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Changing forest structure across the landscape of the Sierra Nevada, CA, USA, since the 1930s

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Abstract. Understanding the dynamics of forest structure aids inference regarding future forests and their distributions around the world. Over the last few decades, several papers have addressed changing forest structure in the Sierra Nevada, CA, USA, but these studies were limited in scope. We carried out a broad comparison of forest density and composition in the 1930s versus the 2000s for the west slope of the central and northern Sierra Nevada, using the two most extensive data sets available. Forests in this region have endured a long, complex history of human disturbance, and are now experiencing climatic shifts. We subdivided the landscape into elevation and latitude zones and compared historical and modern tree densities within each zone. We compared densities in historical plots to burned and unburned modern plots, as well as densities of individual tree species in historical vs. modern plots for their entire elevational distribution. Density of small trees (10.2–30.4 cm dbh) was significantly higher in the modern data set for all elevations and all latitudes, ranging from 20 to 148% higher. However, density of large trees (≥ 61.0 cm) was lower in the modern data set for most elevations and latitudes, ranging from 41% to 60% lower in most zones. Density difference of mid-sized trees (30.5–60.9 cm) was mixed, but was generally higher in modern plots. The pattern of more small trees but fewer large trees held for most individual species as well, but with notable exceptions. Our comparison of burned and unburned plots strongly implicates fire suppression as a driver of increased density of small trees in low- to mid-elevation forests. However, modern high-elevation (>2500 m) forests, where fire suppression impacts should be minimal, were also significantly denser than historical plots. Changing climatic conditions may be driving increased densities of small trees in high elevations, as well as decreased densities of large trees across the region.

Key words: climate change; demography, elevation; fire suppression; historical data; Forest Inventory and Analysis (FIA); forest structure; latitude; Sierra Nevada; tree density; Vegetation Type Mapping (VTM).

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INTRODUCTION

Understanding dynamics in forest structure can improve our knowledge of how trees and forests respond, and will continue to respond, to current and future changes (Swetnam 1993). Forest structure (e.g., tree density or canopy

cover) is intricately linked to biogeochemical cycling and the regional climate (Bonan 2008), and is a key stabilizing process for the geomorphology of hillslope ecosystems (Pawlik 2013). In general, models that predict future biogeographic distributions are lacking good data on population dynamics over time (Kearney and Porter

2009). Empirical data on stand structure can be used to calibrate distribution models (Loehle and LeBlanc 1996), and when combined with historical data, they have the potential to reveal important responses to disturbances and global change factors not properly accounted for by models.

Forests of the Sierra Nevada, California, USA, appear to have experienced dramatic changes in structure during the last several decades. Overall tree density (especially small to medium-sized trees) has increased in many locations (e.g., Vankat and Major 1978, Parsons and DeBenedetti 1979, Ansley and Battles 1998, Millar et al. 2004, Beaty and Taylor 2008, Dolanc et al. 2013*b*), while density of large trees has recently declined (Smith et al. 2005, van Mantgem and Stephenson 2007, Lutz et al. 2009, North et al. 2009, van Mantgem et al. 2009, Dolanc et al. 2013*b*). These studies attributed shifts in structure to a wide range of factors, including fire suppression, logging, grazing, and climate change.

However, most of the research on shifting forest structure in the Sierra Nevada has been restricted to particular elevations (Millar et al. 2004, Dolanc et al. 2013*b*), management units (Vankat and Major 1978, Barbour et al. 2002, Beaty and Taylor 2008, Lutz et al. 2009), certain functional types (Bolsinger 1988), or comparatively small areas (Ansley and Battles 1998, Smith et al. 2005), and application of conclusions regarding causes of change are bound by their more limited scope. There is therefore a need for more broad-scale analysis of structural change in forests across much of the Sierra Nevada, across land ownership boundaries and across the elevational distribution of individual species. Such an approach has the potential to separate localized phenomena from more general causes of change, which should in turn help elucidate the most important conservation and management concerns range-wide.

In this study, we used the two most extensive data sets available on forest structure for the Sierra Nevada to examine trends in historical vs. modern forest structure. Our study area comprised the entire elevational range and 2.7° of latitude of the west slope of the central and northern Sierra Nevada. We used the historical Vegetation Type Mapping (VTM) Project plots, sampled from 1929 to 1936, and modern Forest

Inventory and Analysis (FIA) plots sampled from 2001 to 2010, to compare differences in tree density of different diameter size classes between data sets separated by 65–81 years. Each data set includes hundreds of plots across the region, with plots in all types of forest and land ownerships. Despite differences in protocol, each data set collected tree data on a per area basis and included all species above a minimum diameter size, permitting comparisons of density between data sets.

Taking advantage of the breadth of the VTM and FIA data sets, our main objective was to determine whether differences in forest structure are consistent across the landscape of the Sierra Nevada. Despite the complexity of disturbances in time and space in the Sierra Nevada, such a large analysis has the potential to elucidate underlying trends that most or all forests in the region have in common, from those that are more localized. Since we used unpaired plots for comparison, we stratified each data set into elevation and latitude bins and compared tree densities between data sets in each stratum. We compared tree densities in VTM (historical) plots with burned and unburned (since the VTM era) FIA plots. We also compared differences between VTM and FIA data sets for the most common species, across their entire range in the study area. Thus, four groups of comparisons between data sets are presented in this paper: (1) by elevation; (2) by latitude; (3) burned vs. unburned plots; and (4) by species.

MATERIALS AND METHODS

Study area

Our study area was the west slope of the central and northern Sierra Nevada, an area of approximately 30,500 km² (Fig. 1). Elevations in the study area range from near sea level in the west to c. 4000 m along the Sierra crest in the southeast. Geologically, the region is underlain by Paleozoic and Mesozoic metamorphic rocks and Late Mesozoic granitic plutons. A veneer of Late Cenozoic volcanic rocks overlays the basement rocks in much of the northern portion; granitic rocks dominate in the southern half of the study area. Soil types across the study area are highly diverse (SNEP 1996, Potter 1998, Storer et al. 2004, Hill 2006). Nearly two-thirds

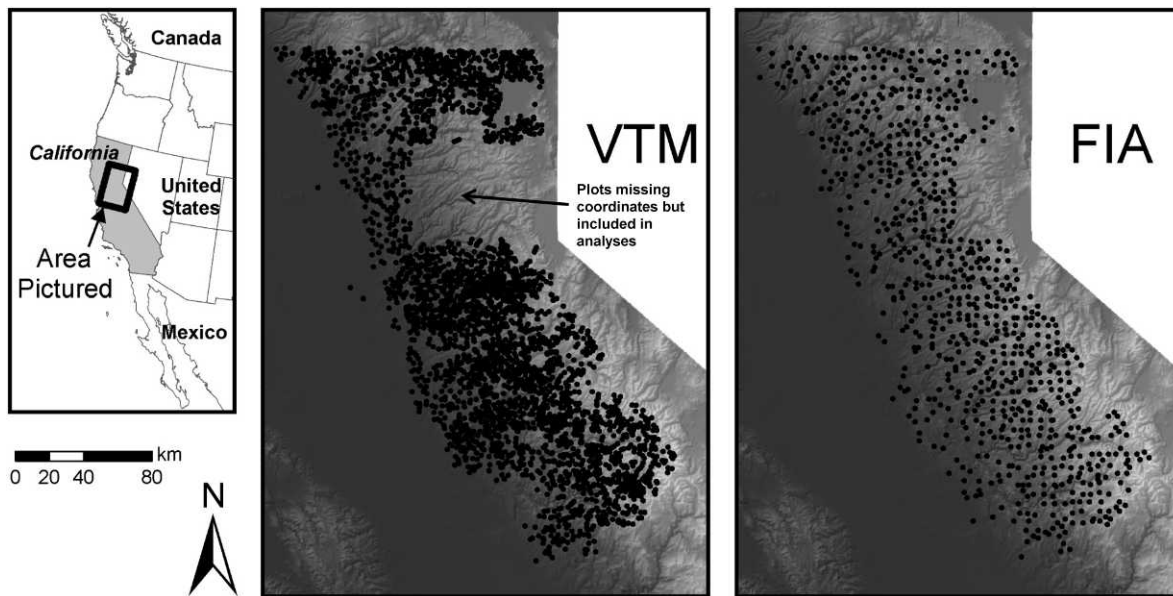


Fig. 1. Map of study area in the central and northern Sierra Nevada ($\sim 30,500 \text{ km}^2$) showing the distribution of Vegetation Type Mapping (VTM) plots and Forest Inventory and Analysis (FIA) plots used in our analyses. All plots analyzed were from the west slope of the range. The area of missing VTM plots actually contains plots but the coordinates are missing, so they cannot be displayed on a map. All other attributes of those plots, including elevation and tree data, exist and were included in the study. When calculating mean latitude for VTM plots in this gap, an average of 39.25° was assumed for each plot as these all come from a quadrangle between 39.0 and 39.5° N latitude. Coordinates are also missing for the quadrangle immediately adjacent to the east and since plots in this quadrangle could fall east or west of the Sierra Nevada crest, all plots were thrown out for both data sets; this is why plots just west of the crest are not shown for FIA plots in this region.

(64%) of land in the Sierra Nevada is publicly owned (36% private), 41% by the US Forest Service, 13% by the Bureau of Land Management and 6% by the Park Service. Approximately 2% is owned by the state, cities or counties and roughly 21% of the range is in protected reserves (SNEP 1996).

The climate of the Sierra Nevada west slope is primarily montane Mediterranean, with warm, dry summers and cool, wet winters (SNEP 1996). Precipitation increases with elevation up to c. 1500 m elevation where it reaches a peak of 1800 mm/yr, and then decreases slightly to the crest (Major 1990). The percent of precipitation that falls as snow varies from 0% near the valley floor, to around 90% near the crest. January mean minimum temperatures range from 3° to 4°C at the lowest elevations (Central Valley) to below -15°C at elevations above 3000 m; July mean maximum temperatures range from about 35°C in the Central Valley, to $<20^\circ\text{C}$ above 3000 m

(SNEP 1996, Potter 1998, Storer et al. 2004).

