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Pedro Nava
Chair, Little Hoover Commission
925 L Street, Ste. 805
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Jan. 31st, 2017

Dear Chairperson Nava,

We sent public comments prior to your January 26th meeting, but part were in letter form and part were in an email. We found that the email comments were not included to your committee, so would like to add them. These comments pertain to forest health, density, and fire.

This was the response from Dr. Chad Hanson, fire ecologist, when we asked him questions regarding a recent op-ed that spoke of tree density in the Sierra Nevada range (the "SNC" he uses refers to the Sierra Nevada Conservancy):

Attached is a study comparing Sierra Nevada forest density--in two different ways--from the early 20th century to current times. In terms of trees per acre, the authors conclude that forest density has increased by 30%, but in terms of basal area, the authors conclude that forest density has decreased by 19% (i.e., somewhat more smaller trees, and somewhat fewer large trees). So, removing a large number of trees across millions of acres, as the SNC representatives suggest, would exacerbate the already below-normal density of basal area (fyi, in many scientific studies, basal area appears to be the most relevant metric of habitat value for numerous species, including Black-backed Woodpeckers, Spotted Owls, Fishers, and others, so their proposal would have serious adverse impacts). Also, the SNC representatives are highly misleading when they mention that some areas that currently have 260 trees per acre had only 20 per acre historically. Of course, this is true of "some areas", and it is also true that other areas have less trees now than they did historically (such as areas that have recently burned). The implication by SNC that tree density has increased 13-fold is mythology. Further, the SNC representatives claim that dead trees increase fire severity/spread, which is consistently contradicted by current science (see excerpt below

from a recent memo of mine on this), and their claim that wildlife habitat is destroyed by high-intensity fire patches (or patches of snags in general) is nothing short of science denial--in fact, snag forest habitat is comparable to old forest in terms of native biodiversity and wildlife abundance. I hope this helps. Please let me know if you have any other questions, and thanks for the work that you do.

Chad

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There are three empirical studies that have investigated the effects of actual fires in areas with known pre-fire snag levels from recent drought and bark beetles, and which pertained to ponderosa pine and mixed-conifer forests. The first, Bond et al. (2009), which I co-authored, was conducted in mixed-conifer and ponderosa/Jeffrey-pine forests of the San Bernardino National Forest in southern California, where fires occurred immediately after a large pulse of snag recruitment from drought/beetles. Bond et al. (2009) “found no evidence that pre-fire tree mortality influenced fire severity”.

The second, Hart et al. (2015), which was published in the Proceedings of the National Academy of Sciences, investigated whether there is a relationship between snag levels from drought/beetles and the rate of fire spread in conifer forests across the western U.S., including ponderosa pine-dominated forests of California. Hart et al. (2015) found the following:

“Contrary to the expectation of increased wildfire activity in recently infested red-stage stands, we found no difference between observed area and expected area burned in red-stage or subsequent gray-stage stands during three peak years of wildfire activity, which account for 46% of area burned during the 2002–2013 period.”

In other words, in both the initial stage of snag recruitment, when dead needles are still on the trees (“red-stage”), and in the later stage, years later, after needles and some snags have fallen (“gray-stage”), fire did not spread faster or burn more area in forests with high levels of snags from drought and native beetles. This was also true specifically in ponderosa pine forests, where there was no significant effect on fire spread of tree mortality from drought/beetles, and where fire spread was nearly identical regardless of snag levels (see Hart et al. 2015, Figure 3D).

The third, Meigs et al. (2016), was conducted in mostly mixed-conifer and ponderosa pine forests of the Pacific Northwest (south to the California border), and found the following:

“In contrast to common assumptions of positive feedbacks, we find that insects generally reduce the severity of subsequent wildfires. Specific effects vary with insect type and timing, but both insects decrease the abundance of live vegetation susceptible to wildfire at multiple time lags. By dampening subsequent burn severity, native insects could buffer rather than exacerbate fire regime changes expected due to land use and climate change.”

Specifically with regard to the mountain pine beetle, a native species associated with the current snag recruitment in California’s ponderosa pine and mixed-conifer forests, Meigs et al. (2016) found that fire severity was the same between stands with high levels of snags from drought/beetles and unaffected forests, when fires occurred during or immediately after the pulse of snag recruitment, and then fire severity consistently **declined** in the stands with high snag levels in the following decades (see Meigs et al. 2016, Figure 3a).

