

## Land ownership and 20th century changes to forest structure in California

Kelly Easterday<sup>a</sup>, Patrick McIntyre<sup>b</sup>, Maggi Kelly<sup>a,c,\*</sup>

<sup>a</sup> Department of Environmental Sciences, Policy and Management, University of California, Berkeley, 134 Mulford Hall #3114, Berkeley, CA 94720-3114, United States

<sup>b</sup> Western North America NatureServe, 1680 38th St., Suite 120, Boulder, CO 80301, United States

<sup>c</sup> University of California Division of Agriculture and Natural Resources (UC ANR), United States



### ARTICLE INFO

#### Keywords:

Forest structure  
Forest change  
Land management  
Land ownership  
California  
Vegetation Type Mapping (VTM)

### ABSTRACT

Forests in California have changed dramatically during the 20th century. Shifts in forest structure including densification, declines in large trees and tree basal area have altered the function, productivity, and resilience of modern day forests. Attributing these changes to specific drivers is increasingly important for effective management of healthy and productive forests. Previous studies focus on climatic (temperature, precipitation, climatic water deficit), disturbance (fire), geomorphological (topography, soil types), and anthropogenic (logging, fire suppression) drivers, but few studies evaluate large scale change in forest structure across land ownership type. In this paper, we investigate 20th century changes to forest structure across six land ownership classes in California. We compare historical and contemporary forest structural data and find that declines in large trees and increases in forest density are consistent across the state. This pattern is most pronounced on private timberlands, which experience up to 400% regional increases in small tree (< 10.2 cm) density since 1930. All land ownership classes experience declines in large trees, while private timberlands, national parks and wilderness areas experience the most extreme change with an average loss of over 83% and 71% respectively. We conclude that understanding patterns of change across land ownership is essential for targeting federal, state, and locally specific policies that foster healthy and resilient forests for the future.

### 1. Introduction

Present-day forests in California are markedly different from their early 20th century counterparts. Numerous studies show changes in the structure and composition of California's forests by documenting shifts towards more small and fewer large trees (Dolanc et al., 2013a; Lutz et al., 2009; McIntyre et al., 2015); more structurally homogenous stands (Maxwell et al., 2014); and changes in species composition (McIntyre et al., 2015; Minnich et al., 1995; Taylor, 2000; van Mantgem et al., 2013). These changes vary over space and time due to the interaction of biophysical and socio-ecological drivers. In California, large tree decline has been attributed to increased temperatures, variable precipitation, and water deficit (Das et al., 2013; McIntyre et al., 2015; van Mantgem et al., 2013, 2009), as well as historical and contemporary legacies of logging (Knapp et al., 2013; Laudenslayer and Darr, 1990; McKelvey and Johnston, 1992; Beesley, 1996). Large scale forest densification, in part, is the result of nearly a century of widespread fire suppression efforts (Dolanc et al., 2014; 2013b; Lutz et al., 2010; Minnich et al., 1995), with previously logged lands showing greater densities than surrounding landscapes (Naficy et al., 2010). The

lack of natural fire and increasing forest density positively correlate with a shift in species composition favoring shade-tolerant species (Miller et al., 2012; Taylor and Skinner, 2003). Such legacies of logging and forest fire suppression have profound impacts that can persist for decades after cessation, altering both the state of contemporary landscapes and influencing future trajectories of change (Perring et al., 2016). These legacies are often specific to the land management practices of a given land owner at a specific time. Given the difficulty in disentangling regional biophysical and socio-ecological drivers, an understanding of forest structure change across land ownership is needed. Additionally, determining how long-term patterns of change vary across ownerships is necessary to help target federal, state, and locally specific management policies that foster healthier more resilient forests for the future.

Land ownership has been used to understand the long-term effects of and variation in land management practices; especially when spatially explicit data on management practices are unavailable or incomplete. In agricultural landscapes for example, Lunt and Spooner (2005) showed that land ownership is predictive of disturbance and therefore can be used to better understand past, current, and future

\* Corresponding author at: Department of Environmental Sciences, Policy and Management, University of California, Berkeley, 134 Mulford Hall #3114, Berkeley, CA 94720-3114, United States.

E-mail addresses: [Patrick\\_McIntyre@NatureServe.org](mailto:Patrick_McIntyre@NatureServe.org) (P. McIntyre), [maggi@berkeley.edu](mailto:maggi@berkeley.edu) (M. Kelly).

<https://doi.org/10.1016/j.foreco.2018.04.012>

Received 26 February 2018; Received in revised form 3 April 2018; Accepted 6 April 2018

Available online 14 April 2018

0378-1127/ © 2018 The Authors. Published by Elsevier B.V. This is an open access article under the CC BY-NC-ND license (<http://creativecommons.org/licenses/by-nc-nd/4.0/>).

patterns of biodiversity in fragmented areas. In forested landscapes, Turner et al. (1996) showed that property boundaries create quantifiable patterns of land use change and that the similarities in these changes across ownerships are reflective of specific management goals. They showed that while forests on private lands were more fragmented than those on public lands, when areas had a common management goal (e.g. active timber harvesting) forests displayed similar spatial patterns.

Studies documenting changes in forest structure across land ownership at a large scale in California are rare. In this paper, we compared historical 1930s Vegetation Type Mapping project (VTM) forest survey plots with modern 2000s Forest Inventory and Analysis program (FIA) forest inventory plots and examined changes in measures of forest structure: stems per ha per size class (small, medium, large, and total) and total basal area ( $\text{m}^2/\text{ha}$ ).

We assessed change over time in these variables across six California land ownership classes: (1) Private Timberland (PT), (2) Non-Wilderness National Forest (NWNF), (3) Non-Wilderness Bureau of Land Management and Tribal Lands (NWBTL), (4) Private Protected lands (PP), (5) State and Regional Parks (SR), and (6) National Parks and Wilderness areas (NPW). We distinguished changes in stand density and size class distributions across land ownership and investigated differences in these measures between the six land ownership classes. We address the following questions: (1) have the numbers and sizes of trees changed significantly over time across all six land ownership classes; (2) how do changes in the number of trees per size class and forest densification vary by land ownership; and (3) do these patterns suggest differing land use legacies across ownership classes.

## 2. Methods

### 2.1. Study area

Our study area includes the forests of the California floristic province including the Northwestern, Sierra Nevada, Central, and South regions. This area has a Mediterranean climate of dry summers and wet winters. Regional differences in climate and soil characteristics are captured by geomorphic regions that are largely determined by the mountain ranges that divide them. The six land ownership classes investigated cover a range of ecoregions and vegetation types and are also representative of regional characteristics that correspond with spatial patterns of ownership.

California is a complex mosaic of land ownership, with federal, state, tribal, and local entities protecting and managing land. Nearly 150,000  $\text{km}^2$  of forest are managed by distinct ownerships with varying degrees of protection, production, and conversion of forests. 48% of California's forested lands (63,130  $\text{km}^2$ ) are managed by the U.S. Forest Service as National Forests, 51,395  $\text{km}^2$  (39%) are managed as private timberland encompassing both industrial and non-industrial private forest land. Approximately 8095  $\text{km}^2$  (6%) is set aside as forest reserves and managed through Wilderness designation or as a National Park, while various other private and public entities manage the remaining ~8900  $\text{km}^2$  (7%) (McIver et al., 2015).

PT includes both industrial and non-industrial forest lands, however the majority of plots investigated in this study were on lands managed for industrial timber. Generally, PTs are located on mixed conifer forests in the Northern Sierras, Klamath, and Cascade Ranges, and in the Douglas Fir and Redwood forests of the North and Central Coasts (Stewart et al., 2016), and tend to occur at lower elevations. NWNF areas are also located extensively in mixed conifer forests, interspersed with pockets of Red Fir, Eastside Pine, and Ponderosa Pine and extending into the hardwood forests and woodlands of the Central and South Coast.

NWBTL lands are distributed in the low elevations of the North Coast, Mojave, Sierra, Central, and South Coast regions, and in our study area, consist of primarily conifer forests and woodlands concentrated in the

Eastern Sierra Nevada, Klamath Ranges, and South Coast Ranges. Very few of our study plots occur on tribal lands, therefore NWBT is primarily illustrative of BLM lands.

PP land is scattered in the matrix of federal, state, and private ownerships, generally representing hardwood woodlands and hardwood forests. SR lands in our study are primarily hardwood woodlands within the greater San Francisco Bay Area. NPW areas are representative of National Parks and all federal agency owned wilderness. These lands are primarily located in the Sierra Nevada region, as well as the Southern Sierra and Transverse Ranges. Forest types in NPW are primarily mixed conifer but also higher elevation Red Fir, Lodgepole Pine, Jeffrey Pine, and hardwood forest types. The spatial distribution of ownership types expresses regional concentrations owing to California's complex land settlement history, therefore the patterns represented in this study are reflective of differences across ownership that are particular to the regions where the plots are located.