Vegetation patterns follow elevation and climatic variability and are thus diverse (Barbour et al. 2007). The western foothill zone is characterized by a mosaic of grassland, oak woodland and chaparral (Allen-Diaz et al. 2007, Bartolome et al. 2007). Conifer forests begin at 300 to 900 m elevation and extend up into the subalpine zone, with treeline occurring at 3000–3300 m, rising in elevation from north to south (Fites-Kaufman et al. 2007). Mixed-conifer forest prevails over much of the middle elevations (roughly 600–2500 m) supplanted by red fir forest and subalpine forest/woodland at higher elevations. For more information on vegetation and individual species of the Sierra Nevada, see Barbour et al. (1993); SNEP (1996); Potter (1998); Barbour et al. (2007); and Sawyer et al. (2009).

Data sources

The Wieslander Vegetation Type Mapping

(VTM) Project sampled about 5000 vegetation plots in the central and northern Sierra Nevada from 1928 to 1940 (1929–1936 for most plots). Plots were intended to provide quantitative information on vegetation structure and composition for maps the VTM crews were producing concurrently. In forested areas, the VTM plots were rectangular, 20.1 m wide by 40.2 m long (809 m²). VTM crews tallied all trees present by species within the 809 m² area in four diameter 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). Crews also collected information on dominant shrub and herb species, as well as site physical data, including elevation, slope inclination and aspect, and soil depth. VTM crews marked plot locations onto maps as they worked but coordinates were added many years later via digitation and georeferencing of their original maps. Kelly et al. (2008) determined that the error likely to be associated with this process ranges from approximately 100 to 400 m.

Researchers have used VTM plot data for comparison with re-sampled VTM plots (Minnich et al. 1995, Franklin et al. 2004, Talluto and Suding 2008, Dolanc et al. 2013*b*) and comparison with independent, modern data sets (Bouldin 1999, Fellows and Goulden 2008, Lutz et al. 2009, Dolanc et al. 2013*a*). Comparisons of change in vegetation distributions between the VTM maps and modern maps have also been published (Freudenberger et al. 1987, Thorne et al. 2008). Details regarding the VTM plot protocol can be found in the VTM field manual, accessible online (Wieslander et al. 1933; <http://vtm.berkeley.edu/>). The VTM plot data are also available online and can be accessed at <http://vtm.berkeley.edu/>.

The Forest Inventory and Analysis (FIA) program is the national forest inventory of the United States and is implemented by the US Forest Service. The program collects, compiles and archives data on forest status and health for all types of land throughout the US, based on a gridded set of plots across the country (Smith 2002). The current national FIA protocol divides plots into four 7.3 m (24 ft) radius circular subplots. Each subplot has a 2.1 m (6.8 ft) radius circular microplot nested within its boundaries. For all subplots, every tree >12.7 cm (5 in) dbh (diameter at breast height [dbh]) is measured and identified to species. Within microplots, every

tree >2.5 cm (1 in) dbh is measured. The total area of all four subplots combined, and thus of the FIA sample, is 672.45 m².

The FIA program does not make plot coordinates publicly available but does release perturbed coordinates for approximate plot locations. These coordinates have been determined to be within 800 m of the actual location (McRoberts et al. 2005). More information on the history and details of FIA protocol can be found in Bechtold and Patterson (2005) and the FIA field manual (Woudenberg et al. 2011). All plots used in this study were from the most recent version of the FIA protocol. FIA data can be accessed at <http://apps.fs.fed.us/fiadownload/datamart.html>.

As with any comparison of independent data sets, it is possible that reported differences between the two data sets are related to their different objectives and methods. The VTM and FIA data sets each include complete information on trees above a certain minimum diameter (i.e., all species, sampled throughout a stated area), allowing for comparisons of trees/area. Contrary to other forest inventories of the time, in which methods focused on timber volume of economically-valuable species (Frayer and Furnival 1999), the VTM protocol included all species and all sizes ≥ 10.2 cm (Wieslander et al. 1933). In an interview conducted in the 1980s, A. Wieslander (the leader and architect of the VTM project) discussed his desire to conduct a survey that was more complete and ecologically sound than typical Forest Service inventories of the time, and how this was initially met with resistance by Forest Service personnel (Wieslander 1985).

Perhaps the greatest concern in comparing VTM and FIA data sets is with how each data set determined plot locations. FIA plot locations are determined randomly based on a grid system (Bechtold and Patterson 2005), but VTM plots were selected subjectively in the field, located in sites that crews felt best represented the vegetation polygon they were mapping concurrently (Wieslander et al. 1933, Wieslander 1935*a*). Because of this subjectivity, it has been suggested the VTM data set is biased toward more mature stand types (Bouldin 2009), meaning crews located plots in sites that were late-successional and avoided (intentionally or not) more dense,

Table 1. Plot number and proportion of total for the Vegetation Type Mapping (VTM) and Forest Inventory and Analysis (FIA) data sets used in this study.

Category	VTM		FIA	
	No. plots	Percentage of total	No. plots	Percentage of total
Total plots	3580	100.0	841	100.0
Elevation				
<500 m	527	14.7	103	12.2
500–999 m	659	18.4	169	20.1
1000–1499 m	769	21.5	199	23.7
1500–1999 m	888	24.8	203	24.1
2000–2499 m	493	13.8	105	12.5
≥2500 m	231	6.5	62	7.4
Latitude				
<38° N	722	20.2	171	20.3
38.0–38.49° N	905	25.3	184	21.9
38.5–38.99° N	819	22.9	172	20.5
39.0–39.49° N	370	10.3	117	13.9
39.5–40.00° N	764	21.3	197	23.4
Warm aspects (SE–NW)	1732	48.4	430	51.1
Cool aspects (NW–SE and level)	1748	48.8	394	46.8

Note: Each subgroup contained at least a few plots with missing values for that attribute, thus most subgroups do not add up to the totals listed.

second-growth forest. Evidence of any sort of directive that might have led to such bias cannot be found in the VTM field manual, or any published documentation of the project (Wieslander et al. 1933, Wieslander 1935*a, b*). What is documented is their objective to locate plots in sites where the vegetation was “representative” of the polygon they were mapping. Previously, we developed scatterplots of tree density/plot by elevation and latitude for all forest types combined and mixed-conifer plots in the central Sierra Nevada (Dolanc et al. 2013*a*). These scatterplots show a remarkably similar spread of tree density/plot between VTM and FIA data sets. Thus VTM crews sampled about the same range of densities as FIA crews do today. This does not rule out a preference by VTM crews for less dense plots, but it does suggest that if such a bias existed, it was not strong.

Since VTM plots were located subjectively, there is also the possibility that they sampled different microsites, forest types or elevations unevenly. Also, since VTM plots were located in areas representative of vegetation types, one might expect that they necessarily avoided disturbed sites. Yet, the VTM data set does appear to have sampled the landscape completely. An examination of VTM plot locations on a map reveals remarkably consistent coverage across the landscape and in our study area they sampled different slope aspects and elevations in

about the same proportions as FIA crews (Table 1). If VTM crews had avoided disturbed sites, large gaps in their sampling would surely be clear on their maps. Large-scale disturbance was already prevalent by the time VTM crews began sampling plots around 1930. Logging had already removed most old-growth forest from lower elevations of the west slope and all of the Lake Tahoe basin by that time (Beesley 1996). Also, the notes that accompany VTM plot data make it clear that some plots were in sites that had recently been logged or burned, just like FIA plots.

Data reduction and analysis

Data were downloaded from publicly available websites. We extracted and adjusted our FIA data with the help of the Remote Sensing Laboratory, Region 5 (California, Hawaii and US Pacific Islands) USDA Forest Service, which generates inventory compilations using FIA plots. Trees from FIA data were converted to the size classes used in the VTM surveys by lumping each tree into one of the four size classes described above based on its dbh. Since FIA surveys use a minimum cutoff of 12.7 cm in their subplots, we downloaded data from both subplots and microplots. In microplots, we included trees >10.2 cm and used an expansion factor to make densities comparable with subplots.

We downloaded all available plots in each data

Table 2. Tree species names, corresponding four-letter code, median elevation, and frequency.

