Twentieth-century shifts in forest structure in California: Denser forests, smaller trees, and increased dominance of oaks

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We document changes in forest structure between historical (1930s) and contemporary (2000s) surveys of California vegetation through comparisons of tree abundance and size across the state and within several ecoregions. Across California, tree density in forested regions increased by 30% between the two time periods, whereas forest biomass in the same regions declined, as indicated by a 19% reduction in basal area. These changes reflect a demographic shift in forest structure: larger trees (>61 cm diameter at breast height) have declined, whereas smaller trees (<30 cm) have increased. Large tree declines were found in all surveyed regions of California, whereas small tree increases were found in every region except the south and central coast. Large tree declines were more severe in areas experiencing greater increases in climatic water deficit since the 1930s, based on a hydrologic model of water balance for historical climates through the 20th century. Forest composition in California in the last century has also shifted toward increased dominance by oaks relative to pines, a pattern consistent with warming and increased water stress, and also with paleohistoric shifts in vegetation in California over the last 150,000 y.

global change | forest | historical ecology | climatic water deficit

Understanding the patterns and causes of recent changes in vegetation structure is essential to predicting ongoing and future vegetation responses to global climate change. Recent changes in forest structure and tree mortality attributed to increases in temperature and drought have been documented for large areas across the globe (1–5). Declines in the abundance of large trees have attracted particular attention, as large trees contribute disproportionately to forest structure and function, carbon stocks, and the cultural values of forests (6–10). Although land-use change and harvesting of large trees contribute to their decline, studies have found that large trees can suffer disproportionate mortality in response to drought in both temperate and tropical systems, and that declines have occurred in protected areas not subject to logging (5, 8, 11, 12). The mechanisms responsible for large tree vulnerability to water deficit are poorly understood but rest largely on interacting effects of increased vulnerability to cavitation, carbon starvation during drought, and vulnerability to natural enemies (13, 14). Here we present, to our knowledge, the first analysis of changes in large tree density across California during the 20th century in relation to changes in water deficit during the same period, and examine changes in species composition that can be linked to historical changes over longer time periods.

In the forests of California, comparisons of historical and contemporary forests in selected areas of the Sierra Nevada and Transverse mountains suggest that forests have in-filled with small trees and exhibited declines in larger trees since the early 1900s, patterns attributed to fire suppression, forest exploitation, and changes in mortality due to increases in temperature and declines in water available to plants (4, 8, 15, 16). In this paper we examine changes in forest structure across the latitudinal extent of California, using an extensive historical forest survey from the 1920–1930s (Vegetation Type Mapping project, VTM) that covered ~60% of forested areas (17–19) and contemporary data from the US Forest Service (Forest Inventory Analysis, FIA) from 2001 to 2010 (20). Comparisons with historical data sets from the early 20th century are powerful tools for documenting and understanding recent patterns of biotic change. Such studies have documented changes in mortality, elevation, and aspect of plant species and vegetation types, and in the distribution of birds and small mammals (e.g., refs. 21–23). Here we address changes in forest density, composition, and basal area across California over the last 70 years. We examine how patterns of forest change from the historical (1929–1936) to contemporary period (2001–2010) relate to modeled estimates of changes in climatic water deficit (CWD, the cumulative annual excess of potential versus actual evapotranspiration) during the same time period. CWD is an integrative measure of water demand relative to availability (values reflect an index of plant

Significance

Declines in the number of large trees in temperate and tropical forests have attracted attention, given their disproportionate importance to forest structure, function, and carbon storage. Yet, factors responsible for these declines are unclear. By comparing historic (1930s) and contemporary (2000s) surveys of California forests, we document that across 120,000 km^2, large trees have declined by up to 50%, corresponding to a 19% decline in average basal area and associated biomass, despite large increases in small tree density. Contemporary forests also exhibit increased dominance by oaks over pines. Both large tree declines and increased oak dominance were associated with increases in climatic water deficit, suggesting that water stress may be contributing to changes in forest structure and function across large areas.