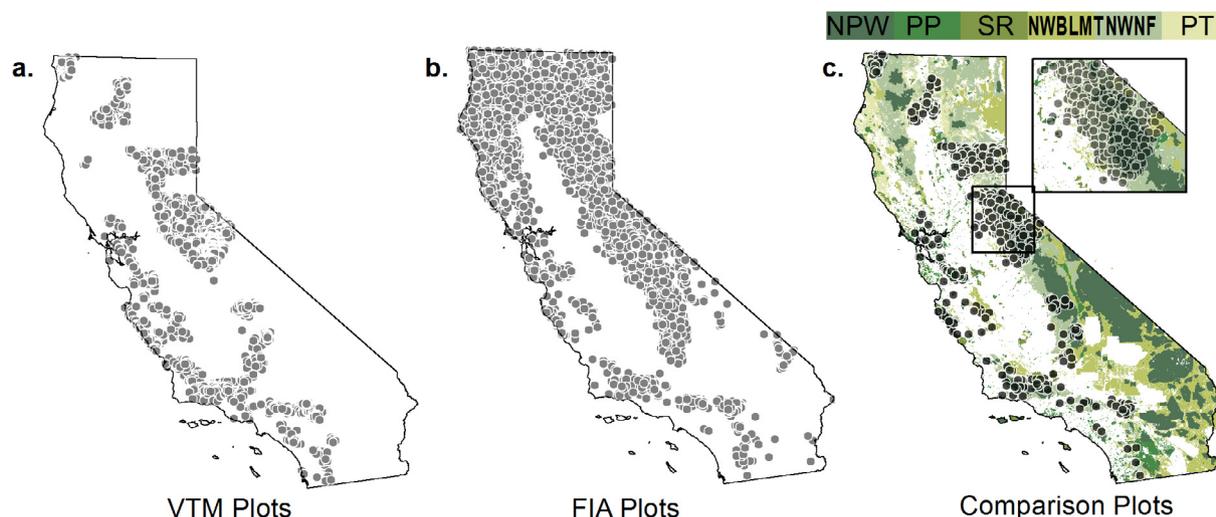
### 2.2. Data

#### 2.2.1. Historical and contemporary forest inventory data

The Vegetation Type Mapping (VTM) project is a series of landscape surveys conducted by the US Forest Service that covered ~40% of California between 1928 and 1940 that resulted in a large collection of 350 vegetation maps, 18,000 vegetation plots, over 3000 photographs and ~20,000 herbarium specimens (Wieslander, 1935). These data are digitized and georeferenced (see Kelly et al., 2005; Kelly et al., 2016; Kelly et al., 2017) and available for download via an open API and for download ([vtm.berkeley.edu](http://vtm.berkeley.edu)). In this study, we use the vegetation plot data, including geolocated information on numbers, diameter, and species of trees as well as other ancillary environmental information (e.g. elevation) associated with the marked plot location (Fig. 1a). The VTM crews conducted complete inventories of all trees over 10.2 cm diameter at breast height (DBH) within 20 m by 40 m (800  $\text{m}^2$ ) rectangular plots. The trees were tallied by species into four individual size classes: 10.2–30.4 cm, (4–12 in), 30.5–60.9 cm (12–24 in), 61.0–91.3 cm (24–36 in), and > 91.4 cm (> 36 in) (Kelly et al., 2005).

The VTM survey began in 1928, just after the beginning of large scale forest fire suppression across the state and in most areas before the 1940s and 1950s peak in forest harvesting. Today, the VTM collection serves as one of the only comprehensive datasets describing the California landscape in the early 20th century. Working with historical datasets requires the acknowledgment and examination of challenges such as plot geolocation error and potential bias. In the VTM dataset for example, plot location is derived from original markings on historical topographic maps and positional error is estimated to be ~200 m (Kelly et al., 2005) per plot which can affect direct plot comparisons or plot resurveys, especially in highly heterogeneous regions (Keeley, 2004).

The protocols behind VTM methods have raised questions about biased sampling favoring undisturbed forests. However, there is no evidence of bias suggested in the original VTM manual (Wieslander et al., 1933), or in the sample plot distributions, yet there are competing patterns of change when comparing FIA and VTM estimates to other historical comparisons. Some studies using alternative comparison datasets or plot resurvey have shown similar patterns of declines in large trees (e.g. Lydersen et al., 2013; van Mantgem et al., 2009) as the VTM dataset, while other studies have shown declines in large trees on some ownership classes but not on others, and increases in basal area across types (Collins et al., 2017; Lydersen et al., 2013). These disparities are difficult to verify as the datasets in question are not directly comparable but do require a cautionary approach to interpreting changes in large trees and biomass. There is no record of intentional bias in the selection of VTM plot locations the locations were chosen as representative samples of vegetation types being mapped (Wieslander et al., 1933), and have been shown to have a similar sampling densities across elevation and latitude as FIA plots which are determined randomly using a grid system (Dolanc et al. 2013a). Despite these potential shortcomings,



**Fig. 1.** Locations of historical and contemporary forest structure plot data for: (a) VTM (1930s–1940s); (b) FIA (2000–2010); and (c) comparison plots used in analysis and spatial distribution of ownership classes. Map 1(c) shows ownership classes with an inset map of the Sierra Nevada region.

recent work finds utility in the VTM dataset (see references in Kelly et al., 2016; Thorne and Le, 2016) and in comparing forest structure and compositions between VTM and FIA datasets (Dolanc et al., 2013a; McIntyre et al., 2015).

The contemporary FIA dataset is a national inventory program implemented by the U.S. Forest Service, which contains systematically collected detailed monitoring data on forests in some regions since its inception. Surveys included detailed data on species, size, tree condition, and other site factors (Smith, 2002). The 2001–2010 FIA protocol uses circular subplots of 7.3 m (24 ft) radius where every tree greater than > 12.7 cm (5 in) is measured, and within which a microplot (2.1 m) is nested and information on stems > 2.5 cm (> 1.0 in) is collected (Bechtold and Patterson, 2005). This information is collected across four subplots giving a total area of 672.45 m<sup>2</sup>. Locations are distributed throughout California's forested areas (Fig. 1b). Although the FIA data collection protocols differ from those used in the earlier VTM surveys, explicit individual tree level information extracted from the FIA dataset allows us to match the size classes determined in the VTM protocol. Data on small trees (> 10.2 cm) from the FIA microplots were added to match the minimum size class of the classes found in the VTM dataset. Due to differences in the VTM and FIA plot sizes, we report accounts of tree numbers per hectare and basal area (m<sup>2</sup>/ha). Other studies (e.g. McIntyre et al., 2015; Dolanc et al., 2013a) provide further information for protocols associated with these data transformations.

### 2.2.2. Spatial depiction of California land ownership

We assembled several freely available datasets to develop a statewide spatial depiction of land ownership classes in California (Fig. 1c, Table 1). We generated categorical descriptions of land management based on ownership using the agency level distinction from the California Protected Area Database (CPAD) to aggregate parcels into six land ownership classes that simplify the diversity of land ownership in California (Table 2). Therefore, the names of the ownership classes may represent multiple owners or distinctions (e.g. BLM includes Tribal lands).

This depiction of California's land ownership suggests a contemporary and static picture; parcel establishment dates and ownership permanence can and have shifted over time within our study period of 1930–2010. However, many of the federal lands were established during the turn of the 20th century. Designation of National Parks and forest reserves between 1880 and 1920 largely protected forest and mountainous landscapes (Santos et al., 2014). These newly protected landscapes were also amongst the first surveyed by the VTM crews and

**Table 1**

The datasets used to create the California land management layer. The California Protected Area Database (CPAD) database was used as the base dataset, the other datasets listed were added to fill in areas where CPAD does not collect information.

Dataset	Reference
California Protected Area Database (CPAD)	CPAD: <a href="http://www.calands.org">http://www.calands.org</a>
Tribal lands	CPAD: <a href="http://www.calands.org/data/related">http://www.calands.org/data/related</a>
BLM grazing lands	BLM: <a href="https://www.blm.gov/ca/gis/index.html">https://www.blm.gov/ca/gis/index.html</a>
Private Timberlands (non-industrial and industrial)	Cal Fire: <a href="ftp://ftp.fire.ca.gov/forest">ftp://ftp.fire.ca.gov/forest</a>
Conservation Easements	CCED: <a href="http://www.calands.org/cced">http://www.calands.org/cced</a>

correspond with the highest densities of VTM plots locations. Other areas experienced shifts in land use and tenure. For example, in the North Coast commercial logging in redwood forests dominated the late 19th and early the 20th centuries yet subsequently many areas became federally and locally protected. After the establishment of federally protected forest and National Park lands many of California's conservation lands were acquired through State Park designations in the 1930s (Santos et al., 2014). Therefore, the majority of the plots used in the analysis are located on lands with relatively stable land tenure and the changes to the forest within those boundaries are likely representative of the management legacies of the land owner.

