



Twentieth century shifts in abundance and composition of vegetation types of the Sierra Nevada, CA, US

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Keywords

Climate change; Fire suppression; Forest Inventory and Analysis (FIA); Historical ecology; Logging; Tree density; Vegetation Type Mapping (VTM)

Nomenclature

Baldwin et al. (2012)

Abbreviations

VTM = Vegetation Type Mapping Project;
FIA = Forest Inventory and Analysis;
DBH = Diameter at breast height

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Introduction

The Sierra Nevada, in California, US, contains an extraordinarily rich suite of vegetation types. These types include grassland and oak woodland/savanna, dense montane forest with snowpack frequently >3-m deep, sub-alpine woodland with trees that live >1000 yrs, alpine tundra and desert-influenced sagebrush steppe (SNEP 1996; Storer et al. 2004; Barbour et al. 2007; Sawyer et al. 2009). The history of human influence in the Sierra

Nevada is equally rich and complex, dating back at least 10 000 yrs to when Native Americans began living in the area (Anderson & Moratto 1996). Modern use by Euro-Americans accelerated after the 1849 gold rush, and since that time has included extensive mining, logging, grazing, urban expansion and fire suppression, each with its own ebb and flow and differential effects on vegetation (Beesley 1996).

In response to these disturbances, the vegetation of the Sierra Nevada has surely been altered, but in a manner

Abstract

Questions: Has tree density changed consistently across vegetation types? Do changes in component species correspond with changes across vegetation types? Do patterns of changes suggest potential drivers of change?

Location: Northern two-thirds of the Sierra Nevada, CA, USA, ca. 45 000 km².

Methods: Using two data sets that cover the span of elevations and land jurisdictions in the study area, we classified 4321 historical plots and 1000 modern plots into nine broad groups of vegetation types that are widely used by land managers and researchers in the region. We compared tree density and composition between historical and modern plots across and within these nine types.

Results: In the modern data set, tree density was significantly higher in eight of nine vegetation types. Total density was significantly higher in modern plots for all west slope types, especially for montane hardwood, where modern forests are 128% denser, and mixed conifer forests, which are 69% denser. Relative density of component species was also very different between data sets in these forests, and suggests a shift in dominance toward shade-tolerant conifers and evergreen oaks. Fire suppression is likely a driving factor in these types but density was also significantly higher in high-elevation types such as sub-alpine forest (+20%), where neither fire suppression nor logging have had major impacts on structure. East slope forest types (eastside *P. jeffreyi* forest and piñon-juniper woodland) were very similar in both modern and historical data sets, with no significant differences in density or composition.

Conclusion: West slope forest types, especially montane hardwood and mixed conifer forest, appear the most altered types of the mountain range. These types are more productive but have also been subject to greater disturbance than high-elevation and east slope forest types. Climate change may also be driving changes across the study area. Species such as *Quercus chrysolepis* and *Calocedrus decurrens*, which have each increased markedly in abundance, appear well positioned to dominate in the near future, especially under continued fire suppression and a warmer climate.

that varies across vegetation types and land jurisdictions. Settlement and grazing in foothill woodland has facilitated invasion by exotic grasses and has impacted oak recruitment, negatively in some places and positively in others (Allen-Diaz et al. 2007). Historical sheep grazing in high elevations had large impacts on meadows and likely affected tree recruitment via browsing or indirectly due to annual fires set by herders (Menke et al. 1996); cattle grazing continues today on many federal lands. Logging in *Pinus ponderosa* and mixed conifer forest has removed most old-growth forest from the Sierra Nevada, leading to reduced structural complexity across the landscape (Franklin & Fites-Kaufman 1996), and facilitating an increase in abundance of hardwood species (Bolsinger 1988). Twentieth century fire suppression has increased stand densities and altered composition in favour of shade-tolerant, fire-intolerant species in these forests (Parsons & Debenedetti 1979; North et al. 2007; Scholl & Taylor 2010). In addition, climate change now appears to be driving additional shifts, contributing to an infilling of previously more open sub-alpine forest and woodland (Millar et al. 2004; Dolanc et al. 2013), and increasing mortality in many types of forest (Guarin & Taylor 2005; Smith et al. 2005; van Mantgem & Stephenson 2007; Lutz et al. 2009). Climatic changes are also linked to more frequent fires, which are further driving shifts in forest structure across the landscape (Westerling et al. 2006; Miller et al. 2009; Miller et al. 2012).

Most of the research related to forest change in the Sierra Nevada has been local or sub-regional in scale and has seldom included multiple vegetation types, making it difficult to apply conclusions broadly – across regions or vegetation types. The Forest Service and the National Park Service of the US, the agencies that manage the majority of public lands in the Sierra Nevada, are both in the initial stages of revising their land and resource management plans. To inform this process, there is an urgent need for broad-scale syntheses of patterns of change across the Sierra Nevada, especially where such syntheses can be nested in ecosystem categories that are widely understood and already utilized in management planning and implementation. Such an approach can highlight vegetation types that have undergone the greatest change, help to distinguish the driving factors behind this change and identify rates of change along geographic, elevation and climatic gradients.

The existence of two broad data sets on forest structure and composition, the Vegetation Type Mapping (VTM) project, sampled from 1929 to 1936, and the Forest Inventory and Analysis (FIA) data set, sampled most recently from 2001 to 2010, provide an opportunity to compare historical and modern conditions across multiple vegetation types and a vast area. By comparing stand densities

between these two data sets, we can ask the following questions: (1) has density changed consistently across vegetation types; (2) do changes in component species dominance correspond with changes across vegetation types; and (3) do patterns of change suggest potential drivers of change?

Methods

Study area

Our study area encompassed the northern two-thirds (ca. 45 000 km²) of the Sierra Nevada. This area stretches from the southern boundary of Yosemite National Park north to 40° latitude in the Plumas National Forest, and from elevations near the Central Valley floor (near sea level) to the crest of the range (>4000 m a.s.l.) and east to its border with the Great Basin (Fig. 1). The Sierra Nevada is a single large mountain range made up mostly of a massive, 100-km wide granitic block uplifted by tectonic activity. Underlying rocks are predominantly granitic, with significant areas of metamorphic rocks in the north, and volcanic rocks along the northern crest and parts of the east slope. Soils are generally nutrient-poor but are highly heterogeneous and can be very productive for conifers (SNEP 1996; Storer et al. 2004). The climate of the range is montane mediterranean, with warm, dry summers and cool, wet winters. The climate of the east slope is more continental, with drier, colder winters than the west slope (Major 1990; Minnich 2007).

