at 250 yr old or older. For the first 15–20 yr after the 1947 establishment of Six Rivers, the federal government projected an annual timber harvest of approximately 300,000 m^3 and their plan encouraged selective cutting of large, high-value trees that have ceased growing (USDA 1947). As a timber-producing forest, Six Rivers had enormous standing stock: An estimated 16,753 million board feet of which 80 percent was Douglas-fir (Conners 1998). (Note that this estimate is presented in board feet to match original reports [Conners 1998] and to avoid confounding harvest estimates by any changes in the scaling system over time [Spelter 2002]). An extensive road network for handling log loads was built and contained some 800 km of roads and 2250 km of trails (Forest Situation Report 1947). The replacement of multi-aged old-growth forests with even-aged stands, coupled with fire suppression, greatly reduced the regional forest heterogeneity. These conditions allowed large wildfires, when they do occur, to become increasingly stand-replacing from the 1970s onward (Skinner et al. 2006, Miller et al. 2012).

Methods

Background on PLSS and PDEs

Across much of the USA, the General Land Office (GLO) through the Public Land Survey System (PLSS) conducted systematic and widespread sampling of species composition. Although PLSS was designed to demarcate territory and catalyze settlement (Schulte and Mladenoff 2001), witness tree surveys provide a widespread and systematic record of species composition from this time period. PLSS survey data consists of 6 × 6 mile townships with 36 embedded 1 × 1 mile sections (Foreman 1882). Permanent monuments mark section corners at the end of the 1-mile section lines, and so-called quarter corners lay halfway between two section corners (Bourdo 1956, Schulte and Mladenoff 2001). Surveyors selected nearby witness trees (bearing trees) as reference points to the corners —one tree in each quadrant (NE, NW, SE, SW) at section corners—recording the distance, direction, species, and stem diameter of each tree (Foreman 1882). Four witness trees were used at section corners, and two bearing trees were used at quarter corners (Foreman 1882). Starting in the southeastern section, surveyors moved north and west, collecting what they called interior tree

data (Fig. 3). Surveyors also collected exterior tree data along the boundary between two townships by the same methodology, that is, recording four trees at section corners and two at quarter corners.

Methods to robustly reconstruct tree density from PLSS records exist (Levine et al. 2017, Cogbill et al. 2018). PDEs rely on tree-to-tree, point-to-tree, or point-angle-tree distances to determine density in an efficient sampling scheme. Many PDEs have been used, but distance-based PDEs developed by Cottam, Pollard, and Morisita have been most frequently applied to PLSS data (Cottam and Curtis 1956, Morisita 1957, Pollard 1971). A full explanation of the historical development and mathematical foundations of the PDE equations is detailed in Cogbill et al. (2018).

In fact, the PDE format was inspired by the public land survey sampling design. Important properties of the survey, however, are not inherent in some PDE models, and therefore, only certain PDEs should be applied to PLSS data (Cogbill et al. 2018). One problem arising from PLSS sampling design is the low sampling density (minimum separation is 0.8 km, i.e., 0.5 mile), which results in regionally non-stationary

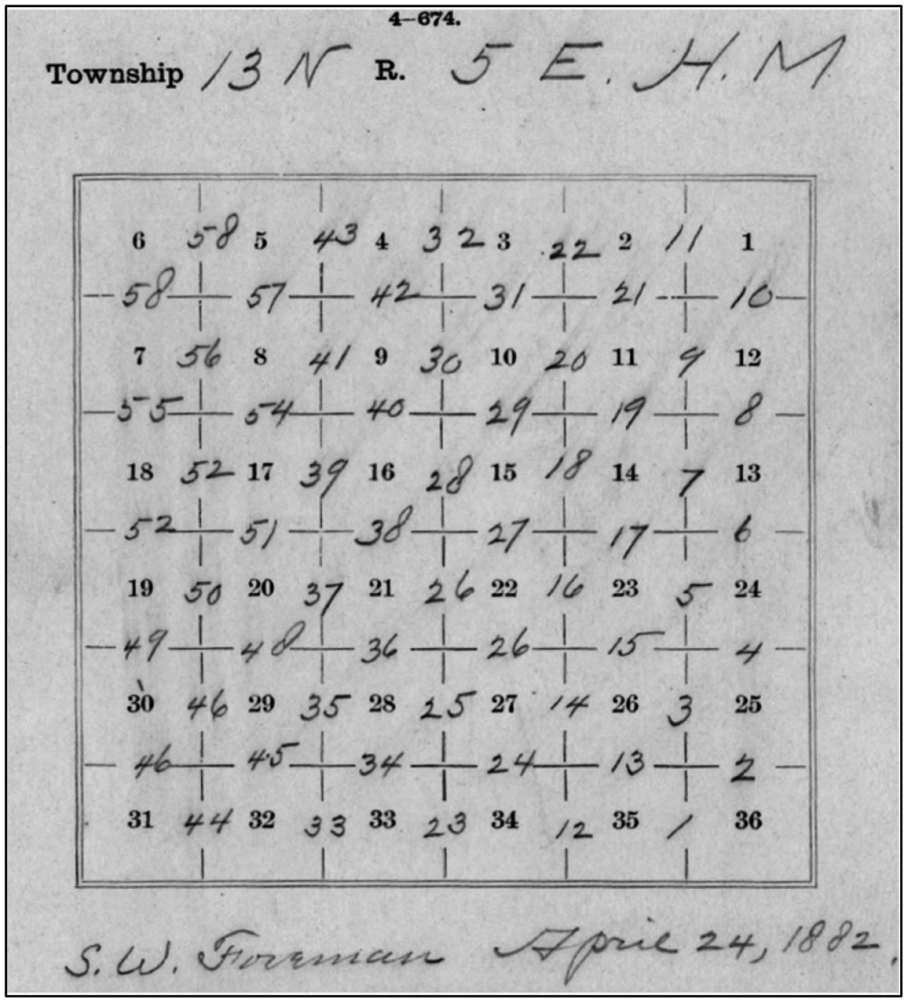

Fig. 3. Township field note index for 13N5E of the Humboldt Meridian in California is a representative example of the surveying pattern used for PLSS data collection (Foreman 1882). Sections are marked in black type. Surveyors marked the direction and sequence of their surveying paths with handwritten numbers (pencil); surveyors started in the southeast section and moved north and west collecting witness tree data.

mean densities and regional heterogeneity (Cogbill et al. 2018). Moreover, the performance of the models depends on the spatial arrangement of trees (Grimm 1984), and trees are often non-randomly dispersed at the local level. Hence, PDEs that assume complete spatial randomness (CSR) or are highly sensitive to non-randomness are not suitable for PLSS data (Engeman et al. 1994, Kronenfeld and Wang 2007, Bouldin 2008, Hanberry et al. 2011). Lastly, PLSS data have an uncertain level of surveyor bias (Bourdo 1956, Grimm 1984, Bouldin 2008, Liu et al. 2011, Kronenfeld 2015).