### 2.3. Analysis

#### 2.3.1. Plot comparison

We employ methodology from McIntyre et al. (2015) to calculate measures per species by plot for each dataset (e.g. VTM and FIA): total numbers of trees per ha, numbers of trees per ha within size class 1 (i.e. small trees; 10.2–30.4 cm DBH), numbers of trees in size class 2 (i.e. medium trees; 30.5–60.9 cm DBH), numbers of trees in sizes class 3 (61.0–91.3 cm DBH), numbers of trees per ha within size class 4 (> 91.4 cm DBH), and total basal area (m<sup>2</sup>/ha). Trees within size class 3 and 4 are combined to create a large tree category (> 61 cm DBH).

Per species measures were summed to represent totals by plot and size class for each period and only plots with more than one tree were used in the analysis. Each VTM and FIA comparison plot was assigned an ownership class based on spatial overlap (Fig. 1c). Error in the VTM and FIA plot locations (Waddell, 2013) can contribute to potential

**Table 2**  
Description of land ownership classes in California (several land owners can be aggregated into a single type), and relevant characteristics.

Land ownership class	Included Land classes	% of CA	Number of unique plots	Average elevation (m)	Average distance between VTM and FIA plots (km)	Average polygon size (km <sup>2</sup> )
NPW: National Parks and Wilderness Areas	Wilderness areas, National Parks, Fish and Wildlife Refuges	17.7%	582	2211	3	23.4
PP: Private Protected	Conservation easements, NGO's	2.4%	28	601	2.5	0.9
SR: State and Regional Parks	State, City, County land	4.4%	94	679	2.5	0.93
NWBT: Non-Wilderness areas, BLM, and Tribal	BLM land and grazing land, Tribal lands	17.7%	59	1290	2.5	13.9
NWNF: Non-Wilderness areas and National Forests	National Forest	15%	1186	1615	2.9	21.6
PT: Private Timberland	Non-Industrial Private Timber, Industrial Private Timber	6.5%	94	1243	2.6	2.95
Total		63.7%	2047			

erroneous assignment of ownership classes, however the potential positional error of 0.2–1.6 km was much smaller than the average area (5.25 km<sup>2</sup>) of individual polygons within ownership classes (Table 2), and further compensated for by the scale of our analysis (Waddell, 2013). Plots where a land ownership description was unavailable were removed from the analysis. We used elevational values derived from a digital elevation model to group plots into 500 m elevation classes. Using these classes, we refined our plot comparison dataset to capture plots that were assigned the same ownership class, elevational class, and were within a 5 km distance threshold. To ensure that the plots adhered to the independence assumptions of our statistical tests, multiple plot matches were evaluated. If the stratification returned more than one FIA plot matching the above criteria, the average of all corresponding plots was used. If a VTM plot matched with a single FIA plot, the plot with the shortest distance was compared. Plot matches were on average no more than 2.9 km apart. From an original dataset of 9388 VTM and 5198 FIA plots, our final comparison dataset was 2047 VTM and 2047 FIA plots.

### 2.3.2. Change over time

To assess if the numbers of trees within each size class (small, medium, large, total) and total basal area changed significantly over time across all land ownership classes we conducted a Wilcoxon test (also known as the Mann-Whitney *U* test, or Wilcoxon rank sum test). The Wilcoxon test is a non-parametric analogue to the *t*-test often used to detect a significant difference in population means or medians (Fay and Proschan, 2010). This interpretation of the test relies on the assumptions that the two populations are independent and have the same shape and equal variance. However, the Wilcoxon-Mann-Whitney test is still valid in situations where the homogeneity of variance assumption is violated (Fay and Proschan, 2010), does not rely on the assumption that the data follow a normal distribution and can be used on data with extreme outliers (MacFarland and Yates, 2016), as was apparent in our data. When the variance assumption is violated, rather than testing for a difference in the medians, the hypothesis tests that a randomly selected value from one sample population will be greater than a randomly selected value from the second sample population. Using the two populations (Time<sub>1</sub> = VTM and Time<sub>2</sub> = FIA), a difference in the population distributions is reflected as a “difference in location” or the median of the differences between a VTM sample and a FIA sample (R Core Team, 2013). To calculate the actual median difference between the two periods we used a bootstrapping approach, generating 5000 iterations of the differences in the population medians from which we took an overall median. We interpret the overall median difference derived from the bootstrapping approach as the median value of change over time in the populations between VTM and FIA within the ownership class. The Wilcoxon test and resultant *p*-value < 0.05 describe the change between the FIA and VTM populations as significantly different. All analyses were implemented with the R statistical software base function `wilcox.test` (R Core Team, 2013), and the boot package (Canty

and Ripley, 2017).

### 2.3.3. Change between ownership class

To assess how changes in the number of trees per size class and total basal area vary by land ownership we used the difference between FIA and VTM (i.e. FIA-VTM) variables at the plot level (as distinct from the difference procedure discussed above in 2.3.2, which looks at difference across the entire population using a bootstrapping method) per ownership class directly. The difference or change values for each of the five variables followed a normal distribution, and so we ran an ANOVA to compare the effect of ownership on each variable as well as calculated overall means and 95% confidence intervals. Statistically significant differences between ownership types were determined for each of the five change variables. We then ran post hoc Tukey tests on the significant ANOVAs to compare specific differences between the ownership classes. This permitted us to determine if the change experienced on one ownership class was significantly different from the change on another class.

### 2.3.4. Spatial pattern of change across ownership class

Additionally, to visualize the spatial distribution of increase, decrease, and extreme change in the five variables we calculated the overall mean of the change values of all plots within 20 km and 5 km resolution grid cells. The 20 km resolution was chosen to be comparable to results from McIntyre et al. (2015), and 5 km resolution represents the maximum allowable distance between the comparison plots. The ownership classes were also aggregated to 20 km and 5 km using the majority method, which does lose granularity as small parcels are subsumed by larger ones. Change values were classed using the Jenks Natural Breaks algorithm, which uses the variance to maximize differences between classes and minimize differences within classes (Jenks, 1977). These classes were reported in terms of increase and decrease, reflecting positive and negative change values. To highlight areas of extreme change, we also classed the values by standard deviations, where extreme change values are defined as change that is three standard deviations from the mean.

## 3. Results

### 3.1. Change over time

When viewed holistically (*n* = 2047 comparison plots), forest structure across California has changed significantly (Table 3). There has been an increase in small trees, medium trees, total trees, and a decline in large trees and TBA. However, critical differences across ownership exist, forests on Private Timberlands, Non-Wilderness National Forests, and National Parks and Wilderness areas (i.e. PT, NWNF, and NPW) showed more pronounced structural changes than do those on State and Regional Parks, Private Protected, and Non-Wilderness BLM and Tribal lands (SR, PP, and NWBT).

**Table 3**

Summary statistics for stems/ha for small, medium, large, and total trees and the average  $m^2$ /ha of total basal area for each ownership class and the average across the whole dataset. We calculated change between FIA-VTM and report percent change. Median differences from are results from 5000 iterations comparing a median value from FIA to a median value in VTM and generating a global median. Significant p-values (from Wilcox) < 0.05 are shown in bold.

	Small trees	Medium trees	Big trees	Total trees	Total basal area
	>24 in dbh				$m^2$ /hectare
	Stems per hectare				
<i>All areas (n = 2047)</i>					
VTM median	99.33	50.94	<b>38.70</b>	235.03	<b>38.96</b>
FIA median	235.43	84.72	<b>18.23</b>	366.60	<b>34.15</b>
% change	137.03	66.32	−52.90	55.98	−12.33
Median Difference (bootstrap)	136.71	33.97	−20.80	131.46	−4.70
P-value (Wilcox)	<b>&lt; 0.001</b>				
<i>PT: Private Timberlands (n = 98)</i>					
VTM median	93.99	78.54	<b>61.96</b>	262.04	<b>56.18</b>
FIA median	469.81	92.49	<b>10.47</b>	626.40	<b>36.19</b>
% change (relative)	399.86	17.77	−83.11	139.04	−35.58
Median Difference (bootstrap)	375.66	10.63	−49.17	371.35	−18.87
P-value (Wilcox)	<b>&lt; 0.001</b>	0.11	<b>&lt; 0.001</b>	<b>&lt; 0.001</b>	<b>&lt; 0.001</b>
<i>NWNF: Non-Wilderness and National Forest (n = 1186)</i>					
VTM median	90.29	49.48	<b>38.70</b>	216.63	<b>38.25</b>
FIA median	262.56	91.16	<b>18.53</b>	407.55	<b>35.85</b>
% change	190.80	84.23	−52.10	88.14	−6.27
Median Difference (bootstrap)	171.91	42.50	−20.40	191.62	−2.40
P-value (Wilcox)	<b>&lt; 0.001</b>	<b>&lt; 0.001</b>	<b>&lt; 0.001</b>	<b>&lt; 0.001</b>	<b>0.002</b>
<i>NPW: National Parks and Wilderness (n = 582)</i>					
VTM median	100.85	66.53	<b>57.63</b>	273.15	<b>50.24</b>
FIA median	187.01	84.72	<b>16.51</b>	318.35	<b>35.91</b>
% change	85.43	27.34	−71.36	16.55	−28.52
Median Difference (bootstrap)	84.41	19.28	−33.56	48.99	−14.42
P-value (Wilcox)	<b>&lt; 0.001</b>				
<i>NWBT: Non-Wilderness BLM and Tribal (n = 59)</i>					
VTM median	112.43	25.80	0.00 <sup>a</sup>	152.82	9.94
FIA median	147.24	28.92	0.00 <sup>a</sup>	185.89	11.79
% change	30.96	12.11	NA	21.64	18.60
Median Difference (bootstrap)	28.96	7.34	0.00	36.84	2.29
P-value (Wilcox)	0.08	0.32	NA	0.10	0.15
<i>SR: State and Regional Parks (n = 94)</i>					
VTM median	196.34	63.89	0.00 <sup>a</sup>	321.33	21.94
FIA median	172.12	67.89	0.00 <sup>a</sup>	262.55	17.42
% change	−12.33	6.27	NA	−18.29	−20.59
Median Difference (bootstrap)	−29.11	3.95	0.00	−58.30	−4.49
P-value (Wilcox)	0.29	0.99	NA	0.15	0.02
<i>PP: Private Protected (n = 28)</i>					
VTM median	141.47	39.27	0.00 <sup>a</sup>	173.14	9.16
FIA median	217.93	39.00	0.00 <sup>a</sup>	247.33	14.84
% change	54.04	−0.68	NA	42.85	61.92
Median Difference (bootstrap)	74.90	3.11	0.00	70.08	4.63
P-value (Wilcox)	0.09	0.46	NA	0.05	0.22