Vegetation of the Sierra Nevada is diverse and heterogeneous, as a result of its wide range of topography and climate. On the west slope, the lowest elevations are a matrix of grassland, oak woodland/savanna and chaparral. The middle elevations (ca. 800–2500 m a.s.l.) are dominated by forested types: montane hardwood, *Pinus ponderosa* var. *pacifica* forest, mixed conifer forest and *Abies magnifica* forest. Higher elevations are dominated by sub-alpine forest and woodland up to tree line (3100–3400 m a.s.l.). On the east slope, alpine and sub-alpine vegetation spill over from locations along the crest. Below that, a mosaic of forest, woodland and *Artemisia* brushland extend to the western boundary of the Great Basin. For more information on vegetation of the Sierra Nevada and its dominant species, see Barbour et al. (2007) and Sawyer et al. (2009).

Data sources

Historical data

The VTM project collected data from >7000 plots in the Sierra Nevada from 1929 to 1936. These plots provided the quantitative detail on stand structure and composition for vegetation maps that were being concurrently produced (Keeler-Wolf 2007; Thorne et al. 2008). Plots were rectan-

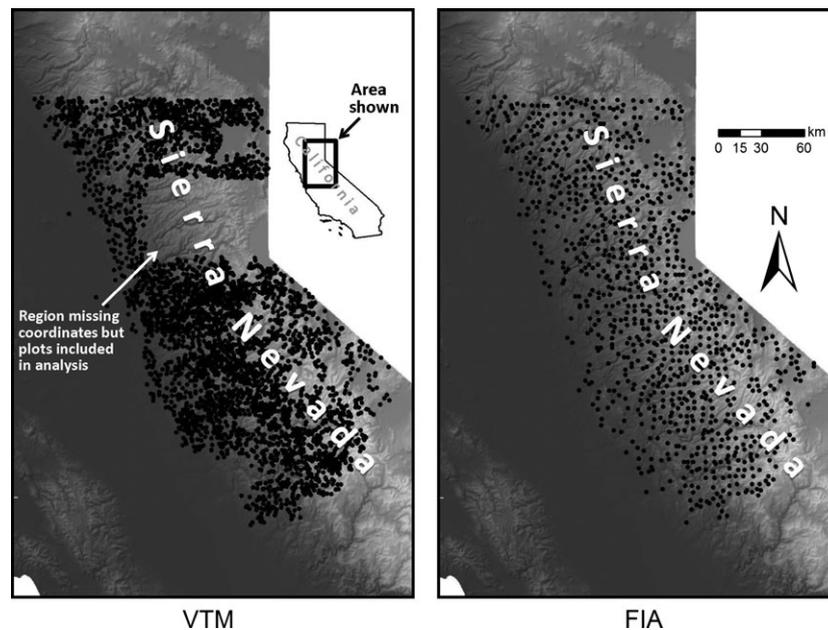


Fig. 1. Study area in Sierra Nevada, CA, USA, showing distribution of Vegetation Type Mapping (VTM) plots (left panel) and Forest Inventory and Analysis (FIA) plots (right panel) included in analysis. The study area includes all elevations and land ownerships of the region shown, which covers ca. 45 000 km² and the northern two-thirds of the mountain range. The rectangular region of ‘missing’ VTM plots does not actually represent missing plots: these plots are missing their coordinates and thus cannot be projected on a map, but retain all other associated data, including elevation and all plot tree data, and were used in analyses.

gular, 20.1-m wide by 40.2-m long (809 m²), and oriented perpendicular to topographic contours or along a cardinal direction in level areas. For the whole area of each plot, VTM crews collected data on stand tree structure by tallying all tree species in four diameter at breast height (DBH) 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). They also estimated cover of shrubs and herbs, and recorded elevation, slope, aspect, soil depth and other environmental variables. Greater detail regarding the VTM plot protocol can be found in the VTM field manual, accessible online (Wieslander et al. 1933). The VTM plot data are also available online and can be accessed at <http://vtm.berkeley.edu/>. The VTM data set is being used as a baseline for historical comparisons with modern conditions in an increasing number of studies. Some studies have resampled VTM plots (Minnich et al. 1995; Franklin et al. 2004; Talluto & Suding 2008; Dolanc et al. 2013), while others have compared VTM data with independent data sets (Fellows & Goulden 2008; Lutz et al. 2009; Crimmins et al. 2011; Dobrowski et al. 2011).

Modern data

The FIA programme collects, compiles and archives data on forest status and health from all types of land throughout the country, re-sampling each plot every 5–10 yrs

(California is re-sampled every 10 yrs; Smith 2002). The FIA protocol divides plots into four 7.3-m radius circular subplots, with one central subplot and three outer subplots arranged at 120° angles from each other at distances of 36.5 m from plot centre to plot centre. Each subplot has a 2.1-m radius circular microplot nested within its boundaries. For all subplots, every tree >12.7 cm (5 in) is measured (DBH, height, etc.) and identified to species. Within microplots, every tree >2.5 cm is measured. The total area of all four subplots combined is 672.45 m². More information on the history and details of FIA protocol can be found in Bechtold & Patterson (2005) and the FIA field manual (Woudenberg et al. 2011). FIA data can be accessed at <http://apps.fs.fed.us/fiadb-downloads/datamart.html>.

A concern when comparing two data sets is that potential bias in either data set can influence the results. While FIA plot locations were determined randomly (Bechtold & Patterson 2005), the VTM plots were subjectively located in stands considered ‘representative’ for the polygon VTM crews were mapping concurrently (Wieslander et al. 1933; Wieslander 1935a). It has been suggested that VTM crews preferentially sampled in old-growth stands (Bouldin 2009). However, this contradicts the VTM project’s stated objectives of locating plots in ‘representative’ stands and is not supported by published documentation of the project or other related sources (Wieslander et al. 1933; Wieslander 1935a,b, 1985; Keeler-Wolf 2007). To check this, we