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drought stress) that has been implicated and associated with patterns of forest mortality and change, and with vegetation distributions more generally (24–27). We calculate CWD using a climatic water balance model that integrates the seasonal course of temperature and precipitation, topographic energy loading, and soil moisture drivers. Our fine-scale (subkilometer) model of CWD for California is based on hydrological modeling of individual watersheds, soil properties, and downscaled climatic and meteorological data (including snow melt, and potential and actual evapotranspiration) between 1900 and 2010 (ref. 28; see *SI Appendix*, Fig. S1) to explore how changes in water availability are related to shifts in forest structure. A recent analysis of change in CWD in California between 1900–1939 and 1970–2009 suggests that although precipitation increased regionally over that time period (29), CWD has also increased across much of the state. Increases in the modeled estimates of CWD are driven by increases in potential evapotranspiration due to 20th century warming, and in montane areas this effect is exacerbated by earlier snowmelt and the limitations of shallow soils to store additional water through the dry summer. However, recent work suggests that trees in Sierra forests may be able to tap deeper reservoirs of water in some locations and that modeled increases in CWD in these areas may overestimate the impacts experienced by the larger trees (30). Modeled decreases in CWD in northern regions are associated with deeper soils in these regions that can store the additional precipitation and maintain lower deficit longer into the dry season (31). We specifically compare changes in tree density relative to changes in CWD for the tree size categories used in the historical data set, as evidence from drought induced mortality suggests that tree size influences vulnerability to water stress, with larger trees exhibiting greater mortality in response to drought (e.g., refs. 13 and 14). In addition, we examine forest composition by looking at changes in the dominance of oaks (*Quercus*) vs. pines (*Pinus*) between time periods. We specifically address *Quercus* and *Pinus* for two reasons: (*i*) These are dominant groups in California forests and woodlands, together comprising 45% of forest basal area within regions covered by the historical and modern surveys, and (*ii*) contemporary changes can be assessed in the context of paleohistoric changes, as these genera are readily distinguishable in pollen records. Oaks and pines have exhibited wide shifts in relative abundance in California associated with climatic change in the past 150,000 y, based on palynological records (32, 33). Oaks have historically increased in abundance during warmer, drier interglacial periods, whereas pines have predominated in colder and more mesic glacial periods. We test the hypothesis that changes in forest structure in the direction of smaller trees and increased oak dominance relative to pines are associated with increases in CWD. By characterizing patterns of forest change over the last 70 y across California as a whole, we provide a broad picture of recent changes in forest structure. Understanding patterns and causes of ongoing vegetation change in relation to climate and hydrology is critical to predict and manage future responses of vegetation to global change.

Results and Discussion

We observed striking declines in large trees [>61 cm diameter at breast height (dbh)] across all regions of California between the historical (1930s) and contemporary (2000s) forest surveys (Fig. 1*B* and *SI Appendix*, Table S1). Differences in large tree density were greatest in the Transverse and Peninsular ranges of southern California, where large tree density in the contemporary period was less than 30% of the density in the historical dataset (40.8 vs. 10.6 trees/ha in the historical vs. contemporary