Mean values for these classes are as follows: SR (VTM: 19.26, FIA: 14.53), PP (VTM: 6.03, FIA: 4.81), NWBT (VTM: 5.56, FIA: 6.19).

<sup>a</sup> Where the values are equal to zero, the majority of plots had zero stem per hectare counts. Wilcox tests were not run on zero values.

PT, NWNF, and NPW represent the largest proportions of managed land in California (Table 2), and these lands have lost significant numbers of large trees (> 61 cm DBH) over the 20th Century (Fig. 2). PT showed the largest declines with a median difference of nearly 50 trees per ha from the 1930s (VTM) to 2010 (FIA), a change of over 83% (Table 3). Rates of large tree declines on Private Timberlands were followed by NPW with a median difference of over 30 trees per ha (71% change) and then NWNF with a 20 tree per ha difference (52%). The median difference on SR, PP, and NWBT land was negligible, as the majority of the plots located on those lands had zero counts of large trees.

Patterns of forest density, primarily driven by significant increases (up to ~137%) in the counts of small trees (10.2–30 cm DBH) per ha were consistent across the state except in SR (Table 3). Private Timberlands (PT) (gains of ~399%), NWNF (gains of ~190%), and NPW (gains of ~85%) had statistically significant increases in small trees (Table 3). Correspondingly, all ownership classes with the exception of State and Regional Parks (SR) experienced increases in total trees per

ha (Fig. 2). Significant increases (up to 55%) in total numbers of trees on the landscape were significant on PT with a median difference of 371 trees per ha (139% increase); NWNF with a median increase of 191 trees per ha (88% increase); and NPW with a median increase of nearly 50 trees per ha (16% increase). PP and NWBT showed slight, but not significant gains in trees per ha.

Declines in large trees were generally reflected by corresponding declines in total biomass as represented by total basal area (TBA  $m^2$ /ha) across ownership classes (Table 3 and Fig. 2). Across PT (35% TBA decline), NPW (29% TBA decline), SR (21% TBA decline), and NWNF (6% TBA decline) forests showed statistically significant declines in total basal area over the 20th century. Private Timberlands had the largest median difference between the two-time periods with decreases of  $19 m^2$ /ha (36%). NPW lost  $14 m^2$ /ha of basal area (29%), and NWNF showed relatively small overall change losing  $2 m^2$ /ha (6%). Conversely, NWBT land experienced non-significant gains in basal area ( $2 m^2$ /ha) (Table 3).

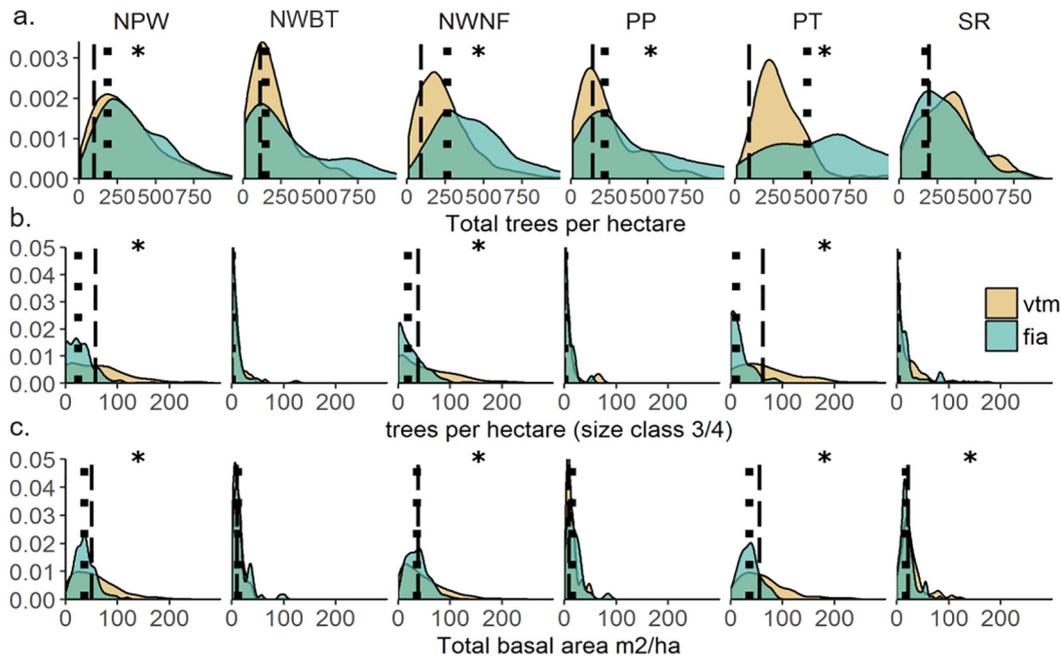


Fig. 2. Change in forest structure over time for: (a) total trees per ha; (b) large trees per ha; and (c) total basal area ( $m^2/ha$ ). Each plot shows the density distribution of each time period for each ownership class. Significant ( $p$ -value < 0.05) indicating dissimilar population distributions are shown with an ‘\*’. Median values of VTM distribution are dashed lines, median values of the FIA distribution are shown with dotted lines. Some plots at the ends of the distribution have been removed to show the part of the distribution with the highest densities.

### 3.2. Change between ownership class

The direct change (FIA-VTM) across management type for **total trees, large trees, and TBA** were significant for PT, NWNF, and NPW (Fig. 3). **PT showed the largest average changes with an increase of 310 (95% CI  $\pm$  5) total trees/ha and average declines of -54 (95% CI  $\pm$  15) in large trees/ha and -26 (95% CI  $\pm$  4) TBA ( $m^2/ha$ ).** NWNF also showed large average increases of 193 (95% CI  $\pm$  21) total trees/ha with declines of -31 (95% CI  $\pm$  3) large tree/ha and -12 (95% CI  $\pm$  3) TBA ( $m^2/ha$ ). Finally, NPW areas showed similar average declines in large trees/ha (-37, 95% CI  $\pm$  5) as NWNF, but compared to PT and NWNF had lower average increases in total trees/ha (53, 95%

CI  $\pm$  25) and corresponding declines of -20 (95% CI  $\pm$  3) in TBA ( $m^2/ha$ ) (Fig. 3).