Scientific name (code)	Common name	Median elevation (m) [†]		Frequency (no. plots) [‡]		Percentage of total plots		Difference in percentage frequency [§]
		VTM	FIA	VTM	FIA	VTM	FIA	
<i>Quercus douglasii</i> (QUDO)	blue oak	396	396	429	100	12.0	11.9	-0.1
<i>Quercus lobata</i> (QULO)	valley oak	488	366	50	12	1.4	1.4	0.0
<i>Pinus sabiniana</i> (PISA)	gray or foothill pine	457	457	477	52	13.3	6.2	-7.1
<i>Quercus wislizeni</i> (QUWI)	interior live oak	457	457	546	105	15.3	12.5	-2.8
<i>Alnus rhombifolia</i> (ALRH)	white alder	792	853	2	16	0.1	1.9	+1.8
<i>Arbutus menziesii</i> (ARME)	Pacific madrone	823	823	20	30	0.6	3.6	+3.0
<i>Acer macrophyllum</i> (ACMA)	big-leaf maple	884	945	12	34	0.3	4.0	+3.7
<i>Pinus attenuata</i> (PIAT)	knobcone pine	914	944	15	7	0.4	0.8	+0.4
<i>Quercus chrysolepis</i> (QUCH)	canyon live oak	1067	823	206	142	5.8	16.9	+11.1
<i>Lithocarpus densiflorus</i> (LIDE)	tan oak	1082	823	24	29	0.7	3.4	+2.8
<i>Taxus brevifolia</i> (TABR)	Pacific yew	1097	945	1	3	0.0	0.4	+0.3
<i>Quercus kelloggii</i> (QUKE)	California black oak	1097	1128	1088	253	30.4	30.1	-0.3
<i>Pseudotsuga menziesii</i> var. <i>menziesii</i> (PSME)	Douglas-fir	1158	1189	624	206	17.4	24.5	+7.1
<i>Pinus ponderosa</i> var. <i>pacifica</i> (PIPO)	Pacific ponderosa pine	1219	1189	1442	251	40.3	29.8	-10.4
<i>Cornus nuttallii</i> (CONU)	mountain dogwood	1189	1402	15	14	0.4	1.7	+1.2
<i>Calocedrus decurrens</i> (CADE)	incense cedar	1463	1433	1001	300	28.0	35.7	+7.7
<i>Pinus lambertiana</i> (PILA)	sugar pine	1524	1494	811	147	22.7	17.5	-5.2
<i>Abies concolor</i> (ABCO)	white fir	1707	1676	1029	324	28.7	38.5	+9.8
<i>Pinus jeffreyi</i> (PIJE)	Jeffrey pine	1920	1861	582	122	16.3	14.5	-1.8
<i>Sequoiadendron giganteum</i> (SEGI)	giant sequoia	2027	NA	3	0	0.1	0.0	-0.1
<i>Abies magnifica</i> var. <i>magnifica</i> (ABMA)	California red fir	2195	2103	503	112	14.1	13.3	-0.7
<i>Juniperus grandis</i> (JUGR)	sierra juniper	2286	2188	89	29	2.5	3.4	+1.0
<i>Pinus contorta</i> subsp. <i>murrayana</i> (PICO)	lodgepole pine	2560	2408	271	100	7.6	11.9	+4.3
<i>Pinus monticola</i> (PIMO)	western white pine	2438	2530	253	46	7.1	5.5	-1.6
<i>Tsuga mertensiana</i> (TSME)	mountain hemlock	2667	2712	125	31	3.5	3.7	+0.2
<i>Pinus albicaulis</i> (PIAL)	whitebark pine	3002	2957	38	7	1.1	0.8	-0.2

Notes: Nomenclature follows The Jepson Manual, second edition (Baldwin et al. 2012). Species in boldface were included in analyses of individual species. Species are arranged in order of ascending elevation, as the mean of median elevation for each data set.

[†] Calculated from plot elevations listed for each data set. Because elevation was recorded in feet, rounded to the nearest 50-100 feet in each data set, conversion to meters and subsequent calculation of the median results in some common values (e.g., 457 m, which is approximately 1500 feet elevation).

[‡] Number of plots where at least one individual >10.2 cm was recorded.

[§] Difference in percentage frequency was calculated as (FIA - VTM).

set for our study area. Though both data sets cover the landscape well, VTM plots were sampled at a slightly higher density in the southern part of the study area. Therefore, we removed by random selection VTM plots from the southern portion and FIA plots from the northern portion until the latitude was not statistically different between data sets (elevation was also not statistically different). The resulting VTM data set (n = 3580) had a median latitude of 38.60 °N and a median elevation of 1402 m; the resulting FIA data set (n = 841) had a median latitude of 38.68 °N and a median elevation of 1372 m.

For group 1 comparisons (by elevation), we lumped plots from each data set into six 500-m elevation bands (0–499 m; 500–999 m; 1000–1499 m; 1500–1999 m; 2000–2499 m; ≥2500 m; Table 1). Determination of elevation category was

determined from elevation data, not coordinates; both VTM and FIA data included elevation in their associated site physical data. For Group 2 comparisons (by latitude), plots were lumped into five latitude categories (37.3–37.99 °N; 38.0–38.49 °N; 38.5–38.99 °N; 39.0–39.49 °N; 39.5–40.0 °N; Table 1). For groups 1 and 2, we compared density (trees/ha) of all tree species combined in VTM vs. FIA plots. See Table 2 for a list of all species.

For group 3 comparisons, FIA plots from all elevations and latitudes were lumped into five categories (unburned, burned once, burned twice, burned three times, burned four times) and compared with all VTM plots. As with Groups 1 and 2, these comparisons included all species present. To determine whether plots had burned in the time between VTM and FIA data collection, we accessed the California fire perim-

eter geodatabase (version 07.1) archived by the California Department of Forestry Fire and Resource Assessment Program (FRAP), available at http://frap.fire.ca.gov/projects/fire_data/fire_perimeters_index.php. This resource is approximately complete for fires ≥ 4 ha (10 acres) back to about 1950, and more or less comprehensive for US Forest Service fires to 1908 (McKelvey and Busse 1996, Miller et al. 2009). Burned FIA plots were determined using perimeters of fires occurring between 1940 and 2000. This process does not guarantee that an individual plot that falls within a burn perimeter actually experienced fire, since fire coverage within a perimeter is sometimes patchy. Miller and Safford (2008) found that about 12% of 94,000 ha assessed for fire severity within Sierra Nevada fire perimeters between 2000 and 2004 had actually not experienced fire. However, the inclusion of hundreds of burned plots in our analysis is expected to overwhelm this type of error.

Since we were working with perturbed coordinates for FIA plots, there is also the possibility that some plots determined to be within burn perimeters were actually located outside the perimeter (false positive), and some plots determined to be outside burn perimeters were actually inside (false negative). Working with the Remote Sensing Lab that helped extract our FIA data, we calculated the average spatial error for each plot (i.e., how far off plots were from their actual locations). This analysis suggested a median error of approximately 400 m (0.4 km). Therefore, using 400 m as a buffer, we used GIS to calculate the area in which the buffer overlapped burn perimeters and concluded that 2.2% of that area was a false positive and 6.4% was a false negative. Thus, we can say that roughly 94–98% of plots are actually in the burn categories used in this analysis.

It is also possible that some VTM plots had recently burned at the time of their sampling in the 1930s. VTM crews did note “year of last burn” in their plots. However, these were largely anecdotal comments that varied from crew to crew and are thus difficult to quantify. Perusing their field notes suggests that roughly 10% of VTM plots in our analyses had experienced some kind of fire within the 15 years prior to their 1929–1936 sampling. They made few comments that convey fire extent or intensity in the plot.

For group 4 comparisons (by species), we compared tree densities for individual species, throughout their ranges in VTM vs. FIA data sets. Analyses were limited to species that occurred in at least 20 plots in each data set (Table 2).

Because the demography of small trees and large trees can be driven by different factors, we compared each of the four VTM size classes separately. However, after running initial analyses, the two largest size classes, which respond similarly, were combined, leaving three size classes for analysis: (small trees: 10.2–30.4 cm; mid-sized trees: 30.5–60.9 cm, and; large trees: >61.0 cm).

All analyses were carried out with R version 3.0.1 (R Core Team 2013). For all comparisons of VTM vs. FIA tree densities, we ran analyses with both Poisson and negative binomial distributions, both of which can accommodate overdispersed, count data (as forest stand data often are). We compared plots of residuals and resulting Akaike Information Criteria (AIC) for each distribution for different comparisons, and the negative binomial distribution was consistently a better fit. Thus, all GLM tests presented in this paper used a negative binomial distribution using the `glm.nb` function available in the MASS package (Venables and Ripley 2002). The response variable for these models was stems:

$$\text{Stems} \sim \text{Data set} + \text{offset}(\log(\text{Area})).$$

In this model, “Data set” represents VTM vs. FIA and “Area” represents the slope-corrected area of each plot. Running the tests directly on stems with area as a parameter in the model effectively tests differences in density (stems/area) while accommodating the integer (count-based) distribution of the negative binomial function.

Separate statistical models were carried out for each stratum (elevation band and latitude category) for each of the three diameter size classes (small, mid-sized and large trees). Since VTM plots outnumbered FIA plots in our study by a ratio of about 4.3:1, we also ran analyses with VTM plots subsampled so that each data set had the same sample size. However, this made no appreciable difference in overall trends, so only the original, uneven samples are presented in this paper.

To examine the variability of tree density

across the landscape in each time period, we also calculated the coefficient of variation (standard deviation of density/mean density) for density by size class for the six elevation strata and five latitude strata. Incomplete or inaccurate data for plot locations for each data set precluded a complete analysis of spatial autocorrelation of the difference in density and plot location across the landscape. However, to gain some understanding of the possibility that spatial autocorrelation could bias our results, we calculated Moran's I for subsets of VTM and FIA tree density data (using the perturbed coordinates for FIA data).

RESULTS

For comparisons by elevation (elev 1, Group 1), density of small trees (10.2–30.4 cm) was significantly higher in FIA plots than VTM plots in all seven 500-m elevation bands (GLM neg. binomial tests, $p = 0.03$ for elev 1; $p < 0.001$ for elevs 2–7), ranging from 21% to 143% higher (Fig. 2; Appendix: Table A1). The greatest differences occurred between 500 and 2000 m elevation. For mid-sized trees (30.5–60.9 cm), FIA densities were significantly higher between 1000 and 2500 m elevation ($p < 0.001$) but not statistically different at other elevations. Density of large trees (≥ 61 cm) was lower in FIA plots in all six elevation bands, ranging from 11% to 60% lower. All elevations except 500–1000 m were statistically significant ($p = 0.014$ for elev 1; $p < 0.001$ for elevs 3–6). Overall (net) density was higher in FIA plots for all elevations (Fig. 2; Appendix: Table A1).

Differences in density were similar across latitude categories. Density of small trees was significantly higher in FIA plots than VTM plots for all five latitude categories ($p < 0.001$) examined, ranging from 75 to 148% more dense (Fig. 3; Appendix: Table A2). Density of mid-sized trees was also significantly higher in FIA plots for four of five latitudes ($p < 0.001$). Density of large trees was significantly lower (45–55% lower) for all latitudes ($p < 0.001$) except 39–39.5° N. As with the elevation bands, all latitudes exhibited higher net densities in FIA plots (Fig. 3; Appendix: Table A2).