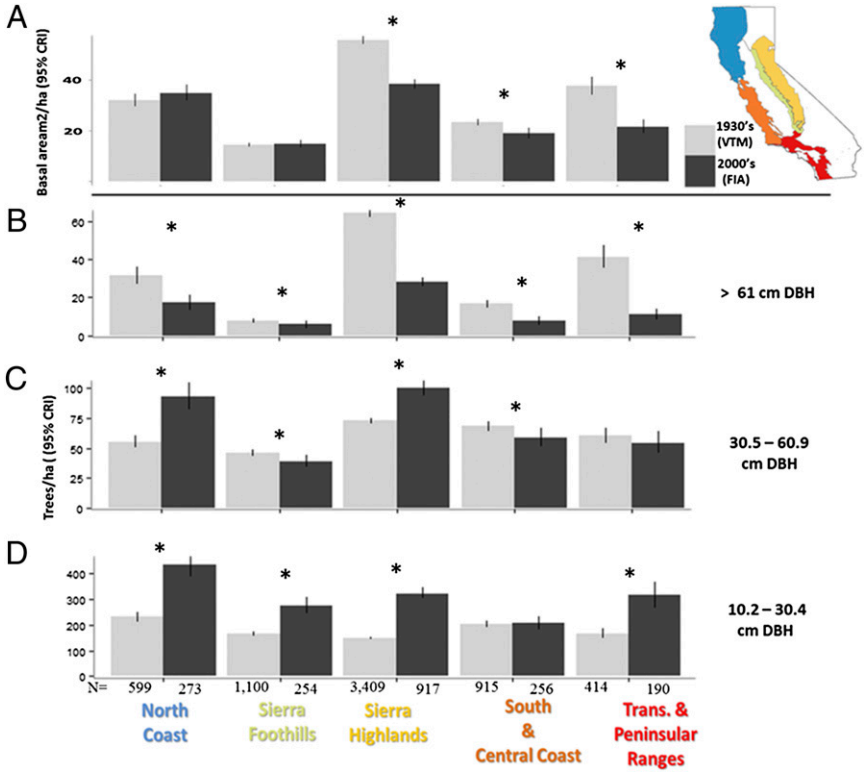

Fig. 1. Basal area has declined across California (*A*), whereas small tree (10.2–30.4 cm dbh) density has increased and large tree density (>61 cm dbh) has declined (*B–D*) between historical (1930s; VTM) and contemporary (2000s; FIA) forest surveys for five ecoregions of California. Asterisks denote nonoverlapping 95% credible intervals (CRI) from Bayesian Generalized Linear Models. Mean values and credible intervals are provided in *SI Appendix*, Table S1. Note ecoregions are color coded in the inset map, with ecoregion names correspondingly colored at the bottom of the figure.

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periods). Declines of ~50% in large tree numbers were observed in the Sierra Nevada highlands (64.3 vs. 28.03 trees/ha), the Coast Ranges of southern and central California (16.6 vs. 7.5 trees/ha), and northern California (30.6 vs. 16.7 trees/ha). Relative and absolute declines were lowest in the Sierra Nevada foothills (7.6 vs. 5.7 trees/ha), where overall densities of large trees were much lower. In contrast to patterns for large trees, we observed dramatic increases in small tree (10-30 cm dbh) density in almost every region of California (Fig. 1*D* and *SI Appendix*, Table S1). Density of small trees within the Sierra Nevada highlands increased over twofold from the historical to the contemporary period (149 vs. 315 trees/ha), whereas small tree density increased over 50% in the Sierra Nevada foothills (165 vs. 268 trees/ha), the North Coast region (229 vs. 412 trees/ha) and the Transverse and Peninsular ranges (165 vs. 301 trees/ha). We did not observe changes in small tree density within the southern and central Coast Ranges (200 vs. 197 trees/ha). Patterns of change for trees in the intermediate size class (31–60 cm dbh) were more variable (Fig. 1*C* and *SI Appendix*, Table S1).

Patterns of change in basal area (Fig. 1*A* and *SI Appendix*, Table S1) across time periods reflected declines in large trees, with declines in basal area of up to 40% in the Transverse and Peninsular ranges (37.8 vs. 21.6 m^2/ha), 30% in the Sierra Nevada highlands (55.9 vs. 38.5 m^2/ha), and 18% in the southern and central Coast Ranges (23.3 vs. 19.0 m^2/ha). We did not detect declines in basal area in northern California or the Sierra Nevada foothills, where reductions in basal area due to large tree declines were balanced by increases in smaller size classes. These changes reflect an important shift in forest structure, with contemporary forests having less biomass (and reduced above ground carbon storage), due to the biomass–basal area relationship (34), and shifts in species composition suggesting that forests have also declined in height (*SI Appendix*, Table S2). Similar changes in biomass were reported from comparisons of a set of historical and contemporary plots located in protected wilderness areas (35). This study covers a much larger area and spans wide latitudinal (32.7–41.95°N) and elevational (10–2,700 m) ranges. Across this historical survey area, we estimate that although total tree density has increased by nearly 40% (Fig. 2*A*), average forest basal area has declined 20% (Fig. 2*B*). On a statewide level, these changes are driven by differences in large tree density, which contribute disproportionately to basal area due to allometric scaling of area with diameter (*SI Appendix*, Fig. S2).