Of the available PDEs, those in the family of non-CSR models are the most applicable to public land survey data, specifically, the Morisita PDEs. Morisita IV uses the nearest tree in each of the four sections and responds to local spatial patterns. Morisita II, however, uses only two trees and is therefore less responsive than Morisita IV to local spatial patterns. Morisita II increases variability, but lowers bias such that it is preferred for PLSS datasets and was used in this work (Picard et al. 2005, Cogbill et al. 2018). Using the Morisita II (Morisita 1957), density is calculated

$$\lambda = K \times \left[\frac{1}{\pi N}\right] \times \left[\sum_{i=1}^{N} \frac{2}{\sum_{j=1}^{2} (r_{ij}^2)}\right] \quad (1)$$

where λ = tree density in trees/ha, N is the total number of points, and r is the distance from point j to tree i. K is the scaling coefficient. Since r_{ij} is measured in meters and density is reported in trees/ha, K = 10,000.

Six Rivers' PLSS data

All surveys in Six Rivers were carried out between 1872 and 1884. Data collection was typically conducted by one compass man, two chainmen, two axemen, and a flagman in a standardized way across each township in their charge. Of the 90 townships encompassed by the Six Rivers' management area, data from 76 townships were available (Fig. 4). PLSS records were obtained from scanned copies of the original field notes, which are stored in the Bureau of Land Management's cadastral survey office in Sacramento, California.

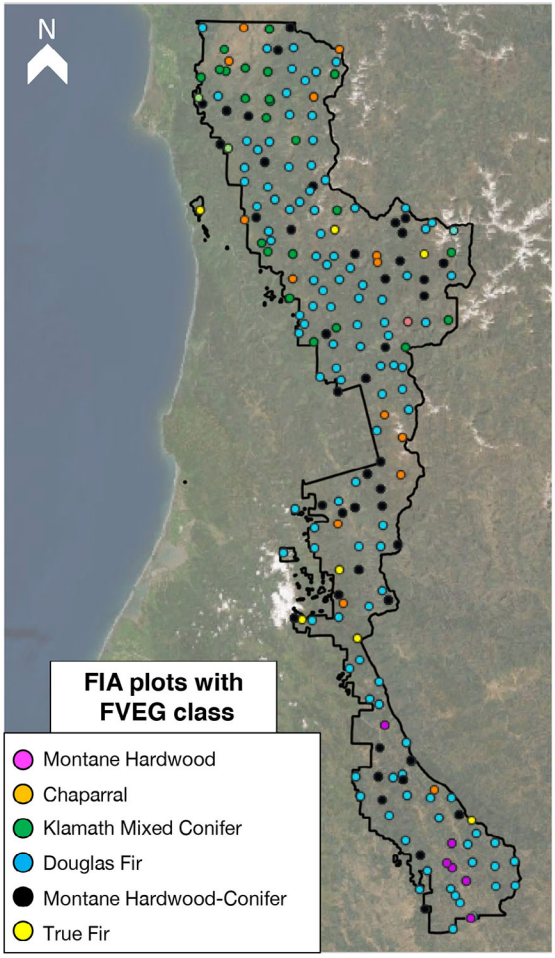

Fig. 4. Witness tree data (green points) collected between 1872 and 1880 within the modern boundaries of Six Rivers National Forest. FIA plots (colored circles) in the Six Rivers' boundary that have been matched to underlying modern FVEG data classifications.

Witness tree data were extracted from the handwritten archive into digital datasets for this analysis. Surveyors commented sporadically about rock type, soil texture, land features, and shrub cover in the original notes, but these details were not transcribed. Although the vast majority of trees were recorded with distance, direction, species, and stem diameter information, surveyors' notes contained three distinct types of omitted/absent data. Surveyors reported no trees within limits when trees were present but were too far away for measurement. They

reported pits impractical when field conditions prevented physical demarcation of witness trees. Lastly, some entries were blank without explanation. These distinctions were recorded into as NTWL, PI, and NA, respectively.

Species identifications were inconsistent across surveyor crews (Appendix S1: Table S1) for some taxa categories. Five surveyor deputies—Brunt, Foreman, Haughn, Holcomb, and McCoy—signed off on 92% of the records in the dataset, although they were not the ones collecting the data (crew names are unknown). The crews under Brunt, Holcomb, and McCoy recorded more species than Haughn and Foreman. Crews from Brunt, Holcomb, and McCoy made distinctions between oaks (Black, White, Live), and Holcomb separated tanoak (*Notholithocarpus densiflorus*) and chinquapin (*Chrysolepis chrysophylla*) from true oaks (*Quercus* spp.). In contrast, Foreman's crews did not differentiate oaks; instead, they lumped them into a generic Oak category that included tanoak and chinquapin; this crew also used a generic Fir for both *Pseudotsuga* and *Abies*. Pine, madrone, and cedar (the latter category including both *Calocedrus decurrens* and *Chamaecyparis lawsoniana* [Port Orford cedar]) were consistently separated across surveyor crews, however.

Given these findings, we created seven taxon categories to account for the variation in taxonomic resolution. They were Douglas-fir, oak, pine, cedar, madrone, other conifers, and other hardwoods. Our Douglas-fir category includes all original Spruce identifications as well as original Fir identifications below 1370 m. True *Picea* is restricted to a very few sites at high elevations in the study area, and Spruce was used extensively as a common name for *Pseudotsuga menziesii* (Peattie 1950). We used 1370-m elevation to discriminate between Douglas-fir and true *Abies* because at that elevation there is a dramatic shift in dominance from *Pseudotsuga* to *Abies* in the modern forest (Appendix S1: Fig. S1a). We kept the generic oak category of Foreman's surveyors because the elevation ranges of tanoak and true oaks overlap significantly, making elevation-based discrimination impossible (Appendix S1: Fig. S1b).

PDE methods

Before analysis, we addressed missing and inconsistent information in the records. Any point with an NA was deleted. Like NA, all PI points were deleted. For NTWL, a maximum distance of 100.5 meters (500 links) was inserted. Since no trees were present at NTWL, basal area was always set equal to zero with a default density = 0.3 tree/ha, the density estimate when the distance to the nearest tree is the 100.3 m from the point. In rare cases (3%), corners had three or one tree recorded, instead of the expected four (section corners) or two (quarter corners), without explanation from the surveyors; these data points were removed. Also, 41 corner points had multiple entries. For these replicated points, we systematically selected the witness tree data from the interior (i.e., first) measurement unless there were missing data.