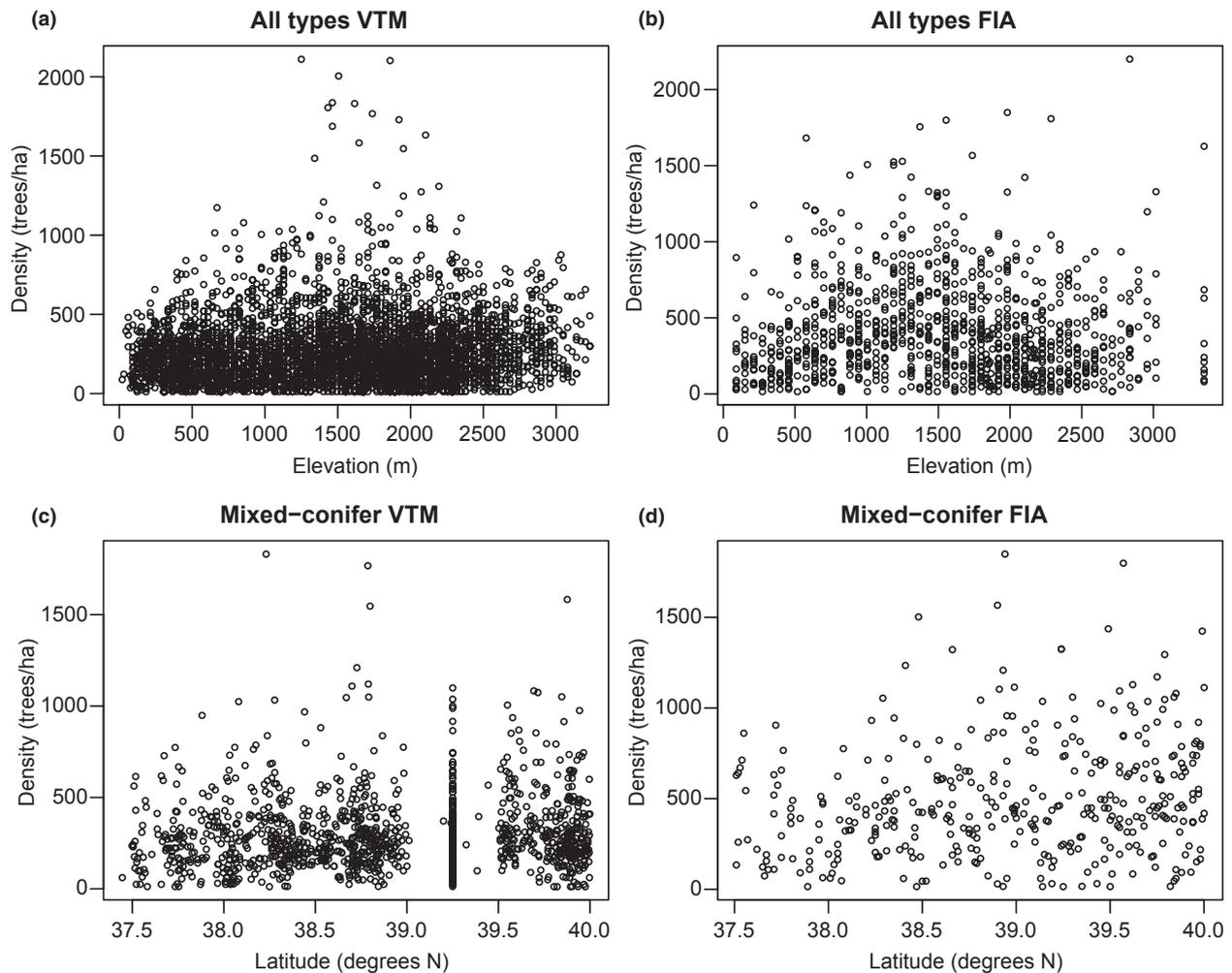


Fig. 2. Total density (trees ha^{-1}) of all trees, all species as a function of elevation (**a**, **b**) and as a function of latitude (**c**, **d**), for all plots in the Vegetation Type Mapping (VTM) data set and the Forest Inventory and Analysis (FIA) data set, for plots classified as mixed conifer forest in each data set. The vertical pattern of points at 39.25 °N latitude in 'C' reflects the estimated midpoint for a group of plots with missing coordinates (see Fig. 1).

developed scatterplots of stand density by elevation for all VTM and FIA plots, and stand density by latitude for mixed conifer forest, which occurs in fairly even abundance north to south in the study area (Fig. 2). These plots show a very similar spread of density across both latitude and elevation for each data set. This does not rule out a modest preference for older, better preserved stands by VTM crews, but it does demonstrate that they sampled as wide a variety of stands, in terms of density, as the FIA programme does today.

Data reduction and analysis

We downloaded all forested (or woodland) plots available for our study area in each data set from the websites listed above. We extracted and adjusted FIA data col-

lected from 2001 to 2010 for our study area, with the help of the Remote Sensing Laboratory, Region 5 USDA Forest Service, which generates Region 5 (California, Hawaii and US Pacific islands) inventory compilations using FIA plots. Since each plot was classified based on tree composition, we only extracted plots with at least one tree. In total, 50 VTM plots with suspect data were removed. Because VTM plots were slightly denser in the southern half of our study area than the northern half, we removed by random selection 600 VTM plots from the southern half (<38.5° latitude) and 70 FIA plots from the northern-most section of the study area (39.5–40.0°). This removal resulted in a total of 4321 VTM plots and 1000 FIA plots with mean latitudes and elevations that were not significantly different from each other (Appendix S1).

Since the VTM tree data were collected in four DBH size classes, it was necessary to reduce the FIA tree data to the same size classes for comparison. The DBH of each tree in the FIA data was lumped into one of the four VTM size classes described above. Since the minimum tree size in FIA subplots is 12.7 cm, we downloaded data from both subplots and microplots and added trees >10.2 cm DBH to the subplot data. FIA microplots have a smaller area, so we multiplied the density of those trees by the difference in area (or expansion factor). All tree species present were included; nomenclature follows *The Jepson Manual*, 2nd Edition (Baldwin et al. 2012).

The 4321 VTM plots and 1000 FIA plots were assigned to vegetation types. We developed rules based on relative basal area (Table 1) to assign plots to one of eight types that reflect agglomerations of the California Wildlife Habitat Relationship (WHR) System (Mayer & Laudenslayer 1988), which is widely used in California (Keeler-Wolf 2007). These eight types are readily defined and recognizable by readers from various backgrounds. They largely reflect a west to east gradient and comprise the full range of elevation and climate in the Sierra Nevada. These eight types are: Foothill Woodland, Montane Hardwood, Ponderosa Pine Forest, Mixed-conifer Forest, Red Fir Forest, Jeffrey Pine Forest, Sub-alpine Woodland and Piñon-juniper Woodland. Since the VTM data set only contains tree density data in four size classes, basal area was estimated

for each tree by assuming the minimum size in each class (e.g. 10.2 for size class 1); basal areas for both VTM and FIA plots were estimated in exactly the same way.

To facilitate classification, we used the hierarchical clustering procedure `hclust` in R version 2.14.1 (R Core Team 2013), using Ward's method on a matrix of Bray–Curtis dissimilarity based on estimated relative basal area for each plot. Resulting dendrograms for each data set were divided into eight groups using the `cutree` function in R. This resulted in eight groups for each data set that largely reflected our eight *a priori* types. We used the rules described in Table 1 to validate the assignment of plots into the eight types, and to refine the classification by relocating some plots into different types. The *P. jeffreyi* forest type was divided further into west-side and east-side types based on the location (coordinates) of the plots on either the west or east side of the crest of the Sierra Nevada, resulting in a final of nine vegetation types used for analysis. Stands dominated by *P. jeffreyi* can occur on both sides of the range, but west-side and east-side types are functionally very different from each other, with quite different physiognomies, substrates and co-dominant species (Fites-Kaufman et al. 2007).