In an analysis of changes in tree abundance across California in relation to CWD, an integrative measure of water stress experienced by plants, we found declines in large tree density correlated with increases in CWD modeled to have occurred since the 1930s based on historical climate data (Fig. 3). Changes in small tree density were not correlated with CWD change. These results are consistent with observations that large trees are disproportionately vulnerable to drought and water stress (11, 14, 36), and suggest that factors leading to increased CWD (increased temperatures, earlier snowmelt, and/or decreased precipitation) have contributed to changes in forest structure. Regional patterns of land use, fire management, and timber harvesting almost certainly contribute to these changes as well (e.g., both large tree declines and modeled increases in CWD are highest in the Sierra Nevada and Transverse mountain ranges, where timber harvesting and air pollution contribute to historical forest changes Fig. 3*C*). However, several lines of evidence suggest that land use practices do not explain the relationship between CWD and large tree declines. First, large tree declines have been consistently found in analyses restricted to National Parks and wilderness areas protected from logging (8, 35). Second, in areas such as northern California where logging has occurred but water deficit has changed little or decreased, there is also less change in large tree density (Fig. 3*C*). The increase in density of smaller trees observed in our study, a well-documented

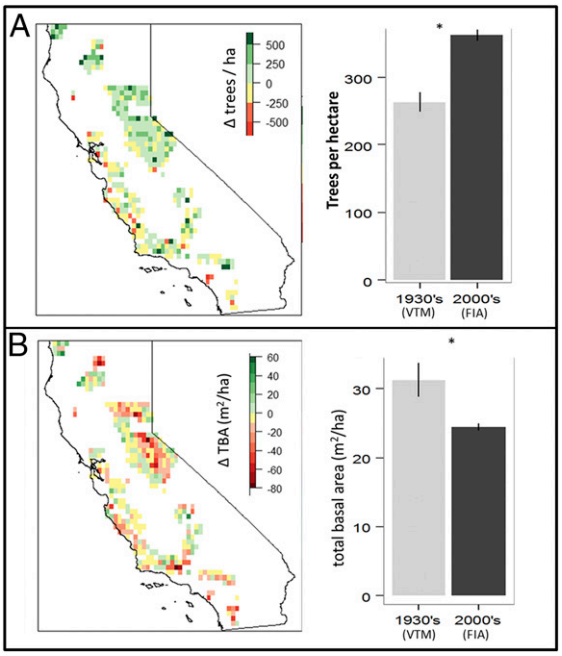

Fig. 2. Maps of change in tree density per hectare (for all size classes) (*A*) and average basal area (*B*) of forest plots between historical (1930s; VTM) and contemporary (2000s; FIA) forest surveys of California. Map and plot values are estimated from mean values of tree density and basal area within 20 km grid cells from each time period. Asterisks denote nonoverlapping Bayesian 95% credible intervals (CRI).

pattern associated with fire suppression (16, 37), could influence competition for moisture but would be unlikely to explain the regional patterns we observe as increases in small tree density were poorly correlated with large tree declines (R^2 = 0.021, n = 359). Further investigation of fire suppression, small tree density, and CWD would be needed to assess whether these factors interact at smaller scales. Similarly, effects of pollution may contribute to the decline in large trees across time periods, especially in the southern Sierra Nevada and lower elevations adjacent to the Los Angeles Basin (38, 39), but are unlikely to explain the consistent declines in large trees we observe across all regions, or the correlations with CWD. Fire suppression has certainly contributed to increases in small tree density, which has the potential to alter competition for water and patterns of CWD experienced by trees (e.g., ref. 40). However, analyses of plots based on evidence of burning in the historic period or in the interval between the survey periods suggests that large tree declines and small tree increases were consistent for burned and unburned areas (*SI Appendix*, Table S4). Taken together, our results suggest that regional shifts in water availability in California may be a mechanism explaining changes in forest structure associated with large tree mortality. However, the dynamics of small tree increases, and potential competition for soil moisture with large trees across differing depths of soils remains largely unexplored.