The clean dataset was analyzed using Morisita II (Eq. 1, Cogbill et al. 2018). First, section corners with four witness trees were reduced to two trees. Care was taken to ensure the closest tree on either side of the survey line was selected. Specifically, the closest tree in the east and west semicircle was included for surveys running N/S (most points). For surveys running E/W, the nearest tree in the north and south semicircle was included. Density in trees/ha (TPH) was calculated for each point using Eq. 1. Basal area per tree (m^2/ha) was calculated as the basal area of the individual tree (m^2, calculated with DBH) multiplied by the point estimate of TPH/2. Basal area per point was calculated as the sum of the basal area of the two neighboring trees. To calculate relative abundance by taxa, the basal area of trees was summed and divided by the total basal area in each vegetation type.

The calculated density and basal area assume that surveyors used a fixed sampling design of the nearest tree on each side of the section line. Surveyors had three documented reasons for bypassing the nearest tree: spatial geometry of less than equal halves; azimuthal censoring; and elimination of trees very near the corner (Manies et al. 2001, Kronenfeld and Wang 2007, Liu et al. 2011, Goring et al. 2016, Cogbill et al. 2018). The base metric was adjusted for these surveyor biases by a multiplier derived from the empirical witness tree bearing and distance measurements recorded by the surveyor. Corrections for surveyor bias followed procedures outlined in Goring et al. (2016). The union of these surveyor biases yields a single correction factor that increases the base density and basal area due to

surveyor biases not sampling the nearest tree (Appendix S1: Table S2).

Density estimates were further corrected to account for the ambiguity in the minimum diameter of witness trees. Many studies have noted the logical absence of very small witness trees. Given their size and longevity, small trees make poor monuments and thus tend to be under sampled (e.g., Bouldin 2010, Hanberry et al. 2012*a*, Goring et al. 2016). To adjust for this bias, we set a lower diameter limit of 20 cm and adjusted the raw density measurement by the proportion of witness trees >20 cm DBH (Goring et al. 2016, Appendix S1: Table S2).

GIS methods

In ArcMap (10.6.1, ESRI 2011), Six Rivers' boundary was obtained from the USDA Forest Service Administrative Forest dataset (USDA 2019). All datasets used the North American Datum of 1983 (NAD 83). Vector data of townships and ranges were obtained from BLM California cadastral PLSS standardized data (USDOI 2019). A digital elevation model for Six Rivers was built from seven 1/3 arc-second tiles with a resolution of 10 meters (USGS National Elevation Dataset 2013). Vegetation data from Cal-Fire Fire and Resource Assessment Program (called "FVEG," hereafter) were used (California Department of Forestry and Fire Protection 2015). The wildlife habitat relationship class code in FVEG (Appendix S1: Table S3) was used to distinguish forest cover types at 30 × 30 m resolution. (Note that forest cover types, e.g., Klamath Mixed Conifer or Montane Hardwood, were capitalized in descriptions from FVEG and capitalization is preserved in this document [USFS 2010]. Douglas Fir refers to the cover type from FVEG, whereas Douglas-fir refers to *Pseudotsuga menziesii*.)

The spatial location of witness trees was determined by linking the unique point identifier from BLM's cadastral PLSS standardized dataset to the historical data. Each PLSS point code incorporates the meridian, township, section, and section/quarter corner and comes with latitude and longitude and elevation information (BLM 2006, USDOI 2019). PLSS codes were created for 13,600 witness trees, and FVEG vegetation polygon data were matched to those points.

The contemporary composition and structure of the forests in the Six Rivers' management area were quantified using the most recent 10 yr (2008–2017) of Forest Inventory and Analysis (FIA) data from the database version 1.8.0.0.1. FIA plots were clipped to the Six Rivers' extent and matched to FVEG classification types (Fig. 4). There were a total of 184 FIA plots sampled in Six Rivers. For trees >20 cm in diameter, we calculated density, basal area, and aboveground live tree biomass by FVEG vegetation type. To ensure a sufficient number of samples in each vegetation type, we combined the two chaparral habitat types present in Six Rivers, namely Mixed Chaparral and Montane Chaparral, into one. While the Mixed Chaparral tends to be floristically richer than Montane Chaparral, these two broadly defined types overlap and shrub species from two genera, *Ceanothus* and *Arctostaphyllus,* are common constituents (CDFW 2020). We also merged the red fir and white fir alliances into one True Fir alliance (Appendix S1: Table S3).

Fire and harvest spatial information were obtained from state and federal agencies, respectively. Fire perimeter data from 1908 to 2018 were obtained from Cal-Fire's ArcGIS geodatabase file, grouped by decade, and clipped to Six Rivers' boundary. Harvest and salvage spatial information in Six Rivers began as Ecological Unit inventory (EUI) classification and mapping starting in the late 1980s. (FACTS data were not available for Six Rivers National Forest, and data from the Ukonom region were unavailable). EUI's purpose was multi-pronged and included the following: estimating land productivity, understanding plant communities, determining long-term landscape processes, and identifying renewable products. In 1995, Six Rivers' office obtained ArcInfo and the ability to digitally map on the fly using geo-referenced Digital Ortho-photo quads (USDA Forest Service 2001). Between 1994 and 1999, Six Rivers' vegetation was mapped based on seral stage and potential natural vegetation type using aerial photography and orthophotograph quadrangles (USDA Forest Service 2001). An estimated 25% of the survey areas were ground-truthed (USDA Forest Service 2001).

Analyses

We evaluated the differences in forest composition and structure between the two periods by comparing means. Significant differences were defined as non-overlap in 95% confidence

intervals. A drawback with the Morisita II is that variance is not defined (Cogbill et al. 2018). Thus, we estimated confidence intervals using resampling methods (Crowley 1992). Specifically, we resampled with replacement our point estimates of density and basal area 1000 times. For each vegetation type, we reported the mean and 95% confidence interval of these 1000 realizations. For FIA results, we reported the mean and calculated 95% confidence intervals using the t-distribution.

To estimate aboveground live tree biomass (AGL) for the settlement era, we developed a plot-level basal area to AGL transfer function from the contemporary FIA data. We explored several different functional forms to predict AGL as a function of basal area. We also tested for differences by vegetation type. We compared our candidate models using the Akaike information criterion corrected for small sample sizes (AIC_c). The linear log–log functional form with a single equation for all forest types best fits the data ($\Delta AIC_c = 7.1$). Specifically,

$$\ln(\text{AGL}) = 0.997 \times 1.234 \times \ln(\text{basal area}) \quad (2)$$

with AGL measured in Mg/ha and basal area in m^2/ha ($p < 0.001$ and $R^2_{adj} = 0.97$). We used Eq. 2 to calculate AGL for each point based on the bias-corrected basal area. We then summarized AGL by vegetation type using the resampling approach described above. These analyses were conducted using R statistical software (R Core Team 2018; version 3.5.1).