Ken Pimlott, Director of CalFire, recently stated that he does not dispute this science (<http://www.sandiegouniontribune.com/news/2016/jul/25/california-gov-wildfire-prevention-strategies/>). Yet the State of California continues to disseminate information—web-based and otherwise—claiming that snag patches substantially increase fire intensity and spread, and the Governor’s emergency proclamation, which makes this same incorrect assertion, has not been withdrawn or modified. Nor has the State withdrawn the proposal, which is promoted on this same incorrect basis, to facilitate widespread logging of recent snags across vast areas of public forestlands in remote “Tier Two” forests (forests that are not immediately adjacent to roads, powerlines, and homes).

Please find attached the study Dr. Hanson mentions in the opening paragraph: McIntyre PJ, et al. (2015) *Twentieth-century shifts in forest structure in California: Denser forests, smaller trees, and increased dominance of oaks. Proc Natl Acad Sci USA 112(5):1458–1463*

Sincerely,

A handwritten signature in black ink that reads "Marilyn Woodhouse". The signature is fluid and cursive, with the first name "Marilyn" written in a smaller, more compact script than the last name "Woodhouse".

Director

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

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Edited by Gregory P. Asner, Carnegie Institution for Science, Stanford, CA, and approved December 15, 2014 (received for review June 2, 2014)

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 km², 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.

Author contributions: P.J.M., J.H.T., C.R.D., M.K., and D.D.A. designed research; J.H.T., C.R.D., A.L.F., L.E.F., M.K., and D.D.A. contributed data and analytic tools; P.J.M. analyzed data; and P.J.M., J.H.T., C.R.D., A.L.F., L.E.F., M.K., and D.D.A. wrote the paper.

The authors declare no conflict of interest.

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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 paleo-historic 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; VTM) and contemporary (2000s; FIA) 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

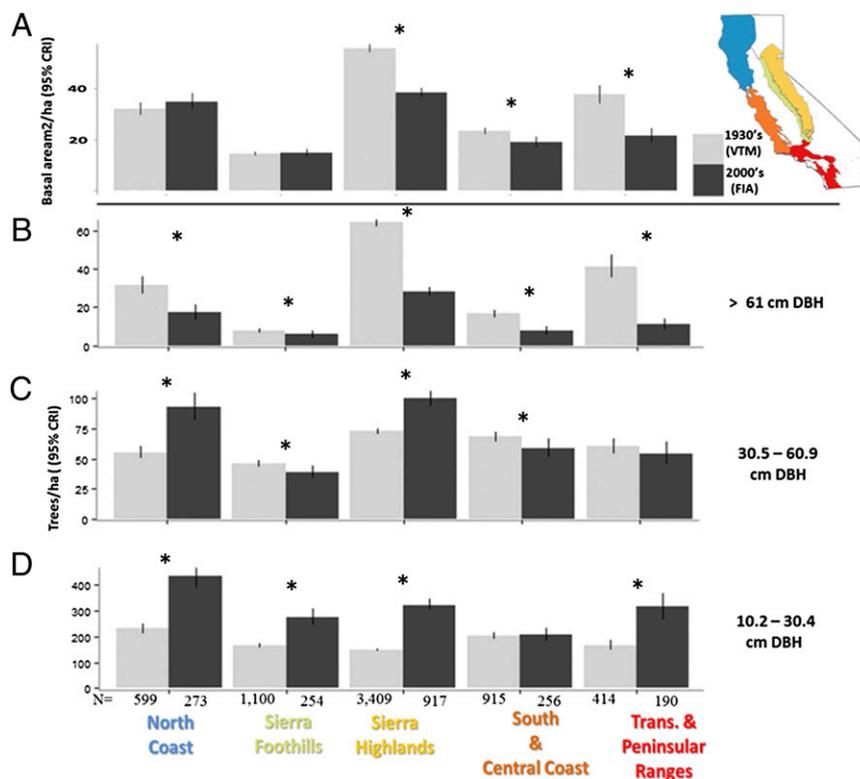


Fig. 1. Basal area has declined across California (A), whereas small tree (10.2–30.4 cm dbh) density has increased and large tree density (>61 cm dbh) has declined (B–D) between historical (1930s; VTM) and contemporary (2000s; FIA) forest surveys for five ecoregions of California. Asterisks denote non-overlapping 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.