Several comparisons of VTM vs FIA data sets were made after classifying each plot into one of nine vegetation types: (1) the number, or proportion of plots in each vegetation type as a measure of extent; (2) total mean density (trees

Table 1. Vegetation types, with codes and classification rules used to subdivide Vegetation Type Mapping (VTM) project plots and Forest Inventory and Analysis (FIA) plots into groups. Vegetation types reflect agglomerations of the California Wildlife Habitat Relationship (WHR) system of classification (Mayer & Laudenslayer 1988).

Vegetation Type	Rules	WHR Type Crosswalk
Foothill woodland (FOOTWD)	≥50% relative basal area (RBA) by <i>Quercus douglasii</i> , <i>Pinus sabiniana</i> , <i>Q. wislizeni</i> , <i>Q. lobata</i> or any combination	Blue oak woodland; valley oak woodland; blue oak – foothill pine; valley foothill riparian
Montane hardwood forest (MTNHAR)	≥50% RBA by <i>Q. kelloggii</i> , <i>Q. chrysolepis</i> , <i>Notholithocarpus densiflorus</i> , <i>Acer macrophyllum</i> , <i>Alnus rhombifolia</i> or <i>Arbutus menziesii</i> or any combination	Montane hardwood; montane hardwood – conifer
<i>P. ponderosa</i> forest (PPOND)	≥50% RBA by <i>P. ponderosa</i> ; all other plots with <i>P. ponderosa</i> are lumped into MTNHAR or MIXCON	Ponderosa pine
Mixed conifer forest (MIXCON)	≥50% RBA by <i>Abies concolor</i> , <i>P. lambertiana</i> , <i>Calocedrus decurrens</i> , <i>Pseudotsuga menziesii</i> , <i>Sequoia gigantea</i> or any combination*	Sierra mixed conifer; white fir; Douglas-fir
<i>A. magnifica</i> forest (REDF)	≥50% RBA by <i>A. magnifica</i> ; all other plots with <i>A. magnifica</i> are lumped into MIXCON if mixed with <i>A. concolor</i> , <i>P. lambertiana</i> , <i>P. jeffreyi</i> or <i>C. decurrens</i> , or lumped into SUBALP if mixed with <i>P. contorta</i> , <i>P. monticola</i> , <i>T. mertensiana</i> or <i>P. albicaulis</i>	Red fir
<i>P. jeffreyi</i> forest** (JEFFP)	≥50% RBA by <i>P. jeffreyi</i> ; all other plots lumped into MIXCON, REDF, SUBALP or PINJU, depending on other elements	Jeffrey pine; eastside pine
Sub-alpine forest (SUBALP)	≥50% RBA by <i>P. contorta</i> , <i>P. albicaulis</i> , <i>T. mertensiana</i> , <i>P. monticola</i> , <i>Juniperus grandis</i> or <i>P. flexilis</i> or any combination	Sub-alpine conifer; lodgepole pine; juniper
Piñon-juniper woodland (PINJU)	≥50% RBA by <i>P. monophylla</i> , <i>J. osteosperma</i> or a combination	Piñon-juniper

*Also includes plots dominated by *Pinus attenuata*, which is rare, and does not fit well into any of the major vegetation types listed here. Plots dominated by *P. attenuata* were few in each data set (<3 each) but were included in analyses of all species combined so that no plots were excluded on the basis of vegetation.

**Plots were further divided into west and eastside by their geographic location, west or east of the Sierra Nevada crest.

ha^{-1}) by vegetation type; (3) total mean density of individual species within each vegetation type; and (4) relative total density of each species within each vegetation type. For (1), the number of plots in each vegetation type was tallied. For (2) and (3), we divided data into groups by vegetation type for (2), and by species within vegetation types for (3). To statistically test the differences in mean density between data sets (within vegetation type or component species), separate generalized linear models with a negative binomial distribution were applied to each group. This was done using the `glm.nb` function in R, available in the MASS package (Venables & Ripley 2002).

Stems \sim Data set + Offset (Area).

In this model, stem number was the response variable, with data set (VTM vs FIA) as the predictor variable and slope-corrected area as an additional parameter (an offset). This approach effectively tests the difference in slope-corrected density while retaining the ability to use stems as count data. We tried multiple distributions but negative binomial proved the best fit; this is a count-based distribution, hence the use of stems as the response variable.

For comparison (4), relative density by vegetation type was calculated as the proportion of each species relative to all other species in that type, for each vegetation type in each data set. We also compared densities of mixed conifer and sub-alpine forests within and outside Yosemite National Park, applying the same model described above to test for differences in density.

Results

Extent and density of vegetation types

Montane hardwood, mixed conifer, sub-alpine and piñon-juniper forest types were more abundant in the modern (FIA) data set than the historical (VTM) data set (Fig. 3, Table 2). Mixed conifer forest was 10% more abundant in

modern plots – more than any other vegetation type. Foothill woodland, *P. ponderosa*, *A. magnifica* and both west and east side *P. jeffreyi* forest types were all less abundant in modern plots (Fig. 3). Of these, *P. ponderosa* forest was lowest, relative to historical plots (11% lower in modern plots). The east slope vegetation types (east-side *P. jeffreyi* forest and piñon-juniper woodland) accounted for similar proportions of each data set (Fig. 3).

Total tree density was higher in modern plots than historical plots for eight of the nine types examined, and significantly higher for seven of nine (Fig. 4A, Table 2). No types exhibited significantly lower densities in modern plots. The greatest difference between historical and modern stand densities was in foothill woodland, montane hardwood, *P. ponderosa* forest and mixed conifer forest, ranging in magnitude from 40% to 128% greater in modern plots (Fig. 4A). Both east-side types, east-side *P. jeffreyi* forest and piñon-juniper woodland, were statistically equal in each time period. In historical plots, *A. magnifica* forest was the densest forest type, followed by sub-alpine and mixed conifer forest; in modern plots, montane hardwood and mixed conifer forests, each with roughly 495 trees ha^{-1} , were the densest (Table 2).

Density of mixed conifer forest was not statistically different between data sets for stands within Yosemite National Park, but highly significant for stands outside the park. For sub-alpine forest, both stands within and outside the park exhibited significantly higher densities in modern stands, at about the same magnitude (Fig. 4B).

Density of component species

Differences in tree density by component species were not consistent across species within a vegetation type, leading to shifts in dominant species for some types (Fig. 5, Table 3). Species-level differences between data sets were highest for foothill woodland, montane hardwood forest, *P. ponderosa* forest and mixed conifer forest.



Fig. 3. Proportion of the nine vegetation types used in this study for the Vegetation Type Mapping (VTM) plot data set ($n = 4321$; left panel) and Forest Inventory and Analysis (FIA) data set ($n = 1000$; right panel). Numbers are the percentage of that vegetation type of all plots classified in that data set. Vegetation types are arranged clockwise, starting at 12:00, as they occur from west to east across the long axis of the Sierra Nevada.