Results

Changes in forest structure

The contemporary forest in Six Rivers contains three times more trees than in the settlement era: 255 trees/ha vs 81 trees/ha. For the four of the six vegetation alliances studied, the mean density (trees/ha) was significantly lower (±2 SE) in settlement-era forests than in contemporary forests (Fig. 5, Appendix S1: Tables S4, S5). These alliances included Douglas Fir, Klamath Mixed Conifer, Montane Hardwood-Conifer, and True Fir. The mean densities of Chaparral and Montane Hardwood, however, did not change over time. The vegetation alliance with the largest significant increase in density was Klamath Mixed Conifer with a mean change of

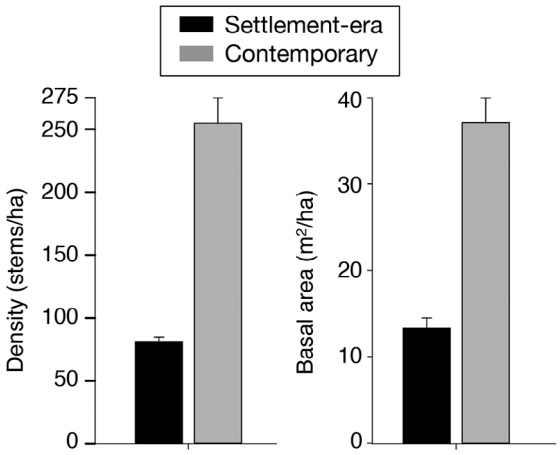

Fig. 5. Changes in forest structure for Six Rivers National Forest. Settlement-era estimates (bias-corrected) from General Land Office survey data (1880s). Contemporary estimates from FIA Phase 2 inventory plots (2008–2017). Results include only trees >20 cm DBH. Means ± 95% confidence interval reported.

300%. The greatest increase in basal area since settlement occurred for Klamath Mixed Conifer with a sevenfold increase. These changes in basal area translated into a net increment in aboveground live tree biomass of 175 Mg/ha since the settlement era (Table 1). The increases in biomass over time by vegetation type ranged from a doubling (Montane Hardwood, Montane Hardwood-Conifer, and True Fir) to a tripling (Douglas Fir) to a ninefold increase (Klamath Mixed Conifer).

Changes in forest composition by relative basal area

Forest composition during the settlement era was predominantly Douglas-fir (34.4%), though pine (24.2%) and oak (21.9%) comprised high percentages of the forest vegetation, with moderate levels of madrone (7.0%), low levels of true fir (6.5%), and less than 5% containing cedars, other conifers and other hardwoods (Fig. 6, Appendix S1: Table S6). Contemporary forests are increasingly Douglas-fir dominant (45.2%), although the pine and true fir alliances also slightly increased (Fig. 6, Appendix S1: Table S7). Oaks, however, decreased by more than half since the 1880s and now make up a percentage of the forest similar to true firs. The compositional changes observed across Six

Table 1. Comparison of aboveground live tree biomass (Mg/ha) at Six Rivers National Forest.

Contemporary Vegetation Alliance	Settlement			Contemporary		
	Mean	SE	CI	Mean	SE	CI
Chaparral	80	13.0	57–107	70.2	25.8	21–119
Douglas Fir	103	10.7	82–124	291.3	20.6	257–326
Klamath Mixed Conifer	42	6.8	29–57	397.8	97.1	202–593
Montane Hardwood	149	26.2	104–203	105.4	37.5	41–170
Montane Hardwood-Conifer	129	24.5	88–181	354.4	47.3	271–438
True Fir	46	9.2	30–66	290.1	32.7	235–346
Other	88	32.9	38–168	120.9	27.4	72–170
All	100	7.1	87–115	261.0	14.7	237–285

Notes: Results for the six most common contemporary vegetation types (alliances). Two types (Chaparral and True Fir) represent higher order aggregations of two alliances. Results include only trees> 20 cm DBH. Means and standard errors (SE) reported for each vegetation alliance. Confidence interval (CI) defined as the range of values between the 2.5% and 97.5% percentiles (Settlement: calculated from resampled estimates; contemporary: calculated using a t-distribution).

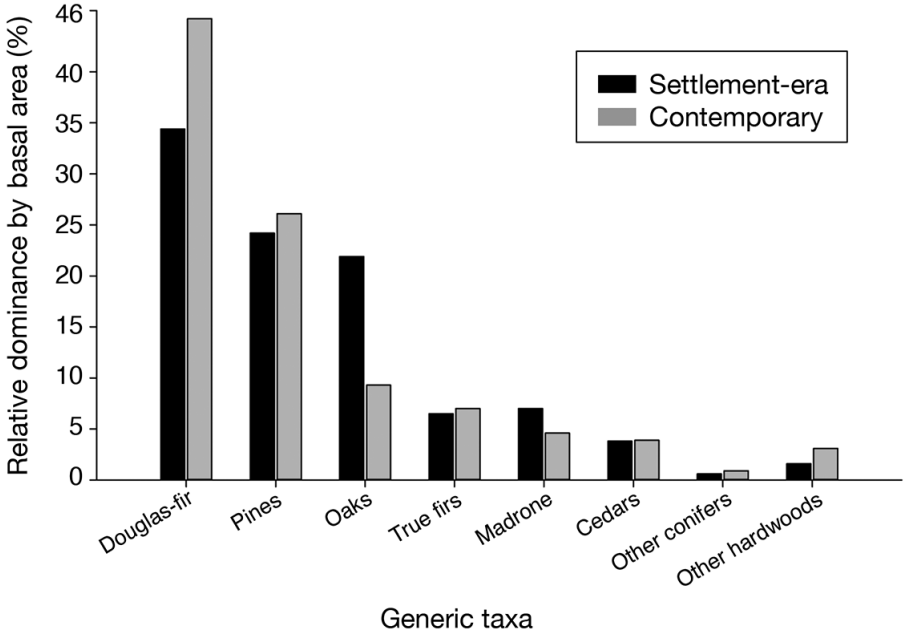

Fig. 6. Changes in forest composition in Six Rivers National Forest. Settlement-era estimates from General Land Office survey data (1880s). Contemporary estimates from FIA Phase 2 inventory plots (2008–2017). Compositional information based on generic taxa; relative dominance defined as relative basal area.