In comparisons of independent datasets gathered with differing methodologies, such as the VTM and FIA datasets, there is potential for biases (e.g., differences in plot locations) to contribute to estimates of change over time (see refs. 41–43 for discussion of potential bias in the VTM surveys). Although the changes in large tree density are large in magnitude, they are consistent with small changes in mortality and recruitment rates over the 70 y between surveys. For example, annual net mortality of 0.7% among large trees would result in declines of 50% over 70 y. The differences in forest structure between the contemporary and historical datasets are also consistent with results of

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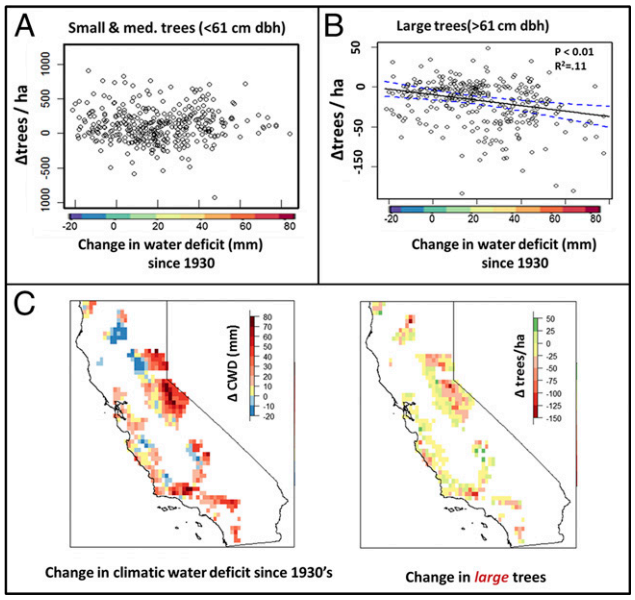

Fig. 3. Changes in tree density and CWD between the historical (1930s; VTM) and contemporary datasets (2000s; FIA) were correlated for large trees (>61 cm dbh; $y = -0\ 0.407x - 11.2$; $F_{1,321} = 34.4$, $P < 0.0001$) (*B*), but not for small (<30) and medium trees (<61 cm) (*A*). Analysis shown is for small and medium trees combined ($y = -0.11x + 113.7$, $F_{1,359} = 0.03$, $P = 0.86$), but neither was significant alone ($y_{small} = -0.13x + 112.03$, $F_{1,367} = 0.05$, $P = 0.82$; $y_{med} = 0.24x + 2.18$, $F_{1,359} = 3.4$, $P = 0.063$). The relationship between large tree changes and changes in CWD held for relative as well as absolute change ($R^2 = 0.09$, $P < 0.001$, Spearman rank correlation). (*C*) Change in CWD since the 1930s and changes in large trees corresponding to the values plotted in *B*.

smaller studies that attempted to relocate and resurvey VTM plots. In the Sierra Nevada, increases of small trees of 63% and declines of large trees of 20% were found in resurveyed plots (15). Similarly, a 79% increase in tree density was found in the Transverse ranges of southern California, attributed to fire suppression (16). Our findings are also consistent with analyses of independent data sets on forest structure in the western US that found large increases in small tree density, attributed to fire suppression (37, 44). Similar patterns of change in abundance from resurvey studies visiting specific VTM plots and from comparison of VTM plots with the independent FIA plots would not be expected if bias in sampling was the driving factor. Additionally, changes due to biased sampling would not lead to significant differences in tree declines associated with the degree of change in CWD.