Table 2. Summary of density, sample size, frequency and statistical inference data for Vegetation Type Mapping (VTM) plots ($n = 4321$) and Forest Inventory and Analysis (FIA) plots ($n = 1000$), for the nine vegetation types used in this study.

	Total Plots		% of Total		Mean density*		Mean SE†		Frequency diff.‡	Density % diff.‡	Estimate§	P-value§
	VTM	FIA	VTM	FIA	VTM	FIA	VTM	FIA				
Foothill woodland	634	127	14.5	12.7	203	288	6.4	25.1	-1.8	+41.8	-0.34	<0.001
Montane hardwood forest	247	105	5.7	10.5	217	496	13.8	35.2	+4.8	+128.3	-0.82	<0.001
<i>P. ponderosa</i> forest	862	89	19.7	8.9	273	383	7.6	28.2	-10.8	+40.2	-0.34	<0.001
Mixed conifer forest	1181	371	27.0	37.1	293	495	8.5	16.7	+10.1	+68.7	-0.52	<0.001
<i>A. magnifica</i> forest	408	60	9.3	6.0	317	390	10.8	38.0	-3.3	+23.1	-0.21	0.010
West-side <i>P. jeffreyi</i>	257	34	5.9	3.4	146	210	8.9	29.2	-2.5	+43.8	-0.36	0.013
Sub-alpine forest	426	140	9.7	14.0	305	368	10.5	27.9	+4.3	+20.6	-0.18	0.012
East-side <i>P. jeffreyi</i>	255	50	5.8	5.0	219	228	9.8	32.9	-0.8	+3.8	-0.03	0.766
Piñon-juniper woodland	51	24	1.2	2.4	234	205	26.6	46.6	+1.2	-14.2	0.14	0.512

*Trees ha⁻¹.

†Standard Error of mean density.

‡Difference between FIA and VTM data sets (FIA-VTM).

§From generalized linear model tests for difference between VTM and FIA density in each group. Significant tests at $P < 0.05$ are in bold.

In foothill woodland, *Pinus sabiniana* total density was significantly lower in modern plots, while *Quercus wislizeni* density was significantly higher. Density of *Q. douglasii*, the historically dominant species in the type, was similar in both data sets (Fig. 5, Table 3). These changes led to large differences in their relative densities: *P. sabiniana* was 13% lower in modern plots, *Q. wislizeni* was 26% higher, and *Q. douglasii* was 8% lower. In terms of density, *Q. douglasii* was the most abundant species in historical plots (82.2 trees ha⁻¹) but *Q. wislizeni* was the most abundant in modern plots (172.5 trees ha⁻¹; Table 3).

In montane hardwood, *Pseudotsuga menziesii*, *Q. chrysolepis* and *Q. kelloggii* densities were all significantly higher in modern plots, while *P. ponderosa* was significantly lower (Fig. 5, Table 3). Notably, the difference in *Q. chrysolepis* density (+175.8 trees ha⁻¹) was more than any other species in any forest type. Relative density of *Q. chrysolepis* was 22% higher in modern plots, while relative density of *P. ponderosa* was 11% lower and *Q. kelloggii* was 14% lower (Table 3).

In *P. ponderosa* forest, all six species analysed had higher densities in modern plots (Fig. 5, Table 3); *Calocedrus decurrens* and *Q. kelloggii* were both significantly more dense. Density of *P. ponderosa* as a species was similar in both data sets and statistically not significant. The relative density of *P. ponderosa* was lower (69% vs 55%) in modern plots, while relative density of all other species in the type was higher (Table 3).

In mixed conifer forest, total density was significantly higher for *Abies concolor*, *C. decurrens*, *Notholithocarpus densiflorus*, *P. menziesii*, *Q. chrysolepis* and *Q. kelloggii* (Fig. 5, Table 3). *Pinus lambertiana* and *P. jeffreyi* densities were significantly lower and *P. ponderosa* density was lower in modern plots but not statistically significant. Differences in

relative density between the two data sets favoured *C. decurrens*, which had a relative density 10.7% more in modern plots. *Abies concolor*, the most dominant species in mixed conifer, had very similar relative densities in both time periods (34% vs 33%; Table 3).

In *A. magnifica* forest, total density of *A. magnifica* was significantly higher in modern plots. No other species in the type exhibited differences that were statistically significant, although density of *P. monticola* was 41% lower in modern plots and was marginally significant (Fig. 5, Table 3). *Abies magnifica* as a species had higher relative density in modern plots; all other species were very similar in both data sets (Table 3).

In west-side *P. jeffreyi* forest, historical and modern densities were not statistically different for any species, although densities of both *A. concolor* and *P. jeffreyi* were higher in modern plots (Fig. 5, Table 3). Differences in relative density between data sets were minor (Table 3).

In sub-alpine forest, three species, *A. magnifica*, *Pinus albicaulis* and *Pinus contorta* ssp. *murrayana* had higher densities in modern plots. Of these, only *A. magnifica* was statistically significant. Differences in relative density were minor for all species (Table 3).

Both east-side forest types (east-side *P. jeffreyi* forest and piñon-juniper woodland) had very similar densities in both data sets, with no significant differences in density by the major species and very little difference in relative density (Fig. 5, Table 3).

Discussion

Our comparisons suggest that most forest types of the central Sierra Nevada are denser on average than they were in the early 1930s. In our data, all west slope vege-