Rivers were consistent within alliance types. For example, the relative abundance of Douglas-fir increased in Chaparral and Douglas Fir types, and the proportion of pines increased in Klamath Mixed Conifer, Montane Hardwood, and Montane Hardwood-Conifer, while the proportion of oaks decreased (Appendix S1: Table S6 and S7).

Drivers of change

During the twentieth century, particularly in the late 1940s, 50s, and 60s, major harvest and logging efforts took place in Six Rivers (Table 2, Conners 1998). Although almost certainly an underestimate, geospatial data indicate management activity (Fig. 7) that occurred on 25% of the total forest area (Appendix S1: Table S8). Of the

Table 2. Total timber harvest estimates for 1920, 1945, 1954, and 1955 in the in Six Rivers' region.

Date	Harvest estimates (million board feet)
1920	0.384
1945	0.480
1954	48.1
1955	76.6

Note: Estimates are presented in million board feet to match original reports (Conners 1998) and to avoid confounding harvest estimates by any changes in the scaling system over time (Spelter 2002).

known harvested areas, three seral stages—pole harvest, shrub harvest, and early harvest—accounted for 80% of the total (USDA Forest Service 2001). Based on assessments in the mid-1990s, stands classified as pole and shrub harvests were considered the result of clearcutting while the early harvest category referred to stands with less intensive methods of harvesting (USDA Forest Service 2001). Extensive logging during the twentieth century was not accompanied by a replanting strategy (Conners 1998) and is not consistent with densification trends.

Mid-century was also a period of active fire suppression. Fire perimeter data show a marked decrease in fire activity, with nearly total cessation between 1940 and 1969 (Fig. 8). Spatially, large recent fires (2000–2018) tended to occur in areas where harvests were not recorded, such as the Ukonom area in eastern Six Rivers and along the California-Oregon border (Fig. 7). The acreage burned gradually increased through the 1970s, 80s and 90s, then quadrupled in the 2000s to 325,000 ha. Compared to the 2000s, fewer hectares burned in the 2010s, but the decadal average was greater than any other decade between 1908 and 1999. Between 2000 and 2018, over 500,000 ha burned, compared to nearly 200,000 ha during the entire previous century (Table 3). Fire rotations (Heinselman 1973) are the number of years needed to burn an area the size of the study area given the extent of burning in that period (Heinselman 1973, Agee 1993). Fire rotations, correspondingly, varied between 1908–1995 and 1908–2018; the fire rotation was three times longer during the twentieth century compared to the last 110 yr (Table 3). Underlying the effects of fire suppression were changes in climate that were consistent with warming trends (Fig. 9). Precipitation trends, however, did not change substantially, suggesting that this region did not experience the pronounced drought of 2012–2015.

Discussion

Our comparison of PLSS data to modern vegetation data indicates stark changes in forest structure—namely statistically significant increases in tree density and basal area—as well as changes in composition. Densification was expected. It has been observed in several locations near Six Rivers: Hayfork in Shasta–Trinity National Forest (Taylor and Skinner 2003), Blacks Mountain Experimental Forest in the Southern Cascades (Dolph et al. 1995, Ritchie et al. 2008), and Lassen Volcanic National Park (Taylor 2000, Skinner and Taylor 2018). However, the magnitude of change shown by this reconstruction was considerable: The contemporary forest in Six Rivers contains three times more trees than in the settlement-era forest and a comparable increase in basal area (Appendix S1: Tables S4, S5). Densification has occurred elsewhere in California, but not to such a degree. For example, a comparison of 1911 inventory data to the contemporary forest revealed a near doubling of live basal area in the central Sierra Nevada (Collins et al. 2017). On the other hand, the density of historical mixed conifer forests in the Oregon Cascades is comparable to the density of Six Rivers' settlement-era forests. A reconstruction of a 1920s timber inventory showed an average of 14 ± 7 m^2/ha (mean $\pm$ SD, Hagmann et al. 2014) compared to our average of 13.3 ± 0.6 m^2/ha.

Despite a lack of causal evidence, fire suppression is the most likely explanation of the widespread differences in forest structure and composition since settlement in Six Rivers. This conclusion is consistent with other settlement-era forest reconstructions from the Oregon Cascade Range and the Sierra Nevada that suggest fire exclusion played a dominant role in forest densification (Collins et al. 2011. 2015, 2017, Hagmann et al. 2013, 2014, 2017, Stephens et al. 2015, Collins et al. 2017). The onset of forest changes in Six Rivers coincides with the start of fire suppression (i.e., between 1903 and 1905; Shrader 1965, Crawford 2012). Fire scar studies from the Klamath Mountains indicate a pre-settlement fire regime characterized by small, low-intensity,