In VTM plots, the coefficient of variation (CV) for small tree density was highest for middle

elevations (1000–2500 m), reflecting greater historical heterogeneity of forests at these elevations (Fig. 4). In FIA plots, the trend is flatter, with lower CV for elevations from 500 to 2000 m and high CV at 2000–2500 m. For most elevations and latitude strata, CV was lower in FIA plots than VTM plots for small and mid-sized trees, but similar for large trees (Fig. 4).

Trends indicate decreasing densities with increasing burn frequency for all size classes (Fig. 5). For small trees, densities of FIA plots that remained unburned and those that burned once were both significantly higher than VTM densities (GLM neg. binomial test, $p < 0.001$ for each) while plots that burned twice ($n = 35$) were not significantly different than VTM levels. Sample size for plots that burned three or more times was too low ($n < 5$) for meaningful analyses. For mid-sized trees, density was significantly higher in unburned FIA plots compared to VTM plots ($p < 0.001$), but not significantly different for plots that burned once or twice. For large trees, densities were significantly lower in all three FIA burned/unburned plots compared to VTM plots ($p < 0.001$ for each; Fig. 5).

Of the 17 individual species analyzed, all but one (gray pine) had higher densities of small trees in the FIA data set and 12 (71%) were statistically significant, with 9 of these 12 highly significant ($p < 0.001$; Fig. 6; see Appendix: Tables A3 and A4 for statistical inference data on all species). Significantly higher densities of small trees was found for both hardwoods and conifers, and for species ranging from low to high elevations. However, the greatest differences were found in tan oak (+169%; $p < 0.001$), canyon live oak (+154%; $p < 0.001$), interior live oak (+143%; $p < 0.001$) and incense-cedar (+130%; $p < 0.001$). Densities of mid-sized trees were significantly higher in FIA plots for six of 16 species analyzed in that size class and significantly lower for one, ponderosa pine (–22.5%; $p < 0.001$). Densities of mid-sized trees for species with the lowest and highest elevational distributions were similar, and generally non-significant (Fig. 6; Appendix: Table A2). For large trees, densities were significantly lower in FIA plots for seven of the 10 species analyzed, ranging from 26 to 40% lower than VTM levels ($p < 0.001$ for ponderosa pine, sugar pine, white fir, red fir, and lodgepole pine; $p = 0.005$ for Jeffrey pine and $p = 0.03$ for western

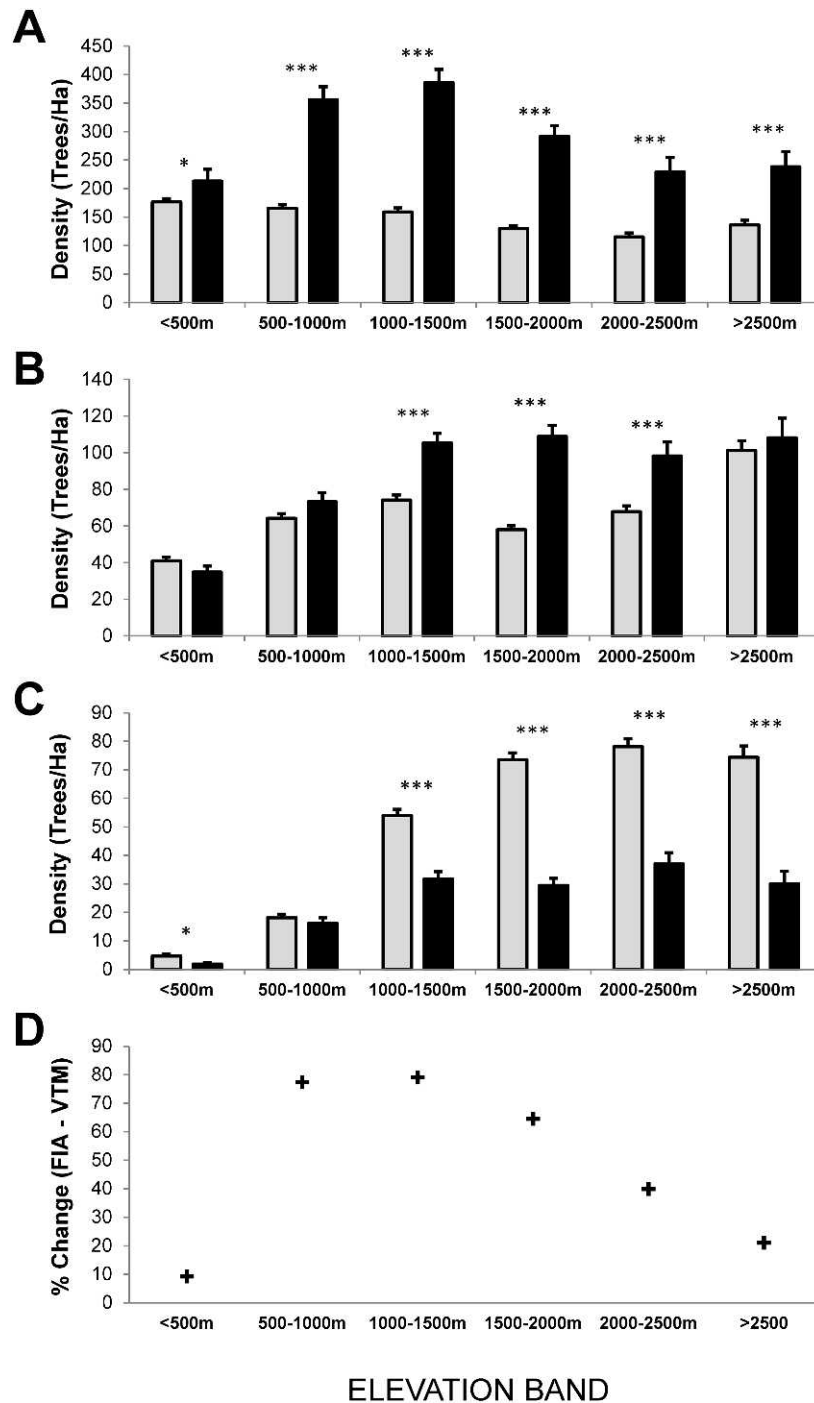


Fig. 2. Density (trees/ha) of Vegetation Type Mapping (VTM) plots and Forest Inventory and Analysis (FIA) plots for all species combined, for elevation bands (0–499 m, 500–999 m, 1000–1499 m, 1500–1999 m, 2000–2499 m and ≥ 2500 m) of the study area for (A) small trees (10.2–30.4 cm dbh), (B) mid-sized trees (30.5–60.9 cm), (C) large trees (≥ 61.0 cm), and (D) the net percent difference in density between VTM and FIA plots, across all size classes. Statistically significant differences for generalized linear model tests with a negative binomial distribution are indicated by * $0.01 < p < 0.05$; ** $0.001 < p \leq 0.01$; and *** $p < 0.001$. See Appendix: Table A2 for greater detail of statistical tests.

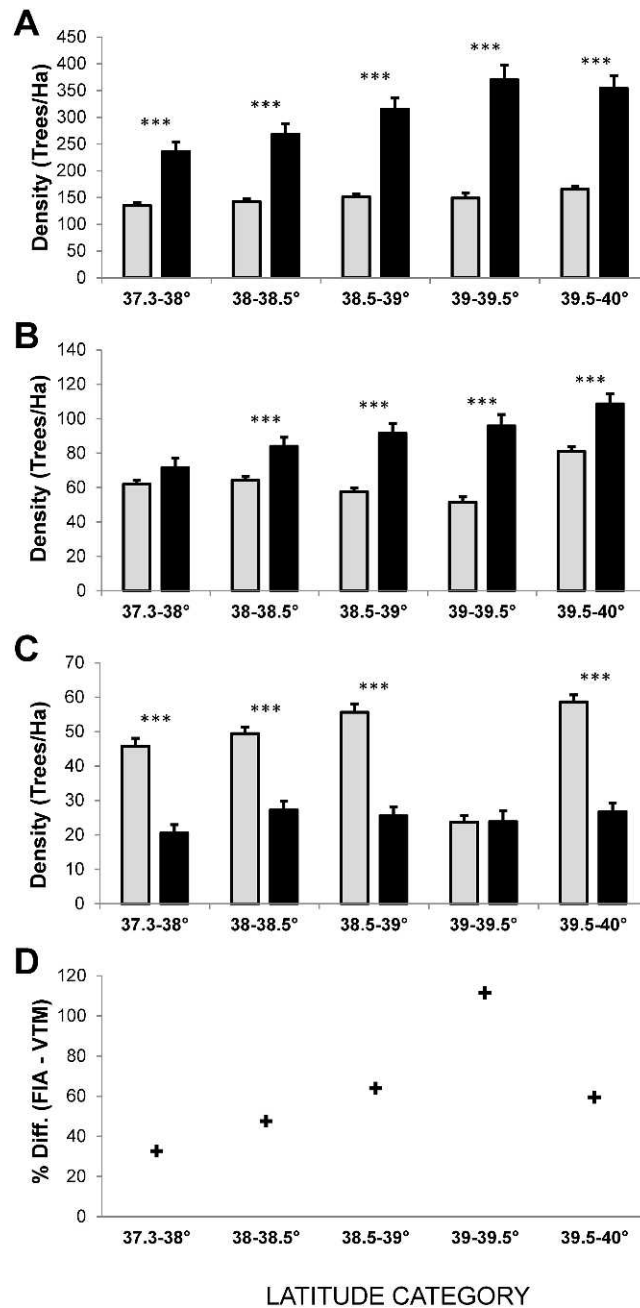


Fig. 3. Density (trees/ha) of Vegetation Type Mapping (VTM) plots and Forest Inventory and Analysis (FIA) plots for all species combined and lumped into five latitude categories (37.3–37.99° N, 38.0–38.49° N, 38.5–38.99° N, 39.0–39.49° N, and 39.5–40.0° N) in the study area for (A) small trees (10.2–30.4 cm dbh), (B) mid-sized trees (30.5–60.9 cm), (C) large trees (≥ 61.0 cm), and (D) the net percent difference in density between VTM and FIA plots, across all size classes. Statistically significant differences for generalized linear model tests with a negative binomial distribution are indicated by $*0.01 < p < 0.05$; $**0.001 < p \leq 0.01$; and $***p < 0.001$. See Appendix 2 for greater detail of statistical tests. Note: Since coordinates were missing for a quad in the 39–39.5° range, it was necessary to remove plots that could not be verified to be located on the west slope. Thus, this group has relatively few high-elevation plots (>2000 m), where large trees are more common.