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. 1D 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. 1C and *SI Appendix, Table S1*).

Patterns of change in basal area (Fig. 1A 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 m²/ha), 30% in the Sierra Nevada highlands (55.9 vs. 38.5 m²/ha), and 18% in the southern and central Coast Ranges (23.3 vs. 19.0 m²/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. 2A), average forest basal area has declined 20% (Fig. 2B). 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. 3C). 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. 3C). The increase in density of smaller trees observed in our study, a well-documented

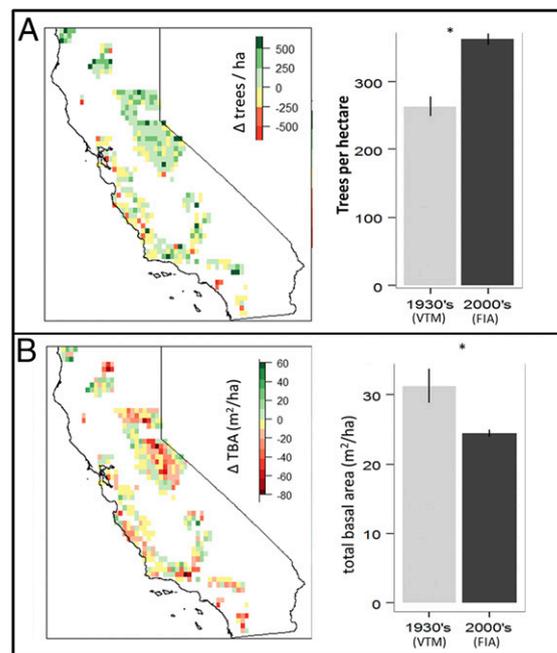


Fig. 2. Maps of change in tree density per hectare (for all size classes) (A) and average basal area (B) of forest plots between historical (1930s; VTM) and contemporary (2000s; FIA) forest surveys of California. Map and plot values are estimated from mean values of tree density and basal area within 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

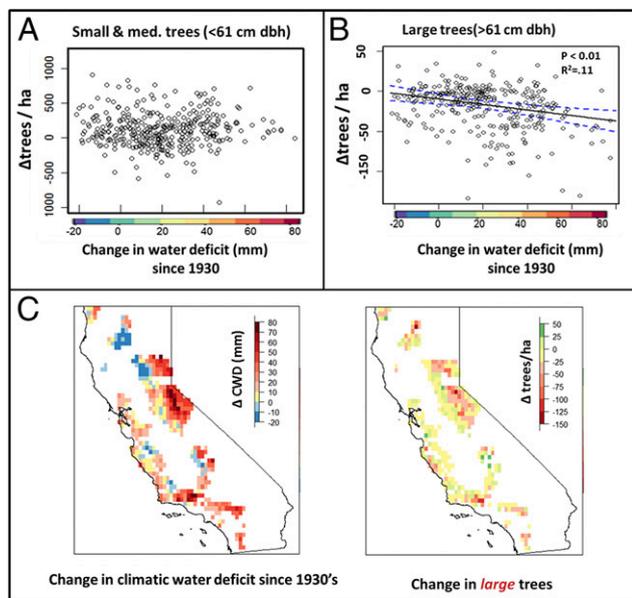


Fig. 3. Changes in tree density and CWD between the historical (1930s; VTM) and contemporary datasets (2000s; FIA) were correlated for large trees (>61 cm dbh; $y = -0.407x - 11.2$; $F_{1,321} = 34.4$, $P < 0.0001$) (B), but not for small (<30) and medium trees (<61 cm) (A). Analysis shown is for small and medium trees combined ($y = -0.11x + 113.7$, $F_{1,359} = 0.03$, $P = 0.86$), but neither was significant alone ($y_{\text{small}} = -0.13x + 112.03$, $F_{1,367} = 0.05$, $P = 0.82$; $y_{\text{med}} = 0.24x + 2.18$, $F_{1,359} = 3.4$, $P = 0.063$). 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