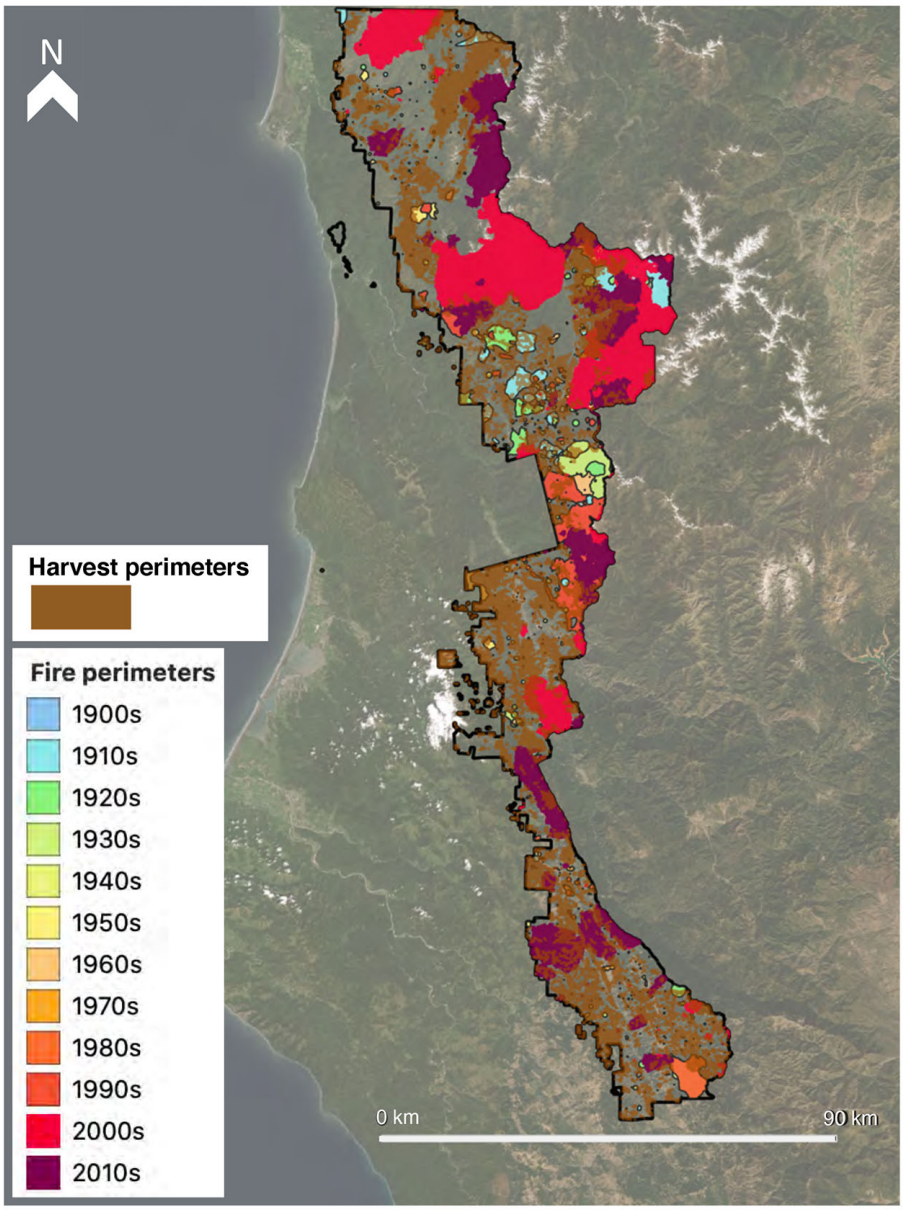

Fig. 7. Harvest and salvage perimeters in Six Rivers (USDA Forest Service 2001) overlaid on fire perimeter data, which has been grouped by decade.

frequent fires and occasional large, intense burns (Crawford 2012). The pre-Euro-American fire rotation of 19 yr increased to 238 yr after 1905 (Taylor and Skinner 2003). Fire perimeter records, too, show a near cessation of fire activity over a 29-yr period (1940–1969) in an area where frequent fire from Native burning and lightning ignitions was common over the last millennia, according to fire scar and charcoal records (Crawford et al. 2015, Skinner et al. 2018).

Fire suppression is also consistent with the compositional changes in Six Rivers. For example, long-term pollen records from two lakes in Six Rivers indicate a compositional shift to shade-tolerant Douglas-fir and tanoak at the expense of shade-intolerant taxa such as oaks during the last

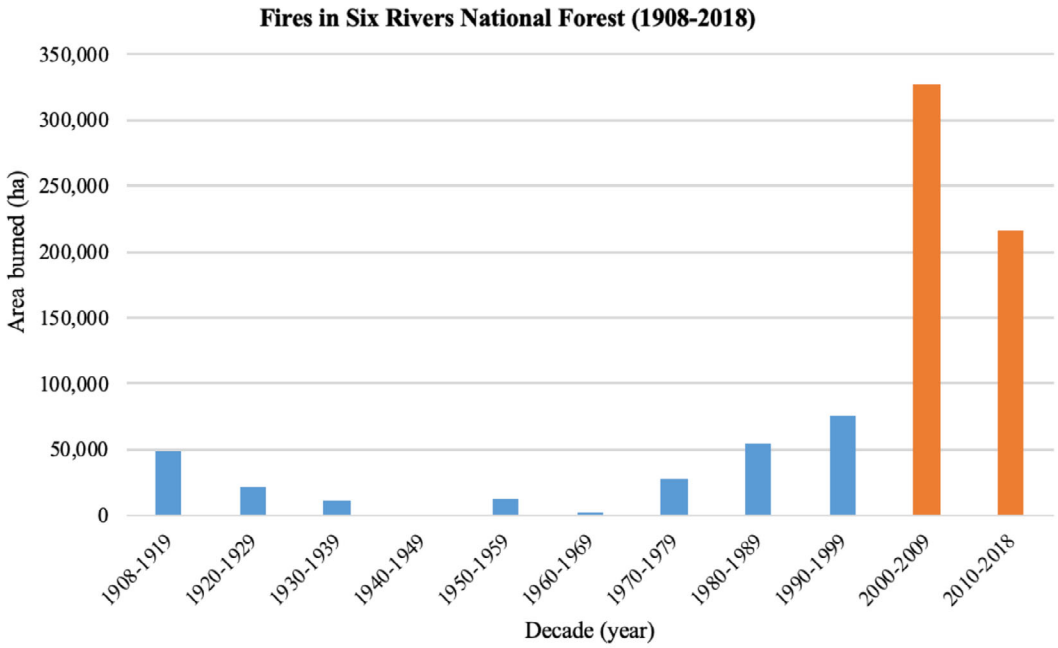

Fig. 8. Area burned (ha) by decade in Six Rivers National Forest from 1908 to 2000 (blue bars) and 2000–2018 (orange bars).

Table 3. Fire rotations (year) in Six Rivers National Forest (394,420 ha) during two time windows in the suppression era.

Time period	Years in observation interval	Area burned (ha)	Fire rotation (year)
1908–1995	87	194,157	176.7
1908–2018	110	801,236	54.1

century (Engber et al. 2011, Crawford 2012, Crawford et al. 2015). Closed-forest indicators such as Douglas-fir strongly increased over the last century, during which time charcoal and fire peak magnitudes dropped off (Crawford et al. 2015). We found similar compositional change—that is, an increase in Douglas-fir abundance and a reduction in oaks—which aligns with the pollen record that shows a 3000-yr historic high of Douglas-fir and coinciding oak decline in modern times (Crawford et al. 2015). In contrast, a study that used PLSS data for canopy cover reconstruction in southwest Oregon found a settlement-era landscape mostly covered by closed forests and woodlands, with a minor amount of open plant community types (Duren et al. 2012). However, this study differs from ours in both its analysis and location. Duren et al. (2012) calculated density (trees/ha) by using "an alternative point-centered quarter method that requires random distribution around a section corner," in place of Morisita's equation. Additionally, they reconstructed canopy cover in valleys and foothills across a greater elevation gradient (280–1480 m) than this study.