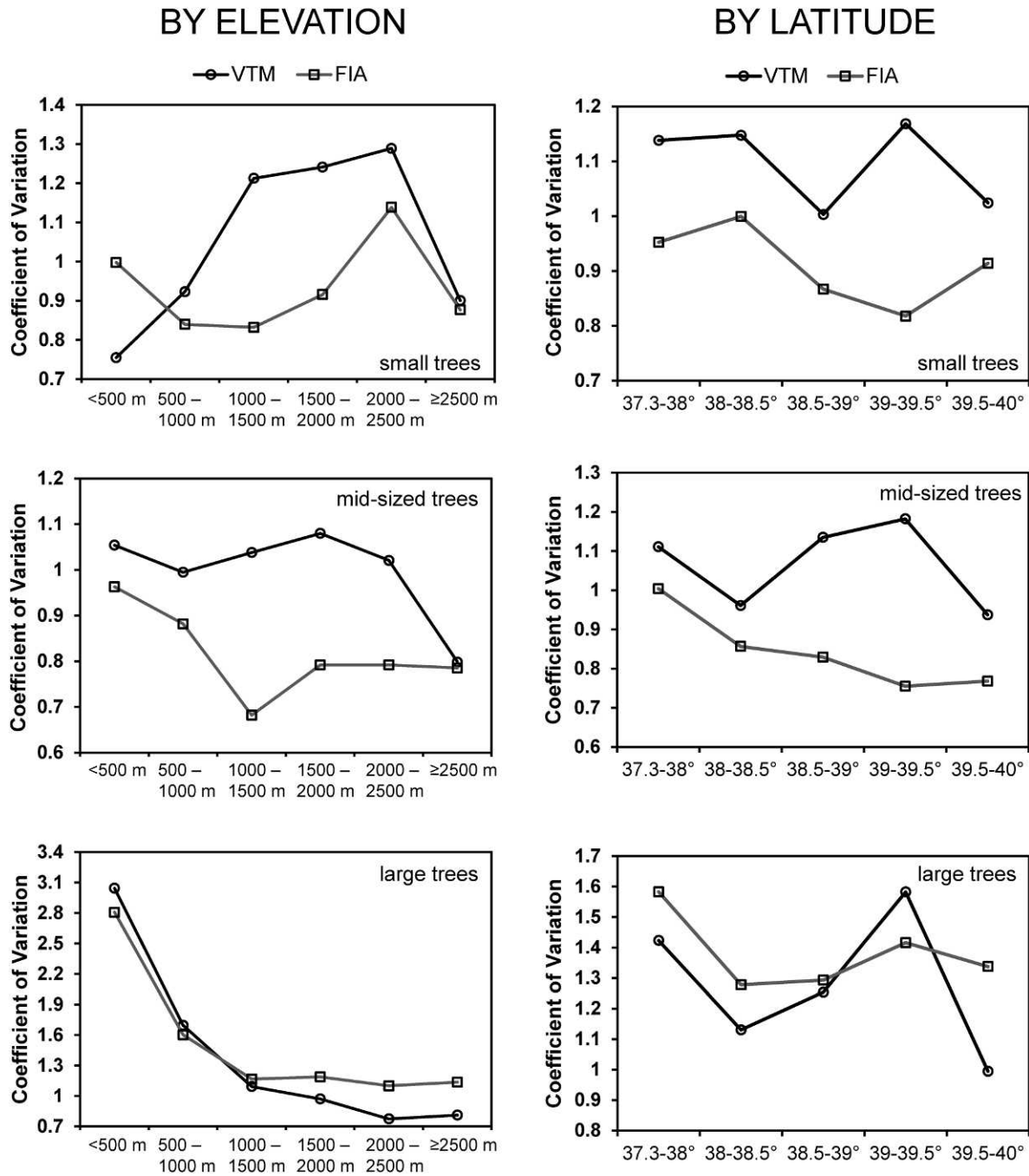


Fig. 4. Coefficient of variation (standard deviation/mean) for forest density (trees/ha) by elevation band (0–499 m, 500–999 m, 1000–1499 m, 1500–1999 m, 2000–2499 m and ≥2500 m), and latitude categories (37.3–37.99° N, 38.0–38.49° N, 38.5–38.99° N, 39.0–39.49° N, and 39.5–40.0° N), and by diameter size class: small trees (10.2–30.4 cm dbh), mid-sized trees (30.5–60.9 cm), and large trees (≥61.0 cm).

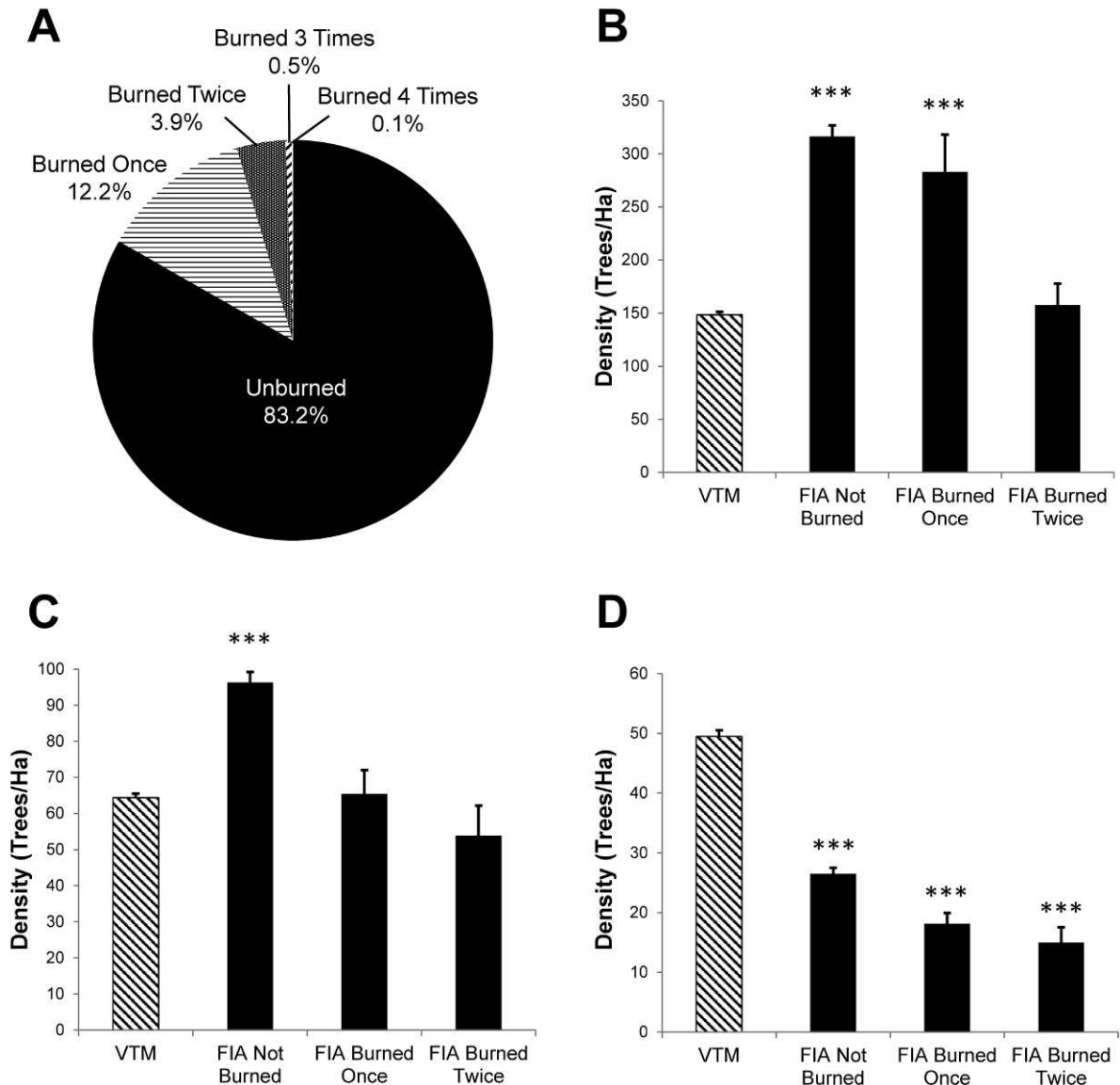


Fig. 5. Comparison of burned and unburned Forest Inventory and Analysis (FIA) plots and their densities relative to historical conditions [Vegetation Type Mapping (VTM) plots]: (A) percent of unburned FIA plots, and plots that burned once, twice, three and four times; (B–D) comparison of change in density (trees/ha) between VTM plots and FIA unburned plots, FIA plots that burned once and FIA plots that burned twice, for (B) small trees (10.2–30.4 cm dbh), (C) mid-sized trees (30.5–60.9 cm), and (D) large trees (≥ 61.0 cm). Statistical significance at $*0.01 < p < 0.05$; $**0.001 < p \leq 0.01$; and $***p < 0.001$ for generalized linear model tests with a negative binomial distribution is indicated above FIA groups and represents that group as compared to the VTM group shown in the same graph.

white pine). Unlike small and mid-sized trees, the trend was not weaker at high elevations. Density of large lodgepole pine was 40% lower in FIA plots and western white pine was 35% lower (Fig. 6; Appendix: Tables A3 and A4).