Despite the constancy in overall patterns of forest densification and shifting tree size class distributions statewide, there are important differences in the amount and direction of change between ownership class (Table 4). Changes in total trees and numbers of small and medium trees per ha on NWNF lands are significantly different from those changes on NPW lands, with NWNF lands experiencing greater increases than NPW. However, NWNF and NPW have changed similarly in terms of declining densities of large trees (Table 4). Changes in NWNF and PT were significantly different from each other in terms of small trees, large trees, and total trees, with PT changes in small trees

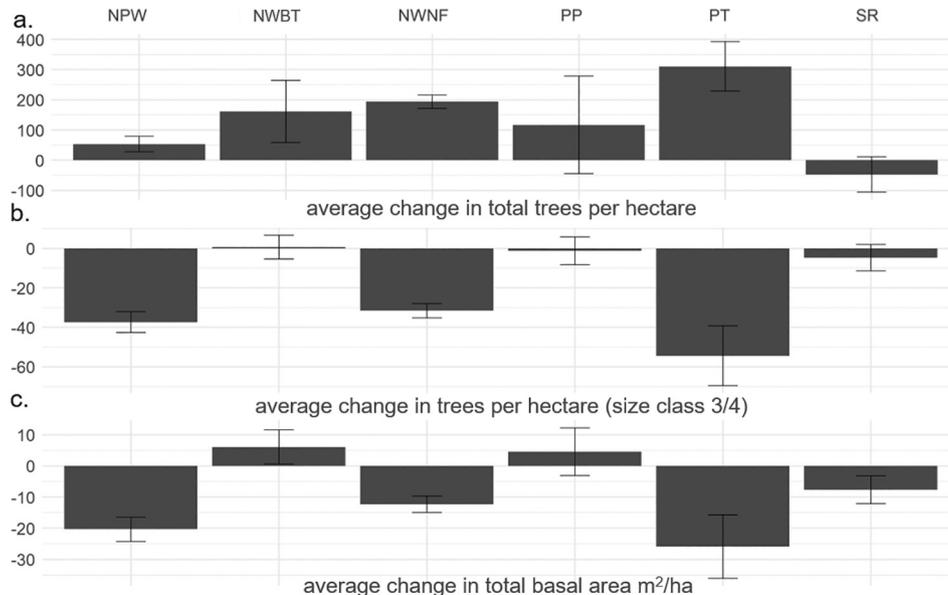


Fig. 3. Average direct change (FIA-VTM) in forest structure by plot and by ownership type for: (a) total trees per ha; (b) large trees per ha; and (c) total basal area ( $m^2/ha$ ) with 95% confidence intervals on change values.

**Table 4**

Significant difference in the change experienced by pairs of ownership class for each variable are demarcated by a “✓” where Tukey Honest Significant Difference test resulted in a P-value < 0.05; pairs that were not significantly different from each other show 0 significant variables.

Management class comparison pair	Small trees	Medium trees	Large trees	Total trees	Total basal area	Number of significant variables
PP-NWBT						0
PP-NWNF						0
SR-PP						0
PP-NPW			✓			1
NWBT-NPW			✓		✓	2
PT-NPW	✓			✓		2
SR-NPW	✓		✓			2
NWNF-NWBT			✓		✓	2
SR-NWBT	✓		✓	✓		2
PT-PP	✓		✓		✓	2
NWNF-NPW	✓	✓		✓	✓	3
PT-NWBT	✓		✓		✓	3
PT-NWNF	✓		✓	✓		3
SR-PT	✓		✓	✓		3
SR-NWNF	✓	✓	✓	✓		4

being significantly different than every other land ownership. Changes on SR were consistently significantly different from other ownership classes, except for PP which due to low samples size is not statistically different than most other ownership types (Table 4). NWBT was most dissimilar in terms of large tree and total basal area decline to NPW, NWNF, and PT (Table 4).

3.3. Spatial pattern of change across ownership class

Increases in small trees and in total trees were widespread throughout the northern Sierra Nevada region, and more scattered throughout the central coast and southern part of the state (Fig. 4b and e). Patterns of medium tree change were variable across ownership class and regions (Fig. 4c). Declines in large trees were widespread throughout the state and pronounced in the Sierra Nevada region

(Fig. 4d). The spatial pattern of large tree declines largely reflected the pattern of decline in total biomass across California (Fig. 4f), however, patterns of TBA exhibited more local heterogeneity particularly in the central coast. The central coast regions depicted strikingly different changes than the Sierra Nevada region, with average decreases in small, medium and total trees in contrast to the increases found in the Sierra Nevada region. These are predominantly SR lands, which showed non-significant changes across most measures (Fig. 2, Table 3). Extreme changes (> 2.0 standard deviation decrease or increase in any measure over the 20th century) are shown in Fig. 5. Extreme changes are scattered throughout the state, with some important local trends. The timber production zones (PT) of the North Coast and Klamath Ranges showed extreme increases (> 2.0 standard deviation from the mean) in the number of small trees and total trees (shown in dark green in Fig. 5b and e). Large tree decline was also most extreme in the higher

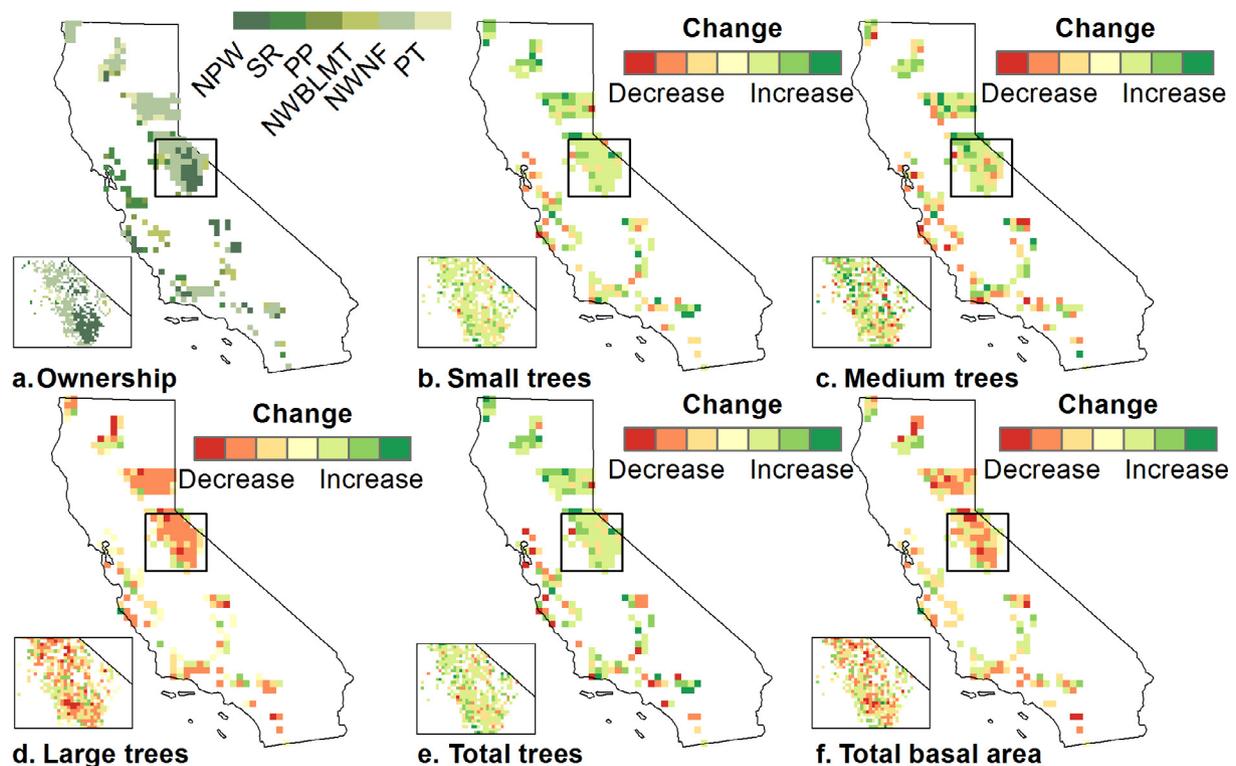
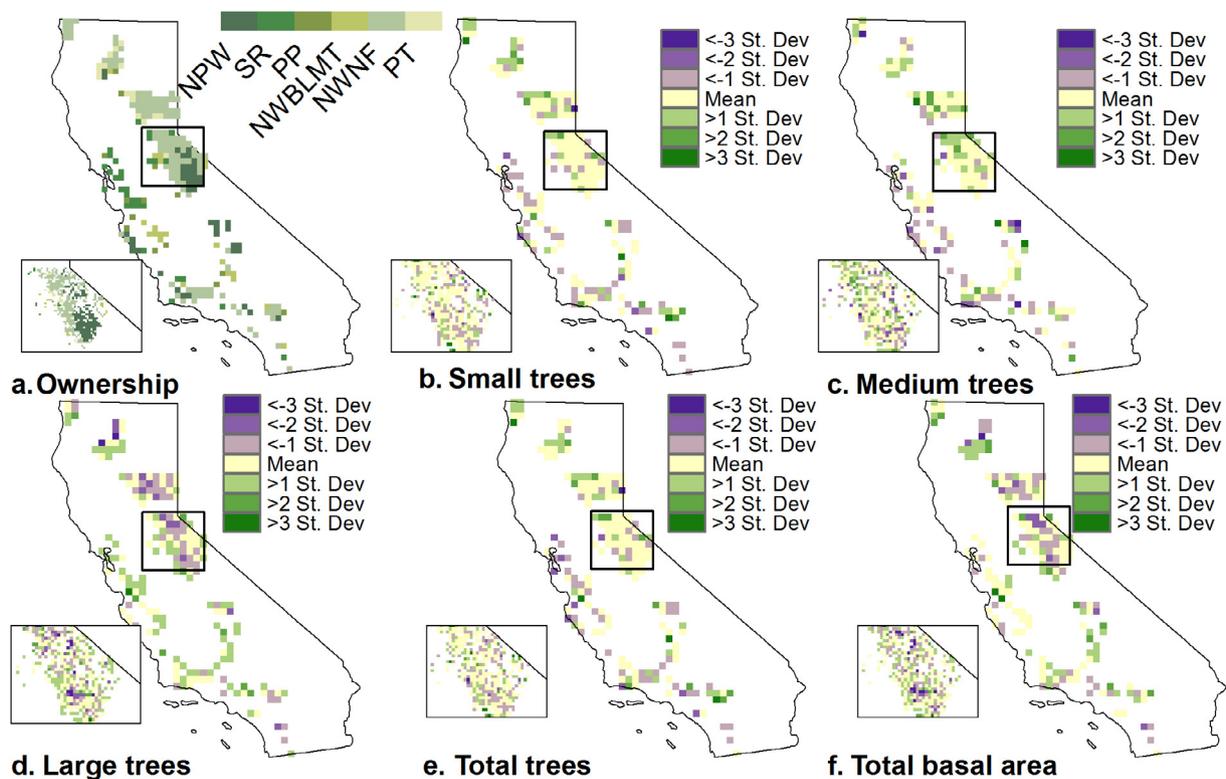