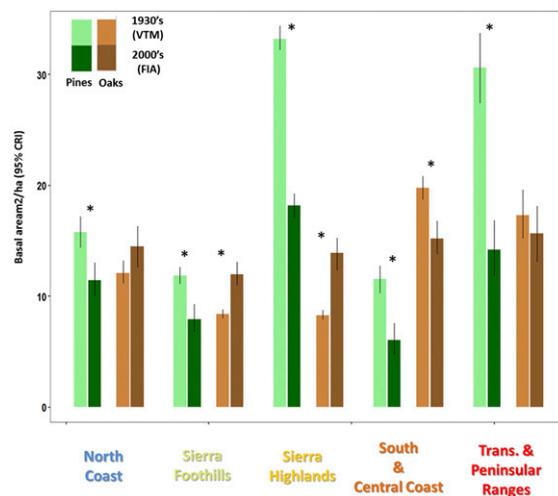


Fig. 4. Changes in basal area of oaks and pines between historical (1930s; VTM) and contemporary (2000s; FIA) forest surveys for five ecoregions of California. Asterisks denote change inferred between time periods based on nonoverlapping Bayesian 95% credible intervals (CRI).

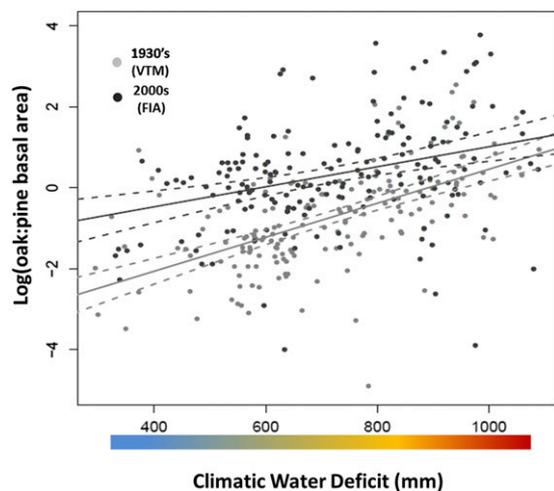


Fig. 5. Relative dominance of oaks versus pines increases with CWD based on correlations between oak:pine basal area and CWD in the historical (1930s; VTM) and recent surveys (2000s; FIA), but is shifted toward increased oak dominance in the recent survey. Points are inferred from mean basal area and 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 \times 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 5 km 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 $\text{m}^2 \text{ha}^{-1}$. 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

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.