Timber harvesting and climate warming are also drivers of vegetation change, but they are likely not the dominant forces shaping the observed shifts in forest structure and composition. The type of timber harvests undertaken in Six Rivers would likely have lowered density. Harvest and salvage data (USDA Forest Service 2001), though incomplete, generally aligned with written records of timber extraction for the forest (Conners 1998). Although some silviculture treatments might increase forest density (e.g., removal and replanting at high density), extensive replanting programs following clearcutting were specifically not undertaken in Six Rivers, according to timber records (Conners 1998). Extraction would therefore be consistent with net forest thinning—the opposite of the trend

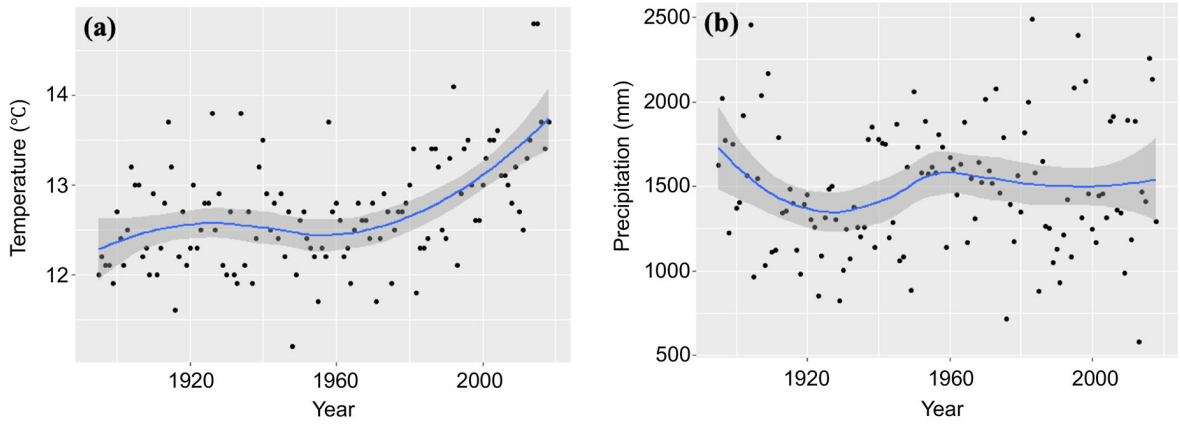

Fig. 9. Trends in (a) mean annual temperature (°C) and (b) total precipitation (mm) at Lake Ogaromtoc, a lake in Six Rivers. Data are from PRISM 4km database from 1895 to 2018. Blue tend lines represent linear splines fit by locally estimated scatter plot smoothing. Gray buffers represent the standard error of the estimate.

reported (Fig. 5). Interestingly, areas without historical harvests were also areas with large recent fires (Fig. 7), possibly because these areas were extremely dense with a high fuel load. Although regional climate warming has occurred in the study area since the end of the Little Ice Age in 1860, the expected impacts of climate warming are not consistent with our results. Under a warming climate, a greater number of fire events and more open forest structure would be expected (Miller and Urban 1999), but the pollen and fire scar record has shown a decrease in fire events and an increasingly closed-forest structure (Crawford 2012, Crawford et al. 2015).

Although we showed that forest structure was substantially less dense during the settlement era, the montane hardwood and chaparral vegetation alliances did not follow this trend. The lack of structural changes in the montane hardwoods might be related to widespread timber improvement efforts that favored conifer recruitment. For example, in the 1970s, hardwoods were systematically killed to support commercial conifers in the Shasta–Trinity National Forest, particularly in areas where conifer regeneration had started in the understory (C. Skinner, *personal communication*). This effort may have occurred in Six Rivers and would be consistent with reduced montane hardwood densification compared to other alliances.

Chaparral in the Klamath is described as persistent shrub-dominated communities with the stability attributed to both edaphic conditions (e.g., moisture limitations) and frequent fires that constrain tree encroachment (Detling 1961). Given the mix of *Ceanothus* and *Arctostaphylos* cover (Appendix S1: Table S3) and the relative abundance of trees in both settlement and contemporary Chaparral (Appendix S1: Tables S6, S7), the Chaparral alliance in Six Rivers appears to be what Cooper (1922) describes as the conifer forest chaparral association. This association is a mix of what Cooper terms "broad-sclerophyll" shrubs and "narrow-sclerophyll" (i.e., needled-leaved) trees. The structure of this alliance has remained notably consistent since settlement, a result that suggests these associations are maintained more by edaphic conditions than the fire regime. However, we cannot explicitly exclude the role of fire given the absence of definitive evidence that fire did not occur in the chaparral zones. In contrast to the constancy in tree density, tree composition has switched from one dominated by pine in the settlement era (40.2%, Appendix S1: Table S6) to Douglas-fir in the contemporary era (39.6%, Appendix S1: Table S7).

Currently, Six Rivers is Douglas-fir and pine dominated. In the settlement era, Douglas-fir and pines were present at high percentages, but oaks were also a dominant feature, in part because they were an important cultivar for Native use. Severe oak decline has been known to follow European settlement in northern and southern California (Mensing 1992, Scholl and Taylor 2010, Cocking et al. 2012, 2014, Stahle et al. 2013). This

decline has been attributed to fire suppression that resulted in composition shift from shade-intolerant, fire-resistant pines, and oaks to fire-intolerant and shade-tolerant firs and cedars (Taylor and Skinner 2003, Scholl and Taylor 2010). We also found this trend. Even though Douglas-fir and mixed conifers (pines) were targeted by logging efforts, their densities still increased.

Debates concerning historic forest density in dry, fire-prone, pine-dominated, and mixed conifer forests are ongoing and unresolved (e.g., Hagmann et al. 2018, Baker and Williams 2018). These discussions have focused on the fire regime that could support reconstructed forest conditions, namely whether the pre-settlement landscape had low- to moderate-severity wildfires that maintained a low-density forest dominated by large trees (e.g., Collins et al. 2011, Hagmann et al. 2013), or whether mixed-severity and high-severity wildfires supported medium- to high-density forests (e.g. Baker and Williams 2018). An important element of this debate is the method used to reconstruct forest conditions from PLSS data. Although our structural estimates are considerably lower than historic estimates from the Sierra Nevada, our PLSS approach nonetheless broadly corroborates other findings, such as 1911 inventory estimates (Collins et al. 2017), tree ring reconstructions that were calibrated with a 1911 timber inventory (Scholl and Taylor 2010), and other western PLSS studies (e.g., Hagmann et al. 2018) and inventory reconstructions (Hagmann et al. 2013, 2014). Additionally, our methodology was consistent with the methodology used in the vast majority of PLSS reconstructions (Bouldin 2010, Goring et al. 2016, Hanberry et al. 2019). That is, we applied methods proven to be accurate for California conifer forests (Levine et al. 2017), supported by PDE sampling theory (Cogbill et al. 2018).