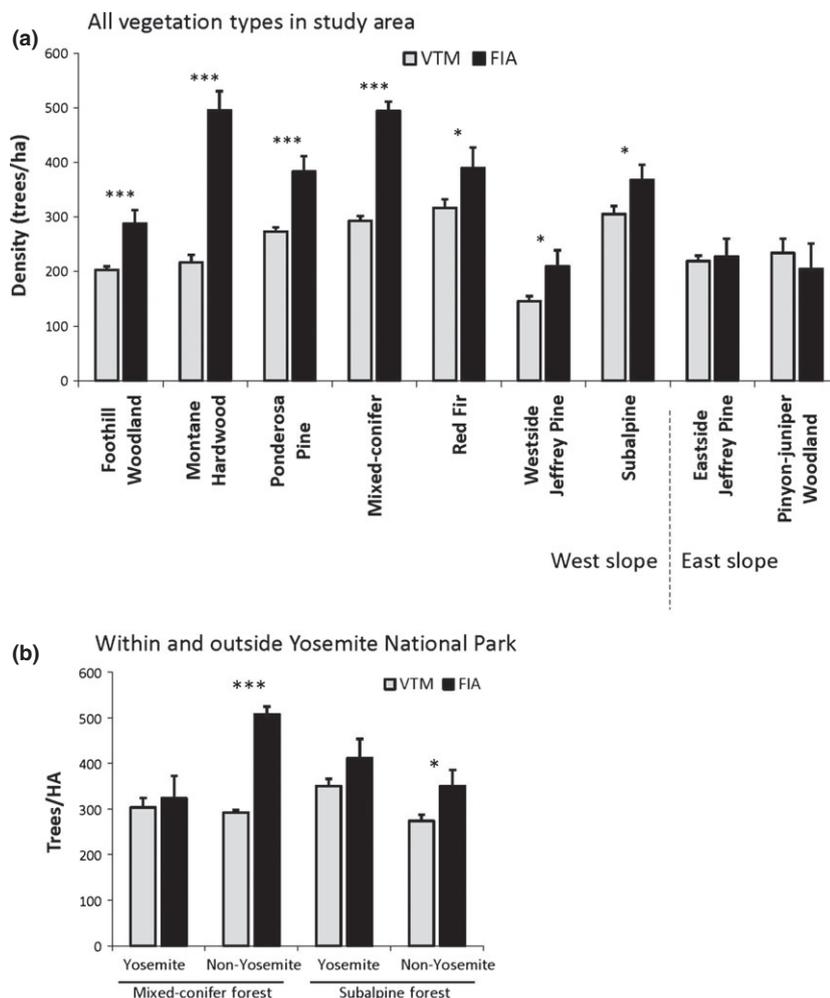


Fig. 4. Difference in mean total tree density (trees ha^{-1}) \pm SE for (a) all species combined between Vegetation Type Mapping (VTM) plots and Forest Inventory and Analysis (FIA) plots, by vegetation type throughout the study area, and (b) all species in mixed conifer forest and sub-alpine forest for VTM and FIA plots within and outside the boundaries of Yosemite National Park. For (a), vegetation types are arranged left to right, as they occur from west to east across the long axis of the Sierra Nevada. See Table 1 for names and descriptions of vegetation types. Statistically significant differences are indicated by * = $0.01 < P < 0.05$; *** = $P < 0.001$.

tation types were denser in modern plots than historical plots, with the largest differences occurring in montane hardwood and mixed conifer forest, while east slope types appear unchanged. Differences in component species abundances between historical and modern data sets reflect stand conditions favouring shade-tolerant over shade-intolerant species (Figs 4, 5, Tables 2, 3). Many researchers have documented general infilling of the forest in the Sierra Nevada over the last few decades across a wide variety of sites and elevations (Vankat & Major 1978; Parsons & Debenedetti 1979; Vale 1987; Taylor 1995; Ansley & Battles 1998; Gruell 2001; Millar et al. 2004; Dolanc et al. 2013). Our study shows, however, that the degree of change varies both among vegetation types and among species.

The strong differences between historical and modern densities observed in montane hardwood, *P. ponderosa* forest and mixed conifer forest are likely related to fire suppression policies that began in the 1920s and 1930s (Husari & McKelvey 1996). Of all forest types in the Sierra Nevada, fire return intervals were historically very low (7–20 yrs) in these types (Skinner & Chang 1996; Van de Water & Safford 2011), making them more likely to have been altered by 20th century fire suppression efforts. Our results are consistent with previous conclusions that current forest densities in mixed conifer forests are considerably higher than pre-suppression levels, and composition has shifted in favour of fire-intolerant species (Ansley & Battles 1998; North et al. 2007; Scholl & Taylor 2010; Collins et al. 2011).

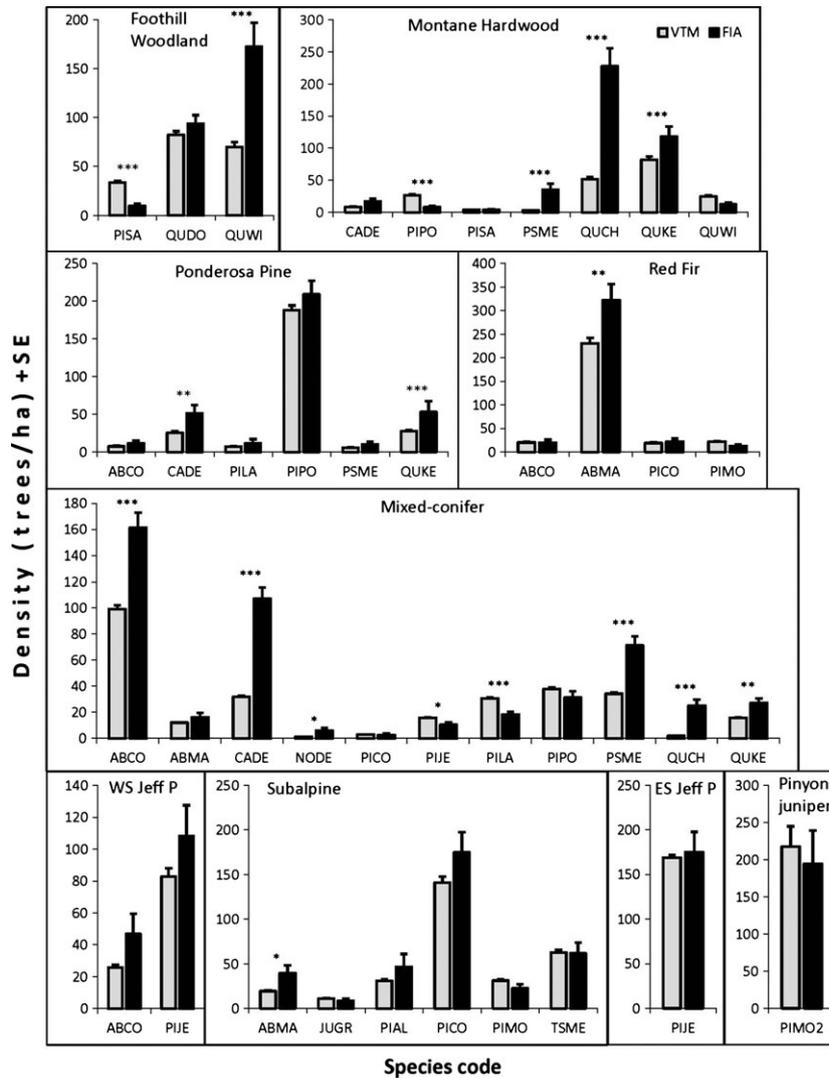


Fig. 5. Difference in mean total tree density (trees ha⁻¹) ± SE for individual species within each of the nine vegetation types analysed in this study, between Vegetation Type Mapping (VTM) plots (light bars) and Forest Inventory and Analysis (FIA) plots (black bars). Only species occurring in at least 20 plots in each data set are shown. Statistically significant differences are indicated by * = 0.01 < P < 0.05; ** = 0.001 < P ≤ 0.01; and *** = P < 0.001. Species are as follows: *Abies concolor* (ABCO); *Abies magnifica* (ABMA); *Calocedrus decurrens* (CADE); *Juniperus grandis* (JUGR); *Notholithocarpus densiflorus* (NODE); *Pinus albicaulis* (PIAL); *Pinus contorta* ssp. *murrayana* (PICO); *Pinus jeffreyi* (PIJE); *Pinus lambertiana* (PIAL); *Pinus monticola* (PIMO); *Pinus monophylla* (PIMO2); *Pinus ponderosa* (PIPO); *Pseudotsuga menziesii* (PSME); *Quercus chrysolepis* (QUCH); *Quercus douglasii* (QUDO); *Quercus kelloggii* (QUKE); *Quercus wislizeni* (QUWI); *Tsuga mertensiana* (TSME).