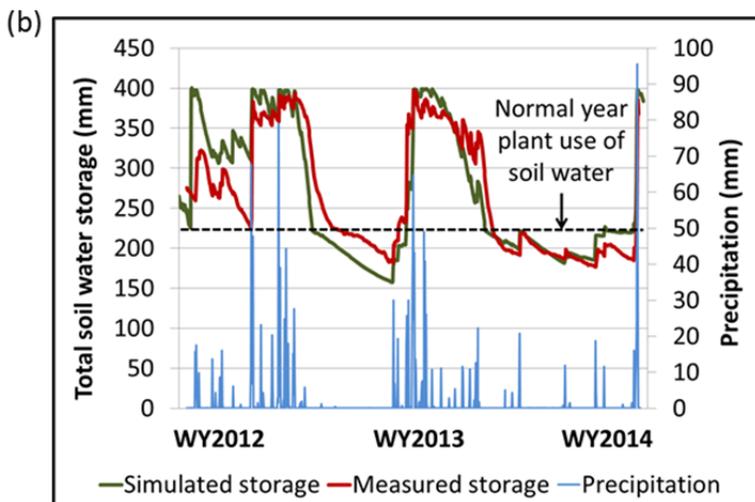
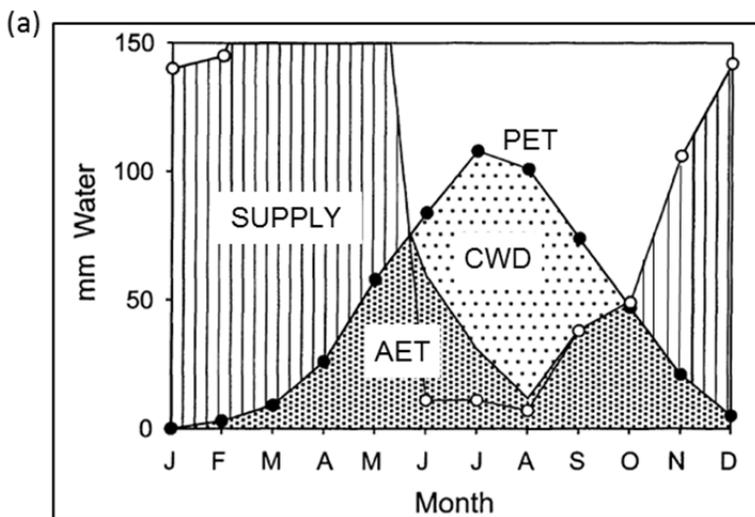
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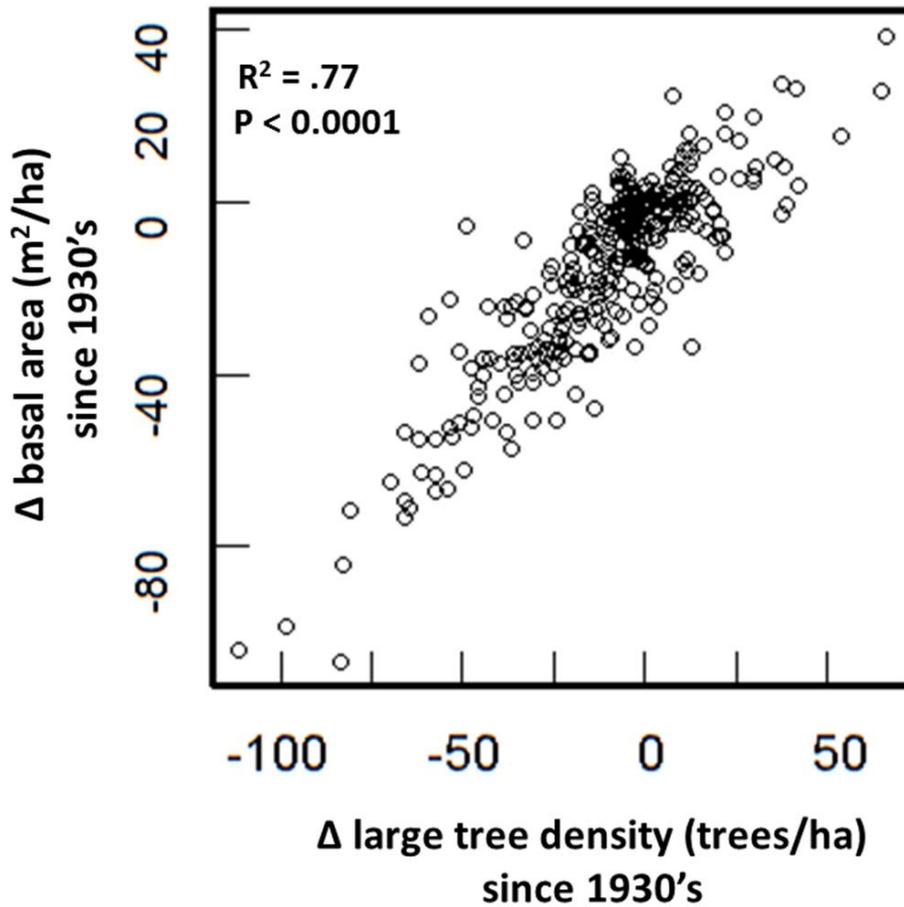
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Supplemental Figure 1. (a) Illustration of climatic water deficit (CWD) calculated as potential (PET) minus actual (AET) evapotranspiration (with monthly values shown), modified from Stephenson (1998) for mixed conifer forest in the Sierra Nevada.