To further investigate patterns of forest change and increased water stress across time periods, we examined how modeled estimates of CWD relate to forest composition within and across time periods, using the relative abundance of oaks (*Quercus*) and pines (*Pinus*). The relative abundance of these two genera has shifted considerably in the past 150,000 y, with oaks dominating in warmer, drier interglacial periods and pines in colder, more mesic glacial periods (32, 33). In an analysis of basal area within ecoregions, we found that pines have declined in all areas, whereas oaks increased in the Sierra Nevada, and decreased in the central and southern Coastal ranges (Fig. 4) (see also ref. 45). Consistent with this, we found that the ratio of oak to pine basal area was positively correlated with estimates of CWD across the survey area in both time periods. In addition, the contemporary survey shows an increased relative dominance by oaks beyond that accounted for by estimates of increases in CWD (Fig. 5). Other factors potentially contributing to shifts in the oak:pine ratio include fire suppression and logging practices. Examination of changes in basal area for common taxa in the historical and contemporary data (*SI Appendix*, Fig. S4) suggests roles for CWD, land use history, and species-specific responses. For example, basal area increased across time periods in the relatively drought tolerant *Pinus monophylla* (46), in contrast to other *Pinus* species. Our emphasis on oaks and pines is not meant to imply a more general hardwood–conifer shift, as conifers such as *Calocedrus decurrens* and *Pseudotsuga menziesii* are more abundant in the contemporary dataset. However, we emphasize oaks and pines due to the clear patterns of paleohistorical shifts associated with climate derived from the palynological record in California. The shift in California forests to a more oak dominated system in the last 70 y is consistent with historical changes over longer time scales associated with temperature and water availability, although land use changes, timber harvesting and successional change likely contribute to this pattern as well (47). An important difference in the contemporary period is the introduction of *Phytophthora ramorum,* the pathogen causing sudden oak death, which was first detected in the mid 1990s and has caused high oak mortality in the central and north coast regions of California (48). This disease is unlikely to result in a signal in the contemporary data, as surveys occurred soon after reports of oak mortality. Thus, although California forests would be predicted to become increasingly oak dominated in response to increased temperature and water stress under scenarios of global climate change (49), if oak mortality rates increase due to introduced pathogens, California's forests may shift in directions not observed in the paleohistorical record.

Summary

We find that declines in large trees across California, and increases in the relative abundance of oaks versus pines are associated with modeled estimates of increases in CWD since the early part of the 20th century. These findings suggest increased temperatures and changes in the timing and levels of water availability are contributing to large area changes in western North American forests. Although other factors likely contribute to this pattern, the association of CWD with changes in forest structure provides evidence that CWD is an integrated metric that can be used in modeling vegetation responses to changing climatic conditions across complex landscapes. Within California, average annual temperature is predicted to increase by up to 5 °C by 2100, resulting in projected increases in water deficit of 30% or more in many areas (absolute increases of up to 100 mm in

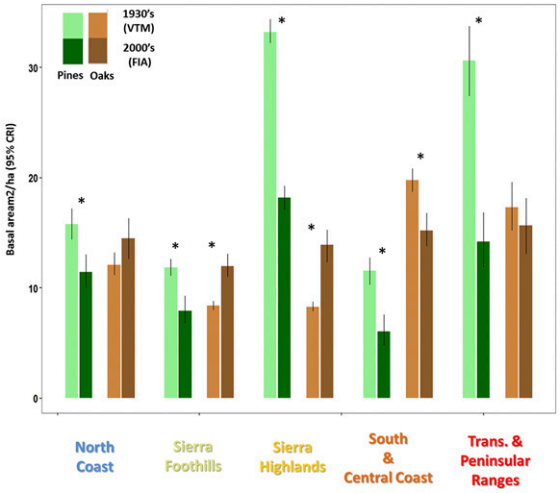

Fig. 4. Changes in basal area of oaks and pines between historical (1930s; VTM) and contemporary (2000s; FIA) forest surveys for five ecoregions of California. Asterisks denote change inferred between time periods based on nonoverlapping Bayesian 95% credible intervals (CRI).