The contrast between change in mixed conifer forest densities within and outside Yosemite (Fig. 4B) may reflect the more aggressive fire management policies in Yosemite compared with other US federal lands in the range (Stephens & Ruth 2005). Vegetation types of the lower half of the west slope have generally been more impacted by other land uses as well, such as mining, logging and development (Beesley 1996). Stand recovery from these types of disturbances might manifest in similar ways to fire suppression response (e.g. more small trees, reduced dominance of *Pinus* spp.).

The lower frequency of *P. ponderosa* forest in modern plots may reflect conversion of these stands to montane hardwood or mixed conifer forest, via in-growth of species such as *Q. chrysolepis*, *Q. kelloggii*, *C. decurrens* and/or *A. concolor*. Historically, frequent fires would have kept recruitment of these species in the understorey low. However, differences could also be related to the different plot selection criteria between the two data sets.

The montane hardwood type in our study exhibited the largest difference between historical and modern stand conditions of all types in the study. Bolsinger (1988) sug-

Table 3. Total and relative density of component species in each vegetation type plus statistical data.

	Total Density*					Relative Density†		
	VTM mean	FIA mean	%Diff. (VTM-FIA)	GLM Estimate‡	GLM P-value§	VTM (%)	FIA (%)	Diff. (%FIA-%VTM)
Foothill woodland								
<i>Pinus sabiniana</i>	33.6	9.9	-70.5	1.22	<0.001	16.6	3.4	-13.2
<i>Quercus douglasii</i>	82.2	93.5	+13.8	-0.13	0.36	40.5	32.5	-8.0
<i>Quercus wislizeni</i>	69.9	172.5	+146.9	-0.90	<0.001	34.4	60.0	+25.6
Montane hardwood forest								
<i>Calocedrus decurrens</i>	8.7	17.2	+97.6	-0.69	0.09	4.0	3.5	-0.5
<i>Pseudotsuga menziesii</i>	3.2	35.5	+1007.6	-2.40	<0.001	1.5	7.2	+5.7
<i>Pinus ponderosa</i>	26.6	8.1	-69.6	1.18	<0.001	12.3	1.6	-10.7
<i>Pinus sabiniana</i>	4.0	4.1	+2.1	-0.02	0.97	1.8	0.8	-1.0
<i>Quercus chrysolepis</i>	51.8	227.6	+339.1	-1.48	<0.001	23.9	45.9	+22.0
<i>Quercus kelloggii</i>	82.0	118.0	+43.9	-0.37	0.007	37.8	23.8	-14.0
<i>Quercus wislizeni</i>	25.2	12.4	-50.6	0.71	0.09	11.6	2.5	-9.1
<i>P. ponderosa</i> forest								
<i>Abies concolor</i>	7.6	11.8	+56.5	-0.44	0.34	2.8	3.1	+0.3
<i>Calocedrus decurrens</i>	25.9	51.6	+99.6	-0.69	0.01	9.5	13.5	+4.0
<i>Pinus lambertiana</i>	7.2	11.7	+63.0	-0.49	0.16	2.6	3.0	+0.4
<i>Pinus ponderosa</i>	188.3	209.3	+11.1	-0.10	0.27	68.9	54.6	-14.3
<i>Pseudotsuga menziesii</i>	5.9	10.3	+74.9	-0.55	0.21	2.2	2.7	+0.5
<i>Quercus kelloggii</i>	28.0	53.2	+89.9	-0.64	<0.001	10.3	13.9	+3.6
Mixed conifer forest								
<i>Abies concolor</i>	99.4	161.4	+62.4	-0.49	<0.001	33.9	32.6	-1.3
<i>Abies magnifica</i>	12.1	16.3	+34.6	-0.30	0.27	4.1	3.3	-0.8
<i>Calocedrus decurrens</i>	32.0	107.1	+235.0	-1.21	<0.001	10.9	21.6	+10.7
<i>Notholithocarpus densiflorus</i>	1.2	6.1	+388.7	-1.59	0.02	0.4	1.2	+0.8
<i>Pinus jeffreyi</i>	15.8	10.5	-33.6	0.41	0.03	5.4	2.1	-3.3
<i>Pinus lambertiana</i>	30.7	18.3	-40.2	0.51	<0.001	10.5	3.7	-6.8
<i>Pinus ponderosa</i>	37.9	31.4	-17.2	0.19	0.15	12.9	6.3	-6.6
<i>Pseudotsuga menziesii</i>	34.3	71.3	+107.8	-0.73	<0.001	11.7	14.4	+2.7
<i>Quercus chrysolepis</i>	1.9	25.1	+1196.1	-2.57	<0.001	0.7	5.1	+4.4
<i>Quercus kelloggii</i>	15.8	27.2	+72.3	-0.54	<0.001	5.4	5.5	+0.1
<i>A. magnifica</i> forest								
<i>Abies concolor</i>	20.4	19.5	-4.4	0.04	0.91	6.4	5.0	-1.4
<i>Abies magnifica</i>	230.8	322.1	+39.6	-0.33	<0.001	72.9	82.7	+9.8
<i>Pinus monticola</i>	22.1	12.9	-41.8	0.52	0.06	6.7	3.3	-3.4
<i>Pinus contorta</i> ssp. <i>murrayana</i>	18.5	22.4	+21.1	-0.15	0.68	5.6	5.7	+0.1
Westside <i>P. jeffreyi</i> forest								
<i>Abies concolor</i>	25.9	46.9	+81.3	-0.59	0.12	17.7	22.3	+4.6
<i>Pinus jeffreyi</i>	82.9	108.2	+30.6	-0.27	0.05	56.8	51.6	-5.2
Sub-alpine forest								
<i>Abies magnifica</i>	19.6	39.7	+102.8	-0.71	0.03	6.4	10.8	+4.4
<i>Juniperus grandis</i>	11.2	8.6	-23.1	0.26	0.48	3.7	2.3	-1.4
<i>Pinus albicaulis</i>	31.0	46.4	+49.8	-0.40	0.38	10.2	12.6	+2.4
<i>Pinus contorta</i> ssp. <i>murrayana</i>	141.2	175.0	+24.0	-0.22	0.19	46.3	47.6	+1.3
<i>Pinus monticola</i>	31.2	22.7	-27.4	0.31	0.13	10.2	6.2	-4.0
<i>Tsuga mertensiana</i>	62.5	61.8	-1.2	0.01	0.97	20.5	16.8	-3.7
Eastside <i>P. jeffreyi</i> forest								
<i>Pinus jeffreyi</i>	168.6	174.8	+3.7	-0.03	0.78	76.9	76.8	-0.1
Piñon-juniper woodland								
<i>Pinus monophylla</i>	217.3	194.3	-10.6	0.11	0.62	92.9	94.8	+2.1

Nomenclature follows *The Jepson Manual, 2nd Edition* (Baldwin et al. 2012).