Fig. 4. Change in forest structure measures at 20 km resolution for: (a) ownership class; (b) number of small trees per ha; (c) number of medium trees per ha; (d) number of large trees per ha; (e) number of total trees per ha; and (f) total basal area (m<sup>2</sup>/ha). The insets of each map show the Sierra Nevada region at 5 km resolution. Change is depicted as increase (> 0), and decrease (< 0).



**Fig. 5.** Extreme change in forest structure measures at 20 km resolution for: (a) ownership class; (b) number of small trees per ha; (c) number of medium trees per ha; (d) number of large trees per ha; (e) number of total trees per ha; and (f) total basal area ( $\text{m}^2/\text{ha}$ ). The insets of each map show the Sierra Nevada region at 5 km resolution. Change is shown as deviations from the mean cell value,  $> 2.0$  standard deviations from the mean is considered to be extreme change.

elevation areas of the Sierra Nevada, and in the Non-Wilderness National Forest and Private Timberlands of the northern Klamath Ranges (shown in purple in Fig. 5d).

#### 4. Discussion

We report overall changes to forests statewide (increases in small trees and total trees and decreases in large trees and total basal area) that are similar to previous results (e.g. McIntyre et al., 2015), however the changes we report uniquely vary across ownership class. For example, large trees declined by 83% on PT, by 71% on NPW, and by 52% on NWNF. The consistency of large tree declines across differing land ownership class aligns with previous research pointing towards systematic influences of climatic drivers such as temperature and climatic water deficit (Das et al., 2013; Lutz et al., 2010; McIntyre et al., 2015) as a primary driver of decline. The lack of variation in large tree decline between PT and NPW is especially surprising given their conflicting logging histories and directly contrast with previous studies that find logging as the primary driver of large tree decline (Knapp et al., 2013). Timber harvesting took place in NWNF and in NPW areas before their establishment, however nearly 95% of the total national timber harvest came from private forests prior to World War II (Hirt, 1994). Increased demand for timber between 1940 and 1960 caused by post-war building led to extensive timber harvesting. Forest stands from private forests and National Forests both contributed to this rapid increase in harvesting. In the late 1940s, timber harvests on National Forests increased dramatically (Winters, 1950). More recently, timber production in California has declined to pre-war averages of about 1.1 billion board feet per year with private lands again producing nearly 95% of California's timber (Stewart et al., 2016). Timber harvesting on PT has been consistent since before WWII, whereas it has been variable on NWNF, and relatively nonexistent on NPW. This consistency in timber harvesting on PT lands may explain why the largest declines in large trees

were on private timberlands, but timber harvesting alone does not explain why declines (71% loss) on relatively unlogged NPW are greater than declines on variably logged NWNF (52% loss) and why losses on NPW are not significantly different than losses on PT (Table 4).

Although an active legacy of timber harvesting may not play the primary role in determining statewide patterns of large tree decline, it might help to explain changes to forest density. Specifically, long term studies of post-harvest forest recovery have shown that logged areas have higher densities than corresponding undisturbed areas (Garcia-Florez et al., 2017; Naficy et al., 2010). This is consistent with historical logging practices of targeting large size classes (Bouldin, 1999; Knapp et al., 2013). Large gaps created by the removal of one large tree allow for several small trees to infill the space left behind (Lydersen et al., 2013). PT, which have been the most actively logged of the ownerships presented here, on average have greater densities than their unlogged or variably logged counterparts (i.e. NPW, NWNF) and showed substantially different changes in numbers of small trees than all other land ownership classes. However, depending on the scale of the study, logging history may not be the primary driver of densification (Knapp et al., 2013; Collins et al., 2017; Merschel et al., 2014), and local and regional drivers maybe more explanatory. Regional differences in ownership types may also play an explanatory role, for example patterns of small tree density on PT could be attributed to the fact that they are largely located at lower elevations and are therefore potentially more productive areas than higher elevation NWNF and NPW areas.

Beyond logging histories, different ways in which fire suppression practices have been implemented also likely played a role in the differing magnitude of changes taking place, particularly on NPW lands and NWNF. The National Park Service adopted a perspective of fire as a critical natural process, allowing wildfire to return to the landscape under specific circumstances nearly a decade earlier than did the Forest Service (Miller et al., 2012). Fire managed for natural resource benefits has taken place primarily in Wilderness areas and in many of the

National Parks whereas fire suppression is still common on other Forest Service lands (Franklin and Agee, 2003; Stephens et al., 2016). Our data showed smaller changes in the number of small trees on the landscape and significantly lower counts of total trees in NPW when compared to NWNF and PT. On PT and NWNF, where immediate fire suppression is still common, significant increases in small trees have contributed to much denser forests overall. In previous studies, where burned and unburned plots were studied with the goal of explicitly understanding the effect of fire suppression, the largest increases in stem densities occurred in unburned mid-elevation conifer forest where fire suppression is argued to have the greatest impact (e.g. Fellows and Goulden, 2008) and which aligns with our results from the majority of PT and NPW plots.

Understanding how forests have changed over long periods of time is increasingly important for contemporary forest managers. Total biomass and forest density measurements are commonly used and relatively simple proxies for forest function (e.g. productivity and diversity); they serve as key indicators of species habitat (Franklin et al., 2002), and are increasingly used in carbon estimation (Balderas Torres and Lovett, 2013; Brown et al., 1989). The forest structure measures we assessed here (e.g. tree counts by size class and basal area) are simple measures used to target silvicultural practices through existing mechanisms (e.g. thinning, controlled burns, fuel reductions, reseeded).

Furthermore, restoration projects, reforestation efforts, and local policies often use trees per area as a baseline or target for success (Crowther et al., 2015). Many of these efforts use historical estimates as restoration targets (Alagona et al., 2012; Rhemtulla and Mladenoff, 2007) yet in this era of both rapid anthropogenic change and potentially novel climatic regimes historical numbers may not be appropriate baselines (Millar et al., 2007). Therefore, understanding how forest structure changes across space and time, is altered by management, and varies across ownership is important for setting appropriate targets.

Significant increases in forest density and declining stand basal area in California over the 20th century has resulted in forests that are profoundly different than they were 100 years ago. In recent decades resilience has become the overarching framework of forest management, especially within public forests (Churchill et al., 2013; Millar et al., 2007; Stephens et al., 2016). Widespread patterns of increasing density reduce important structural and spatial patterns in forests including the distribution of large individual trees, open spaces, and clusters of trees (Churchill et al., 2013; Lutz et al., 2013). As these features are lost forests become increasingly susceptible and less resilient to catastrophic fire, disease, and drought induced mortality (Larson and Churchill, 2012; Lindenmayer et al., 2012; Lydersen et al., 2013; Stephens et al., 2008).

Considering that patterns of forest densification is consistent across the state and across ownership type, large scale forest management strategies that foster greater horizontal and vertical complexity merit further attention. In heavily managed forests strategizing appropriate post-harvest planting densities and expanding seedling genetic diversity (Millar et al., 2007) could contribute to healthier and potentially more resilient forests. Despite the complexity of forest thinning operations in National Forests, National Parks and Wilderness areas, careful deliberation is needed when deciding to abandon these strategies (including selective harvesting, thinning, and the use of prescribed fire) since this could cause an increase in competition for resources such as water, and increase species vulnerability and species stress within a drier climate (Linares et al., 2010). Increasing the amount and scope of management efforts that help to reduce density in forests may help trees survive to become the large trees that we have lost over the last century.

Our work has shown important differences in forest change across land ownership. However, it is important to note that some of this variation could additionally be explained by patterns in regional climate, local differences in tree regeneration, growth, dispersal or disturbance regimes including fire, pests, and disease that may co-vary with ownership. A more nuanced explanation of these changes calls for

further investigation of the aggregating spatial unit (biophysical region, county, land owner), a greater emphasis on collecting and analyzing spatial information on past land use legacies, as well as understanding the interactions between all likely explanatory factors.