DISCUSSION

The structure of Sierra Nevada forests appears to have changed markedly over the last 70+ years, and in a way that is consistent across the

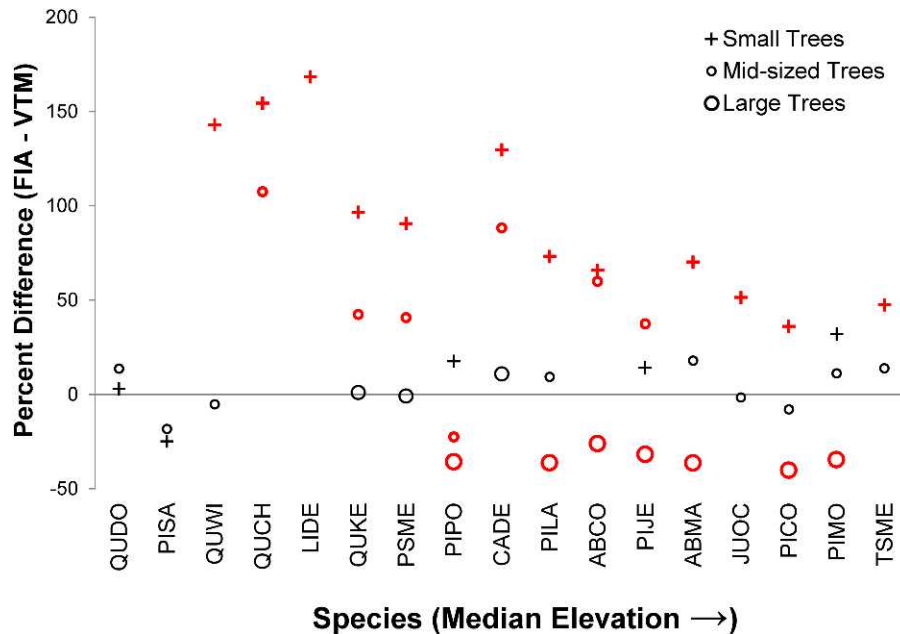


Fig. 6. Percent difference in density (trees/ha) between Vegetation Type Mapping (VTM) plots to Forest Inventory and Analysis (FIA) plots for every species occurring in at least 20 plots in each data set, for each size class: small trees (10.2–30.4 cm dbh), mid-sized trees (30.5–60.9 cm), large trees (≥ 61.0 cm). Species with missing symbols did not meet the 20 plot minimum threshold for that size class. Species are arranged, from left to right, in increasing order of their average median elevation between the two data sets. See Table 2 for median elevations and species names with accompanying four-letter codes. Red bolded data points indicate statistical significance ($p < 0.05$) for generalized linear model tests with a negative binomial distribution. See Appendix: Table A2 for greater detail of statistical inference data.

landscape and across many species. There are currently many more small trees and fewer large trees in most locations and for most species. Densification, or infilling, by small trees has been reported in other studies from the Sierra Nevada that used various methodologies, including repeat photography (Vale 1987, Gruell 2001), dendrochronology and stand reconstruction (Parsons and Debenedetti 1979, Taylor 1995, 2000), historical re-sampling (Ansley and Battles 1998, Dolanc et al. 2013b), and a combination of methods (Vankat and Major 1978). More recently, multiple studies have observed a reduction of large trees as well (Smith et al. 2005, Lutz et al. 2009, Dolanc et al. 2013b). Our analysis adds to this understanding by highlighting the great extent to which these patterns occur on the landscape and in how these patterns suggest possible drivers of change.

Although we compared independent data sets in this study, differences between VTM and FIA

tree densities are similar in magnitude to studies that used re-sampling (Ansley and Battles 1998, Dolanc et al. 2013b), and independent data sets (Lutz et al. 2009) for comparison. Dolanc et al. (2013b) compared historical and modern tree densities by resampling VTM plots in subalpine of the same region as this study. A comparison of their data with this study for plots above 2500 m shows very similar increases in magnitude for small and mid-sized trees (10.2–60.9 cm) and decreases in large trees for both studies (≥ 61.0 cm; Table 3). The two studies show greater difference in magnitude for large tree declines, but both show significant declines. These similarities provide further evidence that the general trend of increasing small trees and decreasing large trees is widespread and prevalent in the Sierra Nevada.

Our analysis of tree densities in unburned and burned plots implicates fire suppression as a major driving factor behind increasing tree

Table 3. Comparison of data (trees/ha) from this study with Dolanc et al. (2013b) for high-elevation tree densities in historical and modern plots.

Size class	This paper†			Dolanc et al. (2013b)‡		
	VTM	FIA	Percentage difference	VTM	Re-sampled	Percentage difference
10.2–30.4 cm	138.1	238.4	+72.7	162.0	264.8	+63.5
30.5–60.9 cm	102.8	108.1	+5.1	100.9	108.6	+7.6
61.0–91.3 cm	55.3	22.3	–59.6	41.3	32.5	–21.3
≥91.4 cm	19.1	7.8	–59.2	18.6	15.0	–19.4

† For all species in plots that occur at or above 2500 m elevation.

‡ For resampled VTM plots above approximately 2300 m elevation in the same region; calculated from Table 1 of Dolanc et al. (2013b).

density in mid-elevation forests. For small trees, FIA plots that remained unburned, as well as those that burned only once, had significantly higher tree densities than VTM plots, but plots that burned twice were not statistically different than VTM levels (Fig. 5). Historically, fire return intervals were short (<30 years) in lower elevations of the Sierra Nevada, and increased with elevation to hundreds of years at high elevations (McKelvey et al. 1996, Skinner and Chang 1996, van Wagtendonk and Fites-Kaufman 2006, Van de Water and Safford 2011). This is probably why we observed the greatest net positive difference between FIA and VTM tree densities from 500 to 1500 m elevation.

Our analysis of burned FIA plot locations across the landscape suggests that fires are still more frequent at low elevations (Appendix: Fig. A1); of the 143 FIA plot locations that burned between 1940 and 2000, 105 (73%) were in the lowest half (<1500 m) of the mountain range. Still, only 22% of FIA plot locations at these elevations experienced fire during this period (15% across all elevations), so most low-elevation sites are likely still well beyond their historical fire return interval. It should be expected that multiple fires might be necessary to return to pre-suppression stand conditions for lower elevations of the Sierra Nevada. Our results for coefficient of variation (CV) of tree density across the landscape suggest that fire suppression is homogenizing forests, as CV is generally lower in FIA plots than VTM plots for small and mid-sized trees (Fig. 4). In other words, there is less variation in stand density, from plot to plot, in the FIA data set for small and large trees. However, differences between VTM and FIA plot location protocol could explain this trend too.

Most of the species with the greatest difference in small tree density between data sets are those with seedlings and saplings that tolerate forest shade but are relatively intolerant of fire, including tan oak, white fir, incense cedar, Douglas-fir, and canyon live oak (Minore 1979, Oliver and Dolph 1992, Allen-Diaz et al. 2007, Fites-Kaufman et al. 2007). An increase in abundance of these species has probably occurred at the expense of shade-intolerant pines, such as ponderosa and sugar pine. Shifts in species abundance under the long-term absence of fire are well-documented trends for mid-elevation Sierra Nevada forests (e.g., Vankat and Major 1978, Parsons and Debenedetti 1979, McKelvey and Busse 1996, Ansley and Battles 1998, Barbour et al. 2002, Sugihara et al. 2006, Fites-Kaufman et al. 2007).

Fire suppression cannot explain all differences in forest structure across the landscape. Our data suggest strong increases in small tree densities at high elevations (>2500 m), where fire suppression has likely had little impact on stand structure. High-elevation forests of the Sierra Nevada are typically sparse with shallow fuel beds and a short growing season (Fites-Kaufman et al. 2007), leading to very long fire return intervals (van Wagtendonk and Fites-Kaufman 2006). These forests are naturally fire-suppressed and thus would not be expected to have been altered by fire suppression efforts at lower elevations. Yet, in our data, small trees were 75% more dense in FIA plots, for areas above 2500 m, with roughly 100 trees/ha more than VTM levels (Fig. 2; Appendix: Table A1).

Fire suppression is also likely not the main factor driving reduced density of large trees. van Mantgem and Stephenson (2007) and van Mantgem et al. (2009) were able to rule out fire suppression as a

cause of their reported increased mortality rates. Van Mantgem et al. (2009) found comparable increases in mortality rates across stands of different historical fire return intervals, including high-elevation stands with very long intervals.

Timber harvest has been suggested as a major factor in the decline of large trees in the Sierra Nevada (Fites-Kaufman et al. 2007). According to Barbour et al. (1993), roughly half of the area of the mixed conifer forest in the Sierra Nevada was logged at least once over the last 150 years. However, significant logging had already occurred by the time the VTM project was underway (Sudworth 1900, Leiberg 1902). Two thirds of the Lake Tahoe Basin had been clearcut by the 1910s, and by World War II large areas of west slope mixed conifer forest had been railroad logged or selectively cut for ponderosa and sugar pine, as well as larger specimens of Douglas-fir (Barbour et al. 2002, Fites-Kaufman et al. 2007).

Yet, the further reduction of large tree densities between the VTM surveys in the 1930s and the FIA inventory of the early 2000s must also be due in some measure to logging (Bouldin 1999). Our comparison of live + dead large tree FIA densities with VTM large tree densities (Appendix: Fig. A2) may support this: the combination of live and dead trees do not come close to VTM era densities, suggesting that many large trees were removed. Still, in Yosemite National Park, where logging has presumably been minimal since the 1930s, large trees appear to be in decline (Lutz et al. 2009). Similarly, our data indicate significant declines in large trees between 37.3° and 38.0°N latitude, which is almost entirely within Yosemite boundaries (Fig. 3).

Changes in forest structure could also be climatically driven. Growing season in the Sierra Nevada is dominated by late summer drought (Peterson 1998) and changes in both temperature and precipitation are likely to play a critical role in current and future demographic trends of trees. Indeed, the climate of the Sierra Nevada has warmed over the last few decades (Dettinger and Cayan 1995, Coats 2010, Millar et al. 2012). The proportion of rain to snow has increased (Knowles et al. 2006, Coats 2010) and snowpack melt dates have moved earlier in the year by an average of one to two weeks across the Sierra Nevada since the early to mid-1900s (Coats 2010, Kapnick and Hall 2010).