*Trees ha⁻¹.

†Density relative to all other species in that vegetation type.

‡Slope estimate coefficient from generalized linear model tests of differences in density between VTM and FIA data sets.

§Significant values at $P < 0.05$ in bold.

gested that increased volume of hardwoods compared with conifers was due to preferential logging of overstorey conifers, followed by rapid resprouting and superior growth of hardwoods. Once established, montane hardwood stands, which are usually dominated by long-lived oaks, can be persistent on the landscape (Allen-Diaz et al. 2007). Our findings are consistent with the modelled predictions of a more substantial increase in areal extent of montane hardwood than other forest types (Hayhoe et al. 2004; Lenihan et al. 2008; montane hardwood forest referred to as 'mixed evergreen forest'). These predictions rest on the assumption that, under warmer conditions, hardwoods will eventually outcompete conifers, especially if precipitation increases and fire activity increases (Lenihan et al. 2003, 2008).

Greater change in forests such as montane hardwood and mixed conifer could also reflect their higher turnover rates (i.e. increased recruitment and mortality). Globally, there is a positive correlation between turnover and productivity, and that manifests as a negative correlation between turnover and elevation in the Sierra Nevada (Stephenson & van Mantgem 2005). Despite widespread increases in small trees in our study area, large tree density appears to be declining (Dolanc et al. *in review*), which is consistent with increased turnover. Higher drought stress via climate change has been suggested as the mechanism behind increased mortality rates (van Mantgem et al. 2009; Allen et al. 2010).

Both foothill woodland and montane hardwood types indicate a shift in overstorey dominance, from deciduous oaks to evergreen oaks – *Q. wislizeni* in foothill woodland and *Q. chrysolepis* in montane hardwood. From 1945 to 1985, Bolsinger (1988) observed that both *Q. chrysolepis* and *Q. wislizeni* had been regenerating very well, and that *Q. douglasii* had not. Increased dominance by live oaks may be related to climate change. Their evergreen leaves and habit give them advantages over deciduous oaks in warmer, drier conditions (Pavlik et al. 1991). Consistent with this, the future range of blue oak under warmer, drier conditions has been modelled to shrink by about 40% (Kueppers et al. 2005).

Differences in species abundance in mixed conifer forest reflect decreased dominance by *Pinus* spp., especially *P. lambertiana*, *P. ponderosa* and *P. jeffreyi*. All other mixed conifer species in our study are generally more shade-tolerant than *Pinus* spp. (Minore 1979; Oliver & Dolph 1992; Fites-Kaufman et al. 2007). Fire suppression, which has led to denser forest (e.g. Ansley & Battles 1998), and logging practices, which targeted overstorey *Pinus* (Sudworth 1900; Leiberg 1902), have created a situation that favours non-pine conifers and hardwoods. *Pinus lambertiana*, *P. ponderosa* and *P. jeffreyi* made up a combined 28.8% of mixed conifer plots in the historical data set, yet make up

only 12.1% in modern mixed conifer stands. Similar trends have been reported elsewhere for mixed conifer forests (North et al. 2007; Scholl & Taylor 2010).

Much of the focus regarding compositional changes due to fire suppression has been on *A. concolor* (e.g. Parsons & Debenedetti 1979), but our data suggest that *C. decurrens* has fared even better. *Calocedrus decurrens* density was 235% higher in modern mixed conifer stands and 100% higher in modern *P. ponderosa* forest, and its relative density in mixed conifer increased much more than any other species (relative density of *A. concolor* actually decreased slightly). Increased abundance of *C. decurrens* may go back to the 19th century. Both Sudworth (1900) and Leiberg (1902) remarked on how well *C. decurrens* was regenerating at the turn of the 20th century. *Calocedrus decurrens* was also generally avoided by early logging operations because of the low value of the wood (Leiberg 1902), and is probably more drought-tolerant than other shade-tolerant conifers (Pharis 1966). In old-growth forests in the Lake Tahoe basin, *C. decurrens* is associated with low-elevation sites that have low snowpack and early melt dates (Barbour et al. 2002). These characteristics seem well suited to a future of warmer temperatures and continued fire suppression.

Changes in east-slope forest types (east-side *P. jeffreyi* forest and piñon-juniper woodland) and higher elevation types (*A. magnifica* forest, west-side *P. jeffreyi* forest, sub-alpine forest) were less pronounced than others types in the range. The higher-elevation and east slope types are generally less productive, with shorter growing seasons (Fites-Kaufman et al. 2007; Thorne et al. 2007), and may also have endured less extensive and/or frequent disturbance.

Our results for sub-alpine forest and woodland are similar to those from a study that re-sampled sub-alpine VTM plots in the same region (Dolanc et al. 2013). In each case, density was higher overall in modern plots but composition was little changed. Dolanc et al. (2013) found this pattern was robust across the landscape. Since the sub-alpine zone has been largely free of the disturbances (including fire suppression) found at lower elevations, they attributed changing structure to climate. Our contrast of mixed conifer and sub-alpine forests within and outside Yosemite lend support to this: change in mixed conifer density inside the park is very different from stands outside, yet in sub-alpine forest, historical and modern differences were quite similar. Since sub-alpine has been minimally impacted by management both inside and outside the park, differences in density are more likely to be driven by climate.

Conclusions

By conducting an analysis across all vegetation types, for a broad region of the Sierra Nevada, we have highlighted which vegetation types have likely changed the most since

the 1930s, in terms of forest density and composition. Our results suggest that montane hardwood and mixed conifer forests, and more generally lower-elevation forests of the west slope, have increased in density and shifted composition more than other types in the range. Interestingly, east slope vegetation types appear to have changed very little. These conclusions help knit together results from previous studies that were more restricted geographically (e.g. Vankat & Major 1978; Vale 1987). Despite differences in sampling protocol and plot selection, trends in our comparisons of VTM and FIA data are similar in direction and magnitude to those reported in these more regional studies using a variety of methods. This not only supports the utility of comparing these two very large, comprehensive data sets, but also suggests the trends in structural and compositional changes in the Sierra Nevada are very real. Changes in density and composition in lower-elevation forests are consistent with fire suppression, but density increases in high-elevation vegetation types are also significant and more likely to be caused by changing climate.

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Supporting Information

Additional supporting information may be found in the online version of this article:

Appendix S1. Comparison of distributions of Vegetation Type Mapping (VTM) and Forest Inventory and Analysis (FIA) data sets by latitude and elevation.