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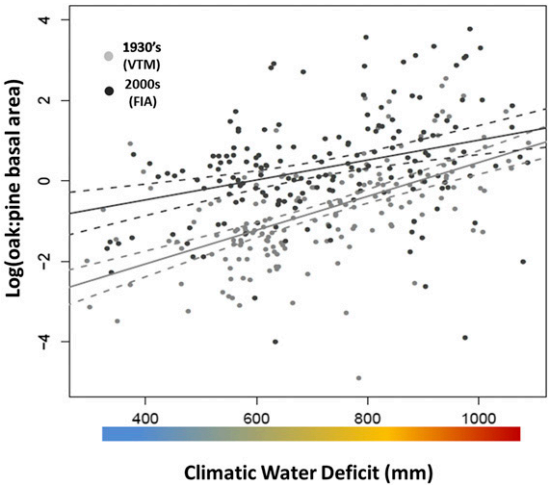

Fig. 5. Relative dominance of oaks versus pines increases with CWD based on correlations between oak:pine basal area and CWD in the historical (1930s; VTM) and recent surveys (2000s; FIA), but is shifted toward increased oak dominance in the recent survey. Points are inferred from mean basal area and CWD within 20 km grid cells from each time period. Coefficient estimates: survey period ($B = -1.93$, $t = 4.17$, $P < 0.001$), CWD ($\beta = 0.0026$, $t = 5.34$, $P < 0.001$), survey period × CWD ($\beta = 0.0015$, $t = 2.4$ $P = 0.0168$).

annual deficit), greatly exceeding the estimated historical changes in this study (8, 50). However, estimates of CWD and our understanding of how plants experience CWD are limited by our understanding of interactions between water storage and the ability of plants to access deeper reservoirs of water (30, 51). Trees in montane areas may avoid deficit by tapping water available below the depth of most current soil models (30), and some areas of California are predicted to exhibit declines in water deficit over the next century due to increases in precipitation in areas with high soil water storage potential (e.g., ref. 25). Refinement of estimates of CWD is needed to better understand these complexities. However, responses of vegetation to declines in CWD due to recruitment and decreased mortality would likely be slow relative to changes from increased mortality with increased deficit, suggesting that rates of change will continue to increase. Continued investigation of integrated effects of water balance on vegetation dynamics is critical to predict and manage vegetation responses to global change.

Methods

Tree Numbers and Basal Area Within Ecoregions. We compared forested plots from the Weislander Vegetation Type Map (VTM) survey plots collected between 1929 and 1936, with US Forest Service Forest Inventory Analysis (FIA) plots collected between 2000 and 2010. Across California, we identified 9,388 VTM plots and 5,198 FIA plots as forested (having at least one tree >10.2 cm dbh, the cutoff for a tree in the VTM data). We kept only plots occurring within 5 km of a plot from the other time period, resulting in 6,572 VTM and 1,909 FIA focal plots. These resulted in sets of plots that were similar in slope, aspect, and elevation, as well as location across latitudinal and longitudinal gradients (*SI Appendix*, Fig. S3). Analyses based on this 5 km distance filter were similar to results using only the nearest neighboring plot within 5km across the two time periods (*SI Appendix*, Table S3) indicating that patterns across the two time periods are robust to rarefaction of the data. Results presented are from the 5 km distance filtering to reduce geographic bias due to differential survey areas and methods while maximizing information from the historical survey (25, 41, 52). We converted FIA data on continuous tree dbh to the VTM size categories (SC1: 10.2–30.4 cm; SC2: 30.5–60.9 cm; SC3 61.0–90.9 cm, SC4: > 91.0 cm) and combined the two largest size classes, which showed similar trends, resulting in 3 size categories (small, medium and large). To compare changes in forest structure across regions of California, we identified plots occurring within the zones of a modified version of the Jepson Manual eco-regions of California (53). The modified regions were: (*i*) South and Central Coast, (*ii*) Transverse and Peninsular Ranges, (*iii*) North Coast, (*iv*) Foothills of the Sierra Nevada and southern Cascades, (*v*) Highlands of the Sierra Nevada and southern Cascades. The Central Valley and desert regions were excluded due to an insufficient number of forested plots. We examined two metrics of forest structure within each region: stems per ha and basal area per ha (by size class) in forested plots. We tested for changes in stems per ha between time periods using estimates from a generalized linear model (GLM) with a negative binomial distribution (because variance of tree numbers was much larger than the mean) and log link for each size class and for total stems across classes. We used slope-corrected area of each plot as a covariate in the model (45), using slope estimates obtained from the FIA database or from a 90-m DEM for the VTM plots. Basal area was estimated from size class data using the quadratic mean of dbh for each tree species in each size class (continuous dbh values in the FIA dataset were converted to VTM size classes for consistency). These mean values per species per size class were applied to both the FIA and VTM dataset by multiplying by the number of trees of each species in each size class to obtain an estimate of basal area in units of m^2 ha^{-1}. Values of basal area were compared across regions and time periods using a GLM with a gamma distribution and a log link. Model parameters were estimated in a Bayesian framework using the R2WinBUGS package (54) with vague priors. The negative binomial distribution was implemented as a Poisson-gamma mixture model to allow for overdispersion. Comparisons between times and regions were based on Bayesian 95% credible intervals (CRIs), which contain 95% of the values from the posterior distribution of parameter estimates, and are analogous to 95% confidence limits (55). CRIs were calculated based on the highest posterior density interval.