Limitations

Within the PLSS research community, many previous studies concerning PDE reconstruction have assumed estimates are accurate (meta-analysis from Cogbill et al. 2018), while other studies have focused on developing statistical techniques to account for known PLSS sampling biases (Bourdo 1956), as well as provide a means to correct for surveyor biases (e.g., Kronenfeld and Wang 2007, Kronenfeld 2015, Goring et al. 2016, Cogbill et al. 2018; Cogbill, *unpublished manuscript*). In a comparison of mapped forest stands in California, the Morista II was consistently the most accurate PDE despite a wide range of tree densities and spatial distributions (Levine et al. 2017). We also used empirically derived bias corrections (Cogbill et al. 2018) to increase the reliability of our historical estimates. Together, these methods accommodate the complexity of the vegetation and limitations of the data.

Correcting for surveyor biases in witness tree selection in PLSS datasets is an active area of research. The four corrections employed in this study (Appendix S1: Table S2) provide a detailed picture of the mechanics of the original survey, as well as an estimate of impact of these mechanics on the results (Goring et al. 2016, Cogbill et al. 2018). Compared to uncorrected results (Appendix S1: Tables S9 and S10), bias-corrected density was an average of 12.7% lower across all alliances due to fewer trees meeting the >20 cm DBH cutoff. In contrast, the corrected basal area was 28.3% larger since the exclusion of smaller trees has little impact on total basal area. The overall small error in witness tree placement (i.e., less than equal halves correction = 1.14 for all points, Appendix S1: Table S2) had the benefit of authenticating Six Rivers' field data, an important conclusion in the wake of fraudulent land surveys found in the eastern USA. Surveyor discrimination against large trees (>35 cm dbh) has also been postulated (Bourdo 1956, Manies et al. 2001, Schulte et al. 2007, Rhemtulla et al. 2009, Bouldin 2010). The comparison of fitted size frequency functions (e.g., Bouldin 2010) and the observed number of large trees (e.g., Bourdo 1956, Williams and Baker 2010, Tulowiecki 2014) are consistent with a quasi-reverse J distribution of trees and not necessarily bias. In any case, bias against small trees is much more important than any large tree bias that would require bypassing a larger tree in order to use a smaller farther tree. In this study, the density of trees ≥50 cm was 11 trees/ha. When using the definition of "large" tree for Douglas-fir (trees ≥ 92 cm, Lutz et al. 2009), the density was 1 tree/ha; the density at the next largest cutoff (≥61 cm, Lutz et al. 2009) was 7 trees/ha. The 95th percentile of tree size for our data was ≥76 cm (5 trees/ha).

We also made corrections to improve taxonomic resolution. We found that some surveyors

were careful taxonomists who identified species with similar forms (e.g., true oaks from tanoaks), while other surveyors lumped taxa. We corrected for Douglas-fir/true fir aggregation using an elevation cutoff (Appendix S1: Figure S1a), but kept the generic oak category because the elevation ranges of tanoak and true oaks overlap, making elevation-based discrimination impossible (Appendix S1: Figure S1b). Knowledge of common names used during settlement allowed us to correct Douglas spruce to Douglas-fir. We encountered incomplete data and noted three types of omissions, which were treated differently (see methods) in accordance with previous reconstructions (Cogbill et al. 2018). Fire perimeter and harvest data are also likely underestimates of landscape-scale management strategies, but they constitute the best available information for the last century.

Lastly, all methodologies used to reconstruct historic forest conditions have tradeoffs. For example, a major strength of PLSS reconstruction lies in its regional coverage and replicated methodology (Bourdo 1956), compared to twentieth-century inventory data which are not as extensive (Collins et al. 2011, 2017), or dendrochronological reconstructions, which provide great detail about stand dynamics but are spatially restricted (Taylor and Skinner 2003, Scholl and Taylor 2010). The type of reconstruction method greatly influences not just the research question that can be answered, but also the management implications of the findings. The basis for management decisions can be greatly strengthened by combining multiple corroborating historic or paleo-records from different spatial resolutions (Maxwell et al. 2014). The reconstructions in this study are geographically extensive but coarse, which may have masked important settlement-era structural or compositional variation. Given that Six Rivers is a highly diverse region—indeed it is unique in California for its floristic diversity—our results should be integrated with other landscape-specific reconstructions (e.g., the Hayfork study, Taylor and Skinner 2003) to inform management decisions.

Potential management implications

Reconstructed baselines have contributed to debates about restoration by illuminating conditions considered to be ecologically resilient (Swetnam et al. 1999), particularly for fire-suppressed forests in western North America (Larson and Churchill 2012, Churchill et al. 2013). Restoration priorities already exist for other California landscapes, such as the Sierra Nevada, but different targets may be needed for northwestern California. Although Six Rivers have greatly densified over the past century, its historical baseline likely supported a more open, smaller-tree landscape, compared to the open, large tree landscape of the Sierra Nevada forests. Hardwood decline since settlement may also factor into the design of restoration treatments for the area. Management objectives must also meet societal demands for ecosystem services and can be informed by understanding forests of the past. For instance, a better understanding of settlement-era forests could inform engaged citizens about the structural diversity of iconic landscapes.

Our findings indicate a doubling of aboveground live biomass in Six Rivers since settlement and are important in the context of climate change mitigation goals. California is one of the few jurisdictions in the world to mandate limits to greenhouse gas emissions and therefore has an urgent need to track and quantify forest carbon (AB-32 2006, Forest Climate Action Team 2018). Fire exclusion in California forests has led to a reduction in large trees and an increase in smaller trees (Taylor et al. 2014, McIntyre et al. 2015). This increase in density boosts carbon stores above that of frequently burned forests, but small-tree carbon storage is unstable in the long-term (Hurteau et al. 2019). Quantitative reconstructions of settlement-era forest carbon stocks can impart crucial ecological information —including tempering expectations around forests' ability to sequester carbon in fire-prone forests—as the state endeavors to meet its climate mitigation goals.

Conclusion

Our work reconstructs a large forested area and provides a landscape-level structural description. For Six Rivers National Forest, we found clear differences between settlement-era forest conditions and modern forest conditions. We also demonstrated a reconstruction methodology that deals with spatial complexity and is

accurate under PLSS conditions (Levine et al. 2017), correcting for biases (Cogbill et al. 2018). These analytical steps are generalizable and can be applied to future PLSS datasets in western landscapes. This work also elucidates the drivers of change in Six Rivers. Fire suppression likely increased forest density despite widespread timber extraction. The area has been actively managed to varying extents for centuries and probably longer, and this snapshot in time captures the rapid transitional era from Native management to settlement. It is one of many potential baselines.

Baselines provide an understanding of relative change: How much did a system change relative to a reference state in the past? For California ecosystems, which have undergone vast change since active fire suppression policies, the settlement era represents a useful historical baseline when restoration targets are predicated on presettlement fire regimes (Churchill et al. 2013). By building a continuum of baselines, ecologists can determine how the current landscape has deviated from previous points in time and impart context for current tree populations, which has implications for ecosystem services and societal demands.

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