Declines in large tree density suggested by our data are consistent with those reported in other studies from the Sierra Nevada, which attributed declines to increased levels of drought-induced mortality (Smith et al. 2005, van Mantgem and Stephenson 2007). However, data on changing water deficit in the Sierra Nevada are equivocal (e.g., Crimmins et al. 2011). Mortality may be exacerbated by factors interacting with climate, such as bark beetles, stand density and mistletoe (Guarin and Taylor 2005, Smith et al. 2005, Millar et al. 2007, van Mantgem et al. 2009, Millar et al. 2012). The relationship between small tree and large tree density in our plots is weak (VTM: $r = -0.1$; FIA: $r = -0.08$), suggesting that increased stand density is not driving the decline in large trees.

Increasing density of small trees in higher elevations may also be climatically-driven. Other studies in subalpine regions of western mountains have documented recent increased recruitment of small trees into meadows, snow fields, forest-tundra ecotones and upland forest (Jakubos and Romme 1993, Rochefort and Peterson 1996, Hessler and Baker 1997, Klasner and Fagre 2002, Millar et al. 2004, Dolanc et al. 2013b), and all attributed the increase to warmer temperatures during the 20th century. Most of these studies note episodic increases: periods during which the climatic conditions were ameliorated relative to “normal” and became conducive to establishment in areas and microsites previously unoccupied. In the subalpine zone of the Sierra Nevada, conditions limiting recruitment and survival of young trees are deep spring snowpack and low summer soil moisture (Peterson 1998). If warmer conditions resulted in longer growing seasons (e.g., via earlier snowmelt) without also exacerbating summer drought stress, that should increase tree recruitment and survival, and eventually increase forest densities.

Bark beetles (*Dendroctonus* spp.) can kill large trees that are already stressed by drought, especially in dense stands (Smith et al. 2005). Similarly, white pine blister rust (*Cronartium ribicola*; WPBR), which is a pathogen that attacks five-needle pines, has been found on sugar pine, western white pine and whitebark pine in our study area (Maloney 2011). The impacts of both bark beetles and WPBR are and will continue to be tied to climate (Thomson 2009, Maloney 2011). So far, impact on forests by each of these factors

has been relatively light in the Sierra Nevada, compared with other regions of western North America (Kurz et al. 2008, Logan et al. 2010, Tomback and Achuff 2010), but they may have greater and greater impact if the climate continues to warm (Allen et al. 2010).

Ozone pollution from upwind valley locations has been shown to increase mortality of ponderosa and Jeffrey pine in the Sierra Nevada (Bytnerowicz et al. 2003). The greatest impacts from ozone have been observed in the southern Sierra, beyond our study area. Both ponderosa and Jeffrey pine exhibited declines in large tree densities in our study but they are roughly in line with that of other species shown to be unaffected by ozone.

Data limitations

Since we were working with perturbed FIA plot coordinates, a complete analysis of the effect of spatial autocorrelation on our models was not possible. This likely contributes to unexplained variance in our models. However, the low degree of spatial autocorrelation of tree density (e.g., Moran's $I \approx 0.02$ – 0.05) for portions of each data set suggests that this effect should be minor, especially considering the magnitude of most trends we report.

The lack of information regarding disturbances such as logging and grazing, both before and after the VTM sampling time period, limits our ability to assess the contributions of these factors to observed differences in forest structure between time periods. For disturbances that occurred more recently, it might be possible to obtain detailed records for a region and focus, for example, on trends on and off of logged sites; this could be particularly valuable in parsing out anthropogenic and natural drivers.

As discussed previously, the different protocols and plot selections of the VTM and FIA data sets are likely to affect our reported trends in differences in forest structure in some way. However, we believe that the consistency and magnitude of these trends, and their similarities with other studies, strongly suggest that profound changes in forest structure of the Sierra Nevada have occurred during the last several decades.

CONCLUSIONS

Forests of the west slope of the central Sierra

Nevada have changed markedly in structure over the last several decades: small trees have increased in density at all elevations, especially between 500 and 2000 m elevation, and across all latitudes; large trees have decreased in density, especially above 1000 m. Fire suppression is likely driving many of the increases in small trees in elevations where fire suppression has had the greatest impact (<1500 m), but other factors such as climate change and logging may be responsible for reductions in large tree density.

An understanding of how the structure of forests in this region has changed over the last several decades is important for understanding their future. For example, Lenihan et al. (2008), based on a dynamic vegetation model, predicted major declines in conifer forest and subalpine/alpine vegetation by the end of the 21st century. Our data suggest that although large trees are declining at higher rates, recruitment by smaller trees is more than compensating in these kinds of forest, meaning displacement by other forest types might take much longer than predicted. However, disruptions to the natural fire cycle, and factors such as bark beetle and white pine blister rust could quickly tip the scales in favor of displacement.

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SUPPLEMENTAL MATERIAL

APPENDIX

Table A1. Summary statistics for elevation band comparisons (Group 1). See *Materials and Methods* for detail on analyses performed.

Metric	Elevation band (m)					
	0–499	500–999	1000–1499	1500–1999	2000–2499	>2500
Small trees (10.2–30.4 cm)						
VTM mean	176.7	165.4	159.1	129.6	115.2	136.4
VTM SE	5.8	5.9	7.0	5.4	6.7	8.1
VTM n	527	659	769	888	493	231
FIA mean	213.0	355.8	386.1	291.6	229.5	238.4
FIA SE	20.9	23.0	22.8	18.7	2.5	26.5
FIA n	103	169	199	203	203	62
Estimate	–0.18	–0.77	–0.89	–0.81	–0.69	–0.56
<i>p</i> value	0.029	<0.001	<0.001	<0.001	<0.001	<0.001
Percent change	20.5	115.2	142.6	125.0	99.1	74.7
Mid-sized trees (30.5–60.9 cm)						
VTM mean	41.0	64.2	74.1	58.0	67.8	101.1
VTM SE	1.9	2.5	2.8	2.1	3.1	5.3
VTM n	527	659	769	888	493	231
FIA mean	34.9	73.2	105.4	108.8	98.2	108.1
FIA SE	3.3	5.0	5.1	6.0	7.6	10.8
FIA n	103	169	199	203	105	62
Estimate	0.17	–0.13	–0.35	–0.63	–0.37	–0.07
<i>p</i> value	0.159	0.143	<0.001	<0.001	<0.001	0.581
Percent change	–15.1	14.1	42.2	87.5	44.8	6.9
Large trees (≥61.0 cm)						
VTM mean	4.7	18.1	53.9	73.5	78.1	74.4
VTM SE	0.6	1.2	2.1	2.4	2.7	4.0
VTM n	527	659	769	888	493	231
FIA mean	1.9	16.2	31.7	29.5	37.0	30.1
FIA SE	0.5	2.0	2.6	2.5	4.0	4.3
FIA n	103	169	199	203	105	62
Estimate	0.94	0.14	0.54	0.91	0.77	0.89
<i>p</i> value	0.014	0.442	<0.001	<0.001	<0.001	<0.001
Percent change	–60.3	–10.9	–41.2	–59.9	–52.6	–59.5
All size classes						
Percent change	+9.3	+77.4	+79.1	+64.5	+39.9	+21.0

Table A2. Summary statistics for latitude category comparisons (Group 2). See *Materials and Methods* for detail on analyses performed.

Metric	Latitude (°N)				
	37.3–37.99	38.0–38.49	38.5–39.99	39.0–39.49	39.5–40.0
Small trees (10.2–30.4 cm)					
VTM mean	134.7	142.5	151.5	149.1	165.6
VTM SE	5.7	5.4	5.3	9.1	6.1
VTM n	722	905	819	370	764
FIA mean	236.2	268.0	315.0	370.0	354.1
FIA SE	17.2	19.7	20.8	28.0	23.1
FIA n	171	184	172	117	197
Estimate	-0.56	-0.63	-0.73	-0.91	-0.76
<i>p</i> value	<0.001	<0.001	<0.001	<0.001	<0.001
Percentage change	75.4	88.1	108.0	148.1	113.8
Mid-sized trees (30.5–60.9 cm)					
VTM mean	61.1	64.3	57.6	51.5	80.9
VTM SE	2.5	2.1	2.3	3.2	2.7
VTM n	722	905	819	370	764
FIA mean	71.6	84.0	91.6	95.8	108.5
FIA SE	5.5	5.3	5.8	6.7	5.9
FIA n	171	184	172	117	197
Estimate	-0.16	-0.27	-0.47	-0.62	-0.29
<i>p</i> value	0.099	<0.001	<0.001	<0.001	<0.001
Percentage change	17.2	30.5	59.0	86.2	34.1
Large trees (≥61.0 cm)					
VTM mean	45.9	49.6	55.7	23.7	58.6
VTM SE	1.7	1.6	2.4	2.0	2.1
VTM n	722	905	819	370	764
FIA mean	20.5	27.2	25.6	23.8	26.8
FIA SE	2.5	2.6	2.5	3.1	2.5
FIA n	171	184	172	117	197
Estimate	0.80	0.60	0.79	0.00	0.80
<i>p</i> value	<0.001	<0.001	<0.001	0.98	<0.001
Percentage change	-55.3	-45.1	-54.1	0.5	-54.4
All size classes					
Percentage change	+33.4	+47.5	+64.0	+111.6	+59.4

Table A3. Summary statistics by species (Group 4) comparisons, for the lower nine species in the study area.