Tree Numbers and Basal Area. To compare changes in forest structure across California as a whole, we calculated raster surfaces of average tree density and basal area in 10 arc-minute grid (~20 km) cells using the VTM-FIA comparison data. Mean values from each raster cell were then used to calculate averages across the VTM survey area in stems per ha and total basal area (mean basal area per ha). Values at each time period were compared using 95% CRI's. Patterns of change between the two time periods across the state were visualized by taking the difference between stems per hectare and basal area between the FIA dataset and the VTM dataset.

Climatic Water Deficit (CWD). Changes in tree density were compared with changes in CWD (56) within the same grid cells between 1910–1940 and 1981–2010 using 30 y averages from each time period. CWD is the seasonally integrated excess in potential evapotranspiration (PET) versus actual evapotranspiration (ref. 26; see *SI Appendix*, Fig. S1). Estimates of CWD were obtained from a fine-scale (subkilometer) hydrological model developed for California (28) that takes into account spatial variation in energy loading, monthly variation in precipitation and temperature, and soil water holding capacity and drainage. Preliminary field assessment of this model suggests good correspondence with field soil moisture (*SI Appendix*, Fig. S1) in addition to internal model evaluation results (28). CWD reflects an estimate of water stress experienced by plants that integrates more indicators than those commonly used (e.g., the simple ratio of annual PET and precipitation). We regressed changes in tree numbers against change in CWD within each tree size class. To address the complexity of soils and estimates of CWD in the montane Sierra Nevada, where forest trees may access water reservoirs deeper than those included in our CWD model (30, 51), we examined the effect of excluding the Sierra Nevada from our analyses. Results were robust to exclusion of the Sierra Nevada (*SI Appendix*, Table S5 and Fig. S5). We further examined the relationship between residuals from the regression of large tree change in relation to soil water storage to determine if changes in tree density beyond those associated with modeled CWD might be associated with the capacity of soils to store additional water and buffer the effects of predicted declines in CWD (*SI Appendix*, Fig. S6). No relationships were observed in this analysis.

Oak and Pine Comparisons. We calculated average basal area of all *Quercus* and all *Pinus* species within plots where they occurred. Basal area rather than abundance was used to infer community level dominance, facilitating comparisons with historic changes in the abundances of these genera based on the palynological record. Pollen data at least coarsely reflect tree basal area on the landscape due to size-dependence of fecundity, and should track basal area better than stem density, which may be driven by small nonreproductive individuals (57, 58). To investigate patterns of oak and pine abundance in relation to CWD, we regressed the ratio of oak to pine basal area with CWD from 10 arc-minute grids within each time period and used ANCOVA to determine if the relationship varied across time periods. To compare changes in basal area

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of oaks and pines within the ecoregions, we compared 95% CRIs from a GLM of basal area with a gamma distribution and log link, as described above.

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