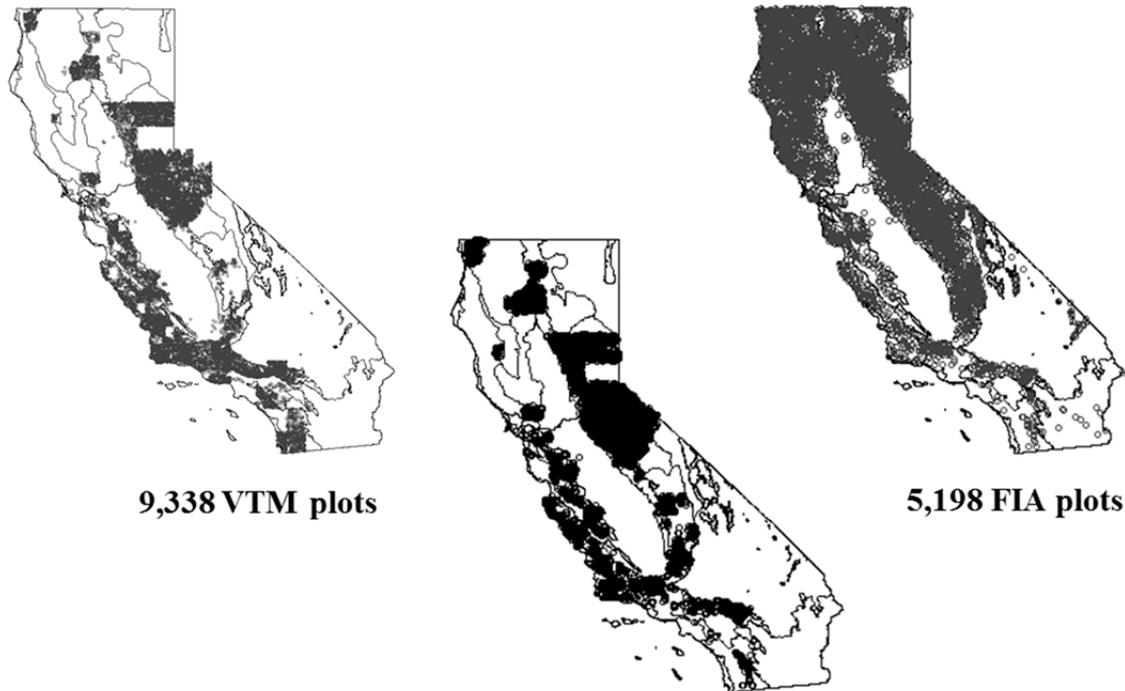
Panel (b) depicts simulated soil water content that is field verified on the basis of measured soil water storage at a grassland site in northern California, the Pepperwood Preserve. As seasonal precipitation (supply) diminishes in Mediterranean climates, AET drives the accumulation of deficit (CWD) as soil moisture declines over the season. Field verification is accomplished as the simulated total soil water storage (simulated over approximately 96.5 cm(38”)) matches measured storage.



Supplemental Figure 2. Changes in large tree (> 61 cm dbh) density are correlated with changes in forest basal area between historical (1930's; VTM) and contemporary (2000's; FIA) forest surveys of California ($y = 1.18x - 9.7$; $F_{1,321} = 940$, $P < 0.001$). Points represent values of tree density and basal area from rasterized grids (~20 km) in each time period (e.g. Fig. 2).



Supplemental Figure 3. Location and number of georeferenced forested plots in the VTM (1929-1936) and Forest Inventory Analysis (2000-2010) surveys within CA. Number and characteristics of plots selected for analyses (those falling within a 5km radius across time periods).



Plots selected for analyses (5 km filter)

	VTM	FIA
No. Plots	6,572	1,909
Elevation(m)	1318	1284
Latitude	38.03	38.05
Aspect	196.5	194.8

Supplemental Table 1. Mean and ranges of 95% credible intervals of tree density and basal area with historic VTM (1930's) and contemporary FIA (2000's) forest survey data. Values are from Bayesian generalized linear models.