## 5. Conclusions

Increased forest density and forest biomass declines over the last century have resulted in profound structural change in the forests of California. Evidence including historical resurveys and contemporary comparisons demonstrate this trend both locally (Dolanc et al., 2013a; Lydersen et al., 2013), and statewide (Fellows and Goulden, 2008; McIntyre et al., 2015). Although these changes are consistent across scales, attributing these patterns to specific drivers is complicated, and a more nuanced understanding requires investigating land use legacies in addition to climate, disturbance, and regional differences. We contribute to this discussion via our investigation into changes in forest structure across differing land ownerships. We compared historical and contemporary forest inventory data and found that contemporary forests in California are denser and have less overall biomass (total basal area) than their 1930s counterparts, and that this pattern is significant at a statewide scale. However, critical differences in forest structural change across ownership exist. Forests on PT, NWNF, and NPW exhibit consistent and more pronounced structural changes (loss of large trees and basal area, increase in small trees and total trees) than those on SR, PP, and NWBT.

Given that the magnitude and directionality of forest structure change differs across ownership class, we argue that land ownership, in part helps explain variations in forest structure. There are also regional differences in forest change (e.g. changes to Sierra Nevada and Central Coast forests are sometimes opposite), and these areas have experienced different management regimes over the 20th century. While we do not explicitly test for such regional differences, we have demonstrated that understanding land ownership and management history is crucial for understanding changing biomass across California, irrespective of region. To further our understanding, predictions, and management of forest ecosystems, consideration of socio-ecological, economic, and biophysical drivers is needed. Our work contributes to the development of a more nuanced understanding of change in California forests that incorporates climate, geomorphology, disturbance and management.

## Acknowledgements

We would like to thank UC Berkeley's Geospatial Innovation Facility (GIF) for hosting the [vtm.berkeley.edu](http://vtm.berkeley.edu) website and providing access to the data. We thank A. Kelly and L. Pitcher for providing early feedback on the manuscript. KE was supported by The Bancroft Library fellowship and The Institute for the Study of Ecological and Evolutionary Climate Impacts (ISEECI) fellowship.

## Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.foreco.2018.04.012>.

## References

- Alagona, P.S., Sandlos, J., Wiersma, Y.F., 2012. Past imperfect: using historical ecology and baseline data for conservation and restoration projects in North America. *Environ. Philos.* 9, 49–70.
- Balderas Torres, A., Lovett, J.C., 2013. Using basal area to estimate aboveground carbon stocks in forests: La Primavera Biosphere's Reserve, Mexico. *Forestry* 86, 267–281. <http://dx.doi.org/10.1093/forestry/cps084>.
- Bechtold, W.A., Patterson, P.L., 2005. The Enhanced Forest Inventory and Analysis Program—National Sampling Design and Estimation Procedures.
- Besley, D., 1996. Past sierra nevada landscapes. In: Sierra Nevada Ecosystem Project: Final Report to Congress. Assessments and Scientific Basis for Management Options,