Metric	QUDO	PISA	QUWI	QUCH	LIDE	QUKE	PSME	PIPO	CADE
Small trees (10.2–30.4 cm)									
VTM mean	102.6	34.4	94.8	89.1	66.5	52.3	64.7	100.2	56.4
VTM SE	4.4	1.6	5.1	13.7	14.1	2.0	3.1	4.1	2.6
VTM n	416	371	511	169	23	886	482	1078	703
FIA mean	105.7	25.9	230.4	226.7	178.6	102.7	123.2	117.8	129.6
FIA SE	10.1	3.0	27.4	20.6	48.8	9.6	10.1	12.7	9.6
FIA n	92	25	103	136	28	203	179	175	265
Estimate	-0.03	0.27	-0.89	-0.93	-0.99	-0.68	-0.64	-0.16	-0.83
<i>p</i> value	0.759	0.141	<0.001	<0.001	<0.001	<0.001	<0.001	0.060	<0.001
Percentage change	3.0	-24.9	143.0	154.4	168.5	96.6	90.6	17.6	129.7
Mid-sized trees (30.5–60.9 cm)									
VTM mean	29.6	31.0	28.3	28.5	...	26.1	34.0	57.0	25.3
VTM SE	1.3	1.3	3.3	2.9	...	0.8	1.8	1.7	0.9
VTM n	256	308	198	94	...	584	351	1051	552
FIA mean	33.7	25.3	26.8	59.1	...	37.2	47.9	44.1	47.7
FIA SE	3.1	3.6	2.8	4.9	...	2.7	3.0	3.2	2.8
FIA n	64	36	36	80	...	157	140	164	195
Estimate	-0.13	0.21	0.06	-0.71	...	-0.35	-0.34	0.25	-0.63
<i>p</i> value	0.173	0.152	0.731	<0.001	...	<0.001	<0.001	<0.001	<0.001
Percentage change	13.7	-18.2	-5.2	107.4	...	42.3	40.7	-22.5	88.3
Large trees (≥61.0 cm)									
VTM mean	20.3	31.1	42.2	22.8
VTM SE	1.1	1.4	1.2	0.8
VTM n	201	291	922	446
FIA mean	20.6	30.8	27.1	25.3
FIA SE	2.0	3.0	2.2	1.5
FIA n	30	77	103	99
Estimate	-0.01	0.04	0.46	-0.10
<i>p</i> value	0.963	0.655	<0.001	0.246
Percentage change	1.1	-0.8	-35.7	10.9
All size classes									
Percentage change	+61.8	+72.2	-10.2	+98.1

Note: See Table 2 for full scientific names.

Table A4. Summary statistics for the by species (Group 4) comparisons, for the upper eight species in the study area.

Metric	PILA	ABCO	PIJE	ABMA	JUOC	PICO	PIMO	TSME
Small trees (10.2–30.4 cm)								
VTM mean	30.5	77.0	57.4	90.7	28.0	104.9	36.1	110.0
VTM SE	1.5	3.7	3.8	6.4	3.1	8.1	2.6	8.8
VTM n	407	812	371	398	52	231	150	111
FIA mean	52.9	127.7	65.5	154.4	42.3	142.7	47.7	162.2
FIA SE	7.5	9.3	9.0	18.8	9.6	22.9	11.2	32.2
FIA n	85	289	82	97	23	80	35	31
Estimate	-0.55	-0.51	-0.13	-0.53	-0.42	-0.31	-0.28	-0.39
<i>p</i> value	<0.001	<0.001	0.289	<0.001	0.038	0.021	0.070	0.024
Percentage change	73.2	65.8	14.2	70.2	51.4	36.1	32.1	47.5
Mid-sized trees (30.5–60.9 cm)								
VTM mean	24.2	42.1	32.8	57.5	28.3	76.7	24.3	63.1
VTM SE	0.9	1.9	1.5	2.8	3.7	5.7	1.4	5.6
VTM n	412	664	372	381	50	219	161	112
FIA mean	26.5	67.3	45.1	67.8	27.9	70.7	27.0	71.9
FIA SE	2.1	4.2	6.0	6.8	4.4	6.5	3.0	13.4
FIA n	74	225	79	93	12	85	21	26
Estimate	-0.09	-0.47	-0.32	-0.17	0.01	0.08	-0.11	-0.12
<i>p</i> value	0.340	<0.001	<0.001	0.074	0.978	0.471	0.528	0.490
Percentage change	9.3	59.9	37.4	18.0	-1.5	-7.8	11.2	14.0
Large trees (≥61.0 cm)								
VTM mean	35.8	43.3	35.8	64.0	...	45.3	32.5	...
VTM SE	1.2	1.4	1.2	2.2	...	3.0	1.8	...
VTM n	569	677	459	438	...	165	173	...
FIA mean	22.9	32.0	24.5	40.8	...	27.1	21.3	...
FIA SE	1.6	2.1	1.5	3.4	...	2.3	1.8	...
FIA n	64	141	74	79	...	57	33	...
Estimate	0.43	0.28	0.32	0.48	...	0.53	0.42	...
<i>p</i> value	<0.001	<0.001	0.005	<0.001	...	<0.001	0.028	...
Percentage change	-36.2	-26.0	-31.7	-36.3	...	-40.2	-34.5	...
All size classes								
Percentage change	+11.7	+64.6	+9.1	+50.8	...	+13.7	+3.1	...

Note: See Table 2 for full scientific names.

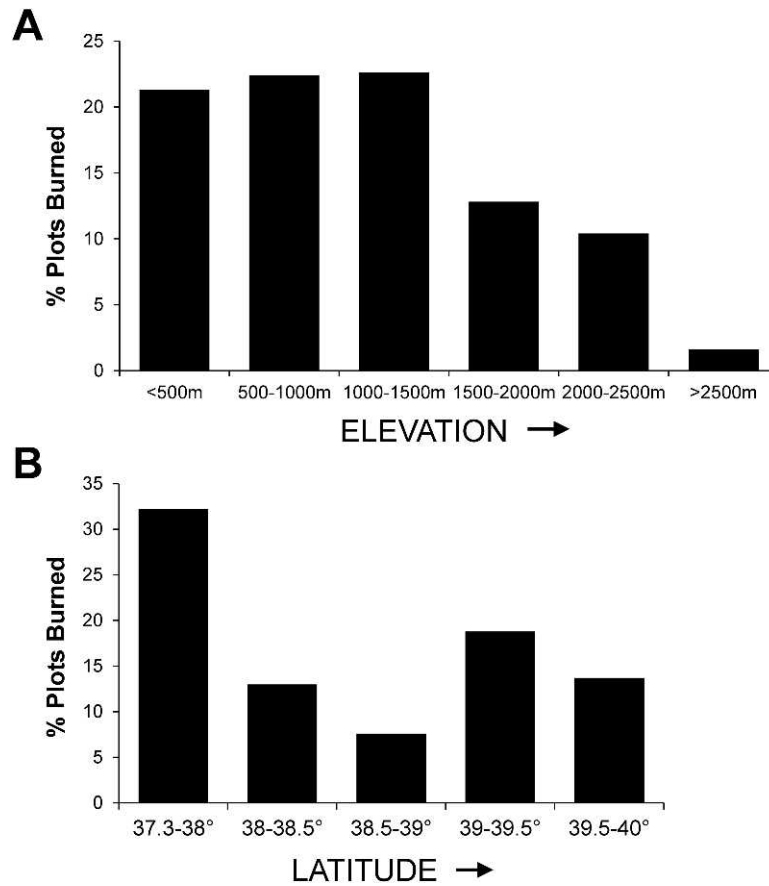


Fig. A1. Percentage of Forest Inventory and Analysis (FIA) plots estimated to have burned at least one time from 1940 to 2000 for (A) elevation bands (0–499 m, 500–999 m, 1000–1499 m, 1500–1999 m, 2000–2499 m and ≥ 2500 m), and (B) latitude categories (37.3–37.99° N, 38.0–38.49° N, 38.5–38.99° N, 39.0–39.49° N, and 39.5–40.0° N) used in this paper.

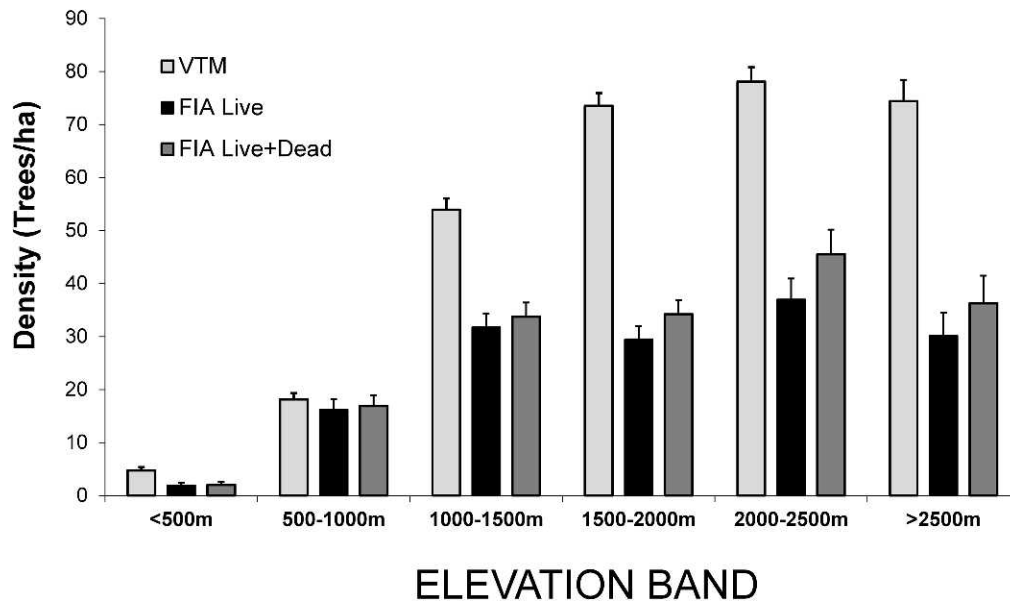


Fig. A2. Comparison of live tree densities (trees/ha) for Vegetation Type Mapping (VTM) plots with live, and live + dead (snag) densities for Forest Inventory and Analysis (FIA) plots across six elevation categories. Error bars represent standard error of the means.