Region	VTM			FIA			Significance based on 95% CRI
	low CRI	mean	upper CRI	low CRI	mean	upper CRI	
Trees per hectare							
Small trees (10.2- 30.4 cm dbh) / ha							
North Coast	224.30	228.79	232.76	402.34	412.16	422.17	*
Sierra Foothills	162.55	165.39	168.01	260.21	267.94	276.17	*
Sierra Highlands	147.53	149.01	150.36	310.35	314.97	319.74	*
South & Cen. Coast	196.76	200.32	203.57	189.92	196.96	204.08	NS
Trans. and Pen. Ranges	160.77	165.13	169.36	291.28	301.05	312.22	*
Medium trees (30.5 - 60.9 cm dbh) / ha							
North Coast	52.61	54.79	56.88	85.85	90.37	95.54	*
Sierra Foothills	43.90	45.45	46.81	35.09	38.12	41.30	*
Sierra Highlands	72.02	73.08	74.00	97.60	100.15	102.65	*
South & Cen. Coast	66.35	68.23	70.11	53.00	57.13	60.70	*
Trans. and Pen. Ranges	57.05	60.08	62.43	48.66	52.79	57.42	NS
Large trees (> 61 cm dbh) / ha							
North Coast	29.02	30.60	32.10	14.80	16.66	18.79	*
Sierra Foothills	7.01	7.57	8.16	4.61	5.69	6.97	*
Sierra Highlands	63.43	64.34	65.24	26.62	28.03	29.32	*
South & Cen. Coast	15.61	16.60	17.51	6.17	7.50	9.01	*
Trans. and Pen. Ranges	38.44	40.85	43.03	8.69	10.67	12.77	*
Total trees (all size classes) / ha							
North Coast	309.51	314.07	319.26	507.86	519.47	530.17	*
Sierra Foothills	215.29	218.40	221.63	303.84	312.03	321.02	*
Sierra Highlands	284.29	286.39	288.30	437.73	443.13	448.90	*
South & Cen. Coast	281.18	285.19	288.88	253.59	261.61	270.01	*
Trans. and Pen. Ranges	260.34	266.10	271.24	353.15	364.77	376.12	*
Total Basal Area (m2/ha)							
North Coast	29.66	32.11	34.65	31.95	34.85	38.25	NS
Sierra Foothills	13.73	14.48	15.24	13.46	14.84	16.29	NS
Sierra Highlands	54.34	55.88	57.47	36.63	38.51	40.32	*
South & Cen. Coast	22.11	23.28	24.66	16.93	18.98	21.18	*
Trans. and Pen. Ranges	34.27	37.79	41.30	19.10	21.59	24.44	*

Supplemental Table 2. Estimates of mean tree height within plots, based on stand composition in the VTM (1929-1936) and FIA (2000-2010) datasets. Height estimates by species, VTM size class, and region were obtained from measurements in the FIA dataset. Using information on mean height by species and size class from the FIA data, we estimated height within region based on species composition and diameter at breast height measurements from the historical VTM plots.

Region	Height (m)	
	VTM	FIA
North Coast	13.51	12.53
Sierra Foothills	11.12	10.76
Sierra Highlands	16.27	12.81
South & Cen. Coast	11.51	11.14
Trans. and Pen. Ranges	14.15	10.86

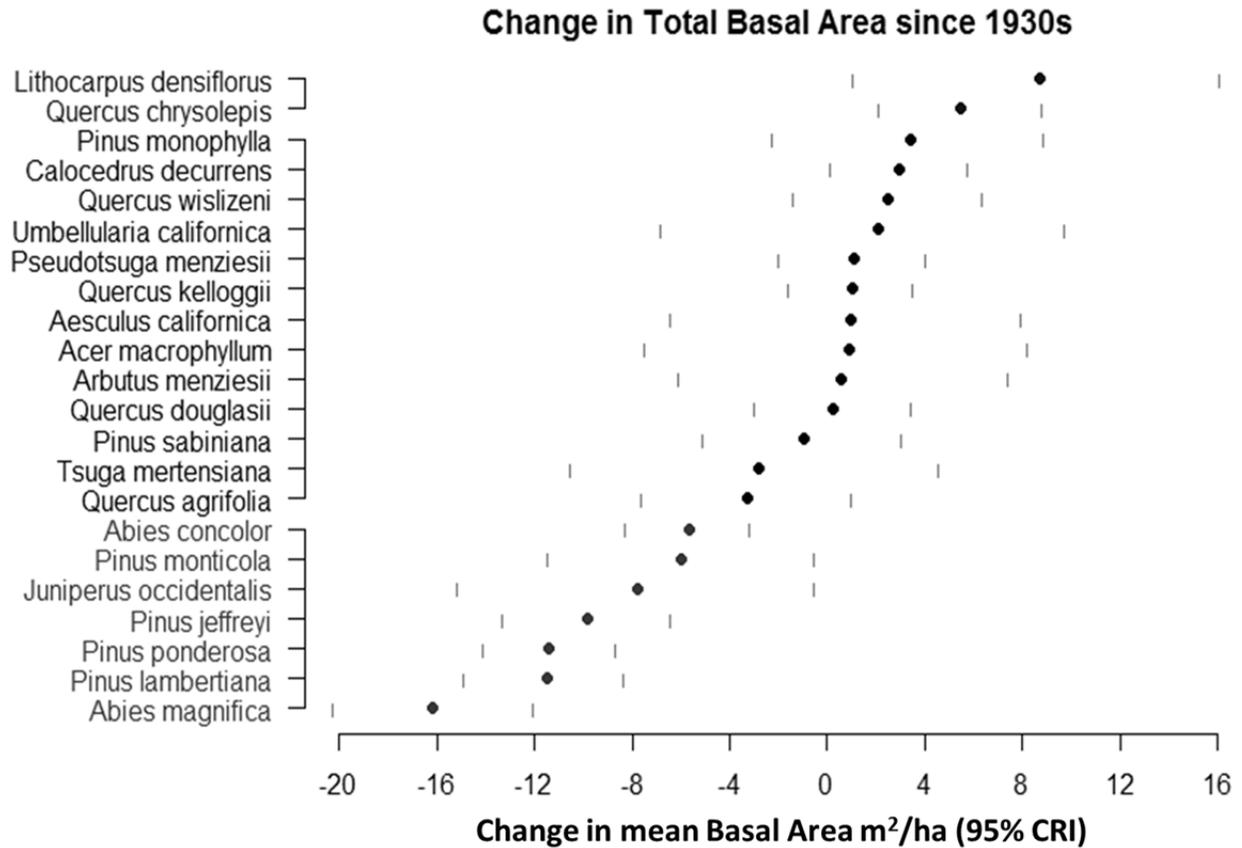
Supplemental Table 3. Mean of trees per hectare for FIA and VTM surveys for small (10.2 - 30.4 cm dbh), medium (30.5-60.9 cm dbh) and large (>61 cm dbh) trees, based on selecting all plots within 5km of a plot from a different time period, and selecting only the nearest plot within 5km. Values are arithmetic means.