- vol. II, pp. 3–24.
- Brown, S., Gillespie, A., Lugo, A., 1989. Biomass estimation methods for tropical forests with applications to forest inventory data. *For. Sci.*
- Bouldin, J., 1999. Twentieth-century changes in forests of the Sierra Nevada, California. Ph.D. Dissertation, University of California, Davis.
- Canty, A., Ripley, B., 2017. boot: Bootstrap R (S-Plus) Functions [WWW Document]. R Packag. version 1.3-20.
- Churchill, D., Larson, A., Dahlgreen, M., Franklin, J., Hessburg, P., Lutz, J., 2013. Restoring forest resilience: From reference spatial patterns to silvicultural prescriptions and monitoring. *For. Ecol. Manage.* 291, 442–457.
- Collins, B.M., Fry, D.L., Lydersen, J.M., Everett, R., Stephens, S.L., 2017. Impacts of different land management histories on forest change. *Ecol. Appl.* 27, 2475–2486. <http://dx.doi.org/10.1002/eap.1622>.
- Crowther, T.W., Glick, H.B., Covey, K.R., Bettigole, C., Maynard, D.S., Thomas, S.M., Smith, J.R., Hintler, G., Duguid, M.C., Amatulli, G., Tuanmu, M.-N., Jetz, W., Salas, C., Stam, C., Piotto, D., Tavani, R., Green, S., Bruce, G., Williams, S.J., Wiser, S.K., Huber, M.O., Hengeveld, G.M., Nabuurs, G.-J., Tikhonova, E., Borchardt, P., Li, C.-F., Powrie, L.W., Fischer, M., Hemp, A., Homeier, J., Cho, P., Vibrans, A.C., Umunay, P.M., Piao, S.L., Rowe, C.W., Ashton, M.S., Crane, P.R., Bradford, M.A., 2015. Mapping tree density at a global scale. *Nature* 525, 201–205. <http://dx.doi.org/10.1038/nature14967>.
- Das, A.J., Stephenson, N.L., Flint, A., Das, T., van Mantgem, P.J., 2013. Climatic correlates of tree mortality in water- and energy-limited forests. *PLoS One* 8. <http://dx.doi.org/10.1371/journal.pone.0069917>.
- Dolanc, C.R., Safford, H.D., Dobrowski, S.Z., Thorne, J.H., 2013a. Twentieth century shifts in abundance and composition of vegetation types of the Sierra Nevada, CA. *US Appl. Veg. Sci.* 1–14. <http://dx.doi.org/10.1111/avsc.12079>.
- Dolanc, C.R., Thorne, J.H., Safford, H.D., 2013b. Widespread shifts in the demographic structure of subalpine forests in the Sierra Nevada, California, 1934 to 2007. *Glob. Ecol. Biogeogr.* 22, 264–276. <http://dx.doi.org/10.1111/j.1466-8238.2011.00748.x>.
- Dolanc, C.R., Safford, H.D., Thorne, J.H., Dobrowski, S.Z., 2014. Changing forest structure across the landscape of the Sierra Nevada, CA, USA, since the 1930s. *Ecosphere* 5, 1–26.
- Fay, M.P., Proschan, M.A., 2010. Wilcoxon-Mann-Whitney or t-test? On assumptions for hypothesis tests and multiple interpretations of decision rules. *Stat. Surv.* 4, 1–37. <http://dx.doi.org/10.1214/09-SS051>. Wilcoxon-Mann-Whitney.
- Fellows, A.W., Goulden, M.L., 2008. Has fire suppression increased the amount of carbon stored in western U.S. forests? *Geophys. Res. Lett.* 35, 1–4. <http://dx.doi.org/10.1029/2008GL033965>.
- Franklin, J.F., Agee, J.K., 2003. Foraging a Science-Based National Forest Fire Policy. Issues Fire. Technol.
- Franklin, J.F., Spies, T.A., Pelt, R. Van, Carey, A.B., Thornburgh, D.A., Berg, D.R., Lindenmayer, D.B., Harmon, M.E., Keeton, W.S., Shaw, D.C., Bible, K., Chen, J., 2002. Disturbances and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir forests as an example. *For. Ecol. Manage.* 155, 399–423. [http://dx.doi.org/10.1016/S0378-1127\(01\)00575-8](http://dx.doi.org/10.1016/S0378-1127(01)00575-8).
- García-Florez, L., Vanclay, J.K., Glencross, K., Nichols, J.D., 2017. Understanding 48 years of changes in tree diversity, dynamics and species responses since logging disturbance in a subtropical rainforest. *For. Ecol. Manage.* 393, 29–39. <http://dx.doi.org/10.1016/j.foreco.2017.03.012>.
- Hirt, P., 1994. A Conspiracy of Optimism: Management of the National Forests Since World War II. University of Nebraska Press.
- Jenks, G., 1977. Optimal Data Classification for Choropleth Maps. University of Kansas, Lawrence.
- Keeley, J.E., 2004. VTM plots as evidence of historical change: goldmine or landmine? *Madrono* 51, 372–378.
- Kelly, M., Allen-Diaz, B., Kobzina, N., 2005. Digitization of a historic dataset: the wieslander California vegetation type mapping project. *Madrono* 52 (3), 191–201.
- Kelly, M., Easterday, K., Koo, M., Thorne, J.H., Mukythar, S., Galey, B., 2017. Geospatial informatics key to recovering and sharing historical ecological data for modern use. *Photogramm. Eng. Remote Sens.* 83, 779–786. <http://dx.doi.org/10.14358/PERS.83.10.779>.
- Kelly, M., Easterday, K., Rapicullio, G., Koo, M., McIntyre, P., Thorne, J., 2016. Rescuing and sharing historical vegetation data for ecological analysis: the California vegetation type mapping project. *Biodivers. Informatics* 11, 40–62.
- Knapp, E.E., Skinner, C.N., North, M.P., Estes, B.L., 2013. Long-term overstory and understorey change following logging and fire exclusion in a Sierra Nevada mixed-conifer forest. *For. Ecol. Manage.* 310, 903–914. <http://dx.doi.org/10.1016/j.foreco.2013.09.041>.
- Larson, A.J., Churchill, D., 2012. Tree spatial patterns in fire-frequent forests of western North America, including mechanisms of pattern formation and implications for designing fuel reduction and restoration treatments. *For. Ecol. Manage.* 267, 74–92. <http://dx.doi.org/10.1016/j.foreco.2011.11.038>.
- Laudenslayer, W.F., Darr, H.H., 1990. Historical effects of logging on the forests of the Cascade and Sierra Nevada ranges of California. *Trans. Western Section Wildlife Soc.* 26, 12–23.
- Linares, J.C., Camarero, J.J., Carriera, J.A., 2010. Competition modulates the adaptation capacity of forests to climatic stress: insights from recent growth decline and death in relict stands of the Mediterranean fir *Abies pinsapo*. *J. Ecol.* 98, 592–603. <http://dx.doi.org/10.1111/j.1365-2745.2010.01645.x>.
- Lindenmayer, D.B., Laurance, W.F., Franklin, J.F., 2012. Global Decline in Large Old Trees. *Science* (80-). 338, 1305–1306. doi: 10.1126/science.1231070.
- Lunt, I.D., Spooner, P.G., 2005. Using historical ecology to understand patterns of biodiversity in fragmented agricultural landscapes. *J. Biogeogr.* 32, 1859–1873.
- Lutz, J.A., Larson, A.J., Freund, J.A., Swanson, M.E., Bible, K.J., 2013. The importance of large-diameter trees to forest structural heterogeneity. *PLoS One* 8, e82784.
- Lutz, J.A., van Wagtenonk, J.W., Franklin, J.F., 2009. Twentieth-century decline of large-diameter trees in Yosemite National Park, California, USA. *For. Ecol. Manage.* 257, 2296–2307. <http://dx.doi.org/10.1016/j.foreco.2009.03.009>.
- Lutz, J.A., van Wagtenonk, J.W., Franklin, J.F., 2010. Climatic water deficit, tree species ranges, and climate change in Yosemite National Park. *J. Biogeogr.* 37, 936–950. <http://dx.doi.org/10.1111/j.1365-2699.2009.02268.x>.
- Lydersen, J.M., North, M.P., Knapp, E.E., Collins, B.M., 2013. Quantifying spatial patterns of tree groups and gaps in mixed-conifer forests: Reference conditions and long-term changes following fire suppression and logging. *For. Ecol. Manage.* 304, 370–382. <http://dx.doi.org/10.1016/j.foreco.2013.05.023>.
- MacFarland, T.W., Yates, J.M., 2016. Mann-Whitney U Test. In: Introduction to Nonparametric Statistics for the Biological Sciences Using R. Springer International Publishing, Cham, pp. 103–132. doi: 10.1007/978-3-319-30634-6\_4.
- Maxwell, R., Taylor, A., Skinner, C., Safford, H., Isaacs, R., Airey, C., Young, A., 2014. Landscape-scale modeling of reference period forest conditions and fire behavior on heavily logged lands. *Ecosphere* 5, 1–28.
- McIntyre, P.J., Thorne, J.H., Dolanc, C.R., Flint, A.L., Flint, L.E., Kelly, M., Ackerly, D.D., 2015. Twentieth-century shifts in forest structure in California: denser forests, smaller trees, and increased dominance of oaks. *Proc. Natl. Acad. Sci.* 201410186. <http://dx.doi.org/10.1073/pnas.1410186112>.
- McKelvey, K.S., Johnston, J.D., 1992. Historical Perspectives on Forests of the Sierra Nevada and the Transverse Ranges of Southern California: Forest Conditions at the Turn of the Century. USDA Forest Service Gen. Tech. Rep. PSW-GTR-133, 225–246.
- McIver, C.P., Meek, J.P., Scudder, M.G., Sorenson, C.B., Morgan, T.A., Christensen, G.A., 2015. California's Forest Products Industry and Timber Harvest, 2012.
- Merschel, A.G., Spies, T.A., Heyerdahl, E.K., 2014. Mixed-conifer forests of central Oregon: effects of logging and fire exclusion vary with environment. *Ecol. Appl.* 24, 1670–1688.
- Millar, C.I., Stephenson, N.L., Stephens, S.L., 2007. Climate change and forests of the future: managing in the face of uncertainty. *Ecol. Appl.* 17, 2145–2151. <http://dx.doi.org/10.1890/06-1715.1>.
- Miller, J., Collins, B., Lutz, J., Stephens, S., van Wagtenonk, J., Yasuda, D., 2012. Differences in wildfires among ecoregions and land management agencies in the Sierra Nevada region, California, USA. *Ecosphere* 3, 1–20.
- Minnich, R.A., Barbour, M.G., Burk, J.H., Fernau, R.F., 1995. Sixty Years of Change in Californian Conifer Forests of the San Bernardino Mountains. *Conserv. Biol.* 9, 902–914.
- Naficy, C., Sala, A., Keeling, E.G., Graham, J., DeLuca, T.H., 2010. Interactive effects of historical logging and fire exclusion on ponderosa pine forest structure in the northern Rockies. *Ecol. Appl.* 20, 1851–1864. <http://dx.doi.org/10.1890/09-0217.1>.
- Perring, M.P., De Frenne, P., Baeten, L., Maes, S.L., Depauw, L., Blondeel, H., Carón, M.M., Verheyen, K., 2016. Global environmental change effects on ecosystems: the importance of land-use legacies. *Glob. Chang. Biol.* 22, 1361–1371.
- Rhementulla, J.M., Mladenoff, D.J., 2007. Why history matters in landscape ecology. *Landscape Ecol.* 22, 1–3. <http://dx.doi.org/10.1007/s10980-007-9163-x>.
- Santos, M.J., Watt, T., Pincetl, S., 2014. The push and pull of land use policy: reconstructing 150 years of development and conservation land acquisition. *PLoS One*.
- Smith, W.B., 2002. Forest inventory and analysis: a national inventory and monitoring program. *Environmental Pollut.* 116, 233–242.
- Stephens, S.L., Collins, B.M., Biber, E., Fule, P.Z., 2016. U.S. Federal fire and forest policy: emphasizing resilience in dry forests. *Ecosphere* 7, 1–19. <http://dx.doi.org/10.1002/ecs2.1584>.
- Stephens, S.L., Fry, D.L., Franco-vizcaino, E., 2008. Wildfire and Spatial Patterns in Forests in Northwestern Mexico: The United States Wishes It Had Similar Fire Problems.
- Stewart, W., Sharma, B., York, R., Diller, L., Hamey, N., Powell, R., Swiers, R., 2016. Forestry. In: Mooney, H., Zavaleta, E. (Eds.), *Ecosystems of California*. UC Press, pp. 817–834.
- Taylor, A., 2000. Fire regimes and forest changes in mid and upper montane forests of the southern Cascades, Lassen Volcanic National Park, California, USA. *J. Biogeogr.* 27, 87–104.
- Taylor, A., Skinner, C., 2003. Spatial patterns and controls on historical fire regimes and forest structure in the Klamath Mountains. *Ecol. Appl.* 13, 704–719.
- R Core Team, 2013. R: A language and environment for statistical computing.
- Thorne, J.H., Le, T.N., 2016. California's historic legacy for landscape change, the Wieslander vegetation type maps. *Madrono* 63, 293–328.
- Turner, M.G., Wear, D.N., Flamm, R.O., 1996. Land Ownership and Land-Cover Change in the Southern Appalachian Highlands and the Olympic Peninsula. *Ecol. Appl.* 6, 1150–1172.
- van Mantgem, P.J., Nesmith, J.C.B., Keifer, M., Knapp, E.E., Flint, A., Flint, L., 2013. Climatic stress increases forest fire severity across the western United States. *Ecol. Lett.* 16, 1151–1156. <http://dx.doi.org/10.1111/ele.12151>.
- van Mantgem, P.J., Stephenson, N.L., Byrne, J.C., Daniels, L.D., Franklin, J.F., Fulé, P.Z., Harmon, M.E., Larson, A.J., Smith, J.M., Taylor, A.H., Veblen, T.T., 2009. Widespread Increase of Tree Mortality Rates in the Western United States. *Science* (80-). 323, 521–524.
- Waddell, K.L., 2013. PNW-FIADB Users Manual: A data dictionary and user guide for the PNW-FIADB database.
- Wieslander, A.E., 1935. A vegetation type map of California. *Madrono* 60, 348–352.
- Wieslander, A., Yates, H.S., Jensen, H.A., Johannsen, P., 1933. Manual of Field Instructions for Vegetation Type Map of California. On File in the Library at Yosemite National Park, Yosemite Valley, CA.
- Winters, R., 1950. Fifty years of forestry in the U.S.A.