Region	Type	5 km radius (VTM 6,407 FIA 1909)			Nearest Neighbor within 5km (VTM 1,909 FIA 1909)		
		Small	Medium	Large	Small	Medium	Large
Trees / ha							
North coast	VTM	231.10	55.13	23.67	200.48	68.37	26.21
	FIA	435.08	93.29	12.61	435.08	93.29	12.61
Sierra Foothills	VTM	165.52	45.60	6.32	164.52	43.14	5.86
	FIA	274.90	39.04	5.17	274.90	39.04	5.17
Sierra Highlands	VTM	148.98	72.88	39.14	162.35	73.99	37.88
	FIA	323.76	100.23	21.39	323.76	100.23	21.39
South & Cen. Coast	VTM	202.23	68.12	14.09	212.38	72.25	14.42
	FIA	208.42	59.16	6.31	208.42	59.16	6.31
Trans. and Pen. Ranges	VTM	166.22	60.58	27.15	172.40	69.27	26.80
	FIA	317.06	54.12	9.12	317.06	54.12	9.12

Supplemental Table 4. Comparison of VTM era plots by burn status (noted to be recently burned or to have signs of burning in notes from the VTM plot data) or without signs of burning, with FIA plots occurring within or outside of at least one known fire based on the California Department of Forestry Fire Perimeter (FRAP; <http://frap.fire.ca.gov/>) maps from 1950-2010. Although the data are coarse (unclear how long a plot from the VTM era would have evidence of burning, whether plots burned in the period between 1930 to 1950, or what portion of plots may occur in areas with undocumented fires in the FRAP data), there was a signal of reduced density with burning. Furthermore, within burn classes across time period there was a consistent increase in stems per hectare for small trees. For large trees, a decrease in stems per ha across time periods was observed in plots with and without evidence of burning,

	VTM			FIA			
	Trees per hectare						
	low CI	mean	upper CRI	low CRI	mean	upper CRI	Significance based on 95% CRI
Burn Status	Small trees (10.2- 30.4 cm dbh)						
unburned	162.20	168.20	174.40	315.70	330.20	344.00	*
burned	112.30	131.90	152.00	255.50	276.20	298.70	*
	Large trees (> 61 cm dbh)						
unburned	43.04	44.35	45.71	18.60	21.36	24.21	*
burned	21.76	25.98	30.44	7.60	12.61	17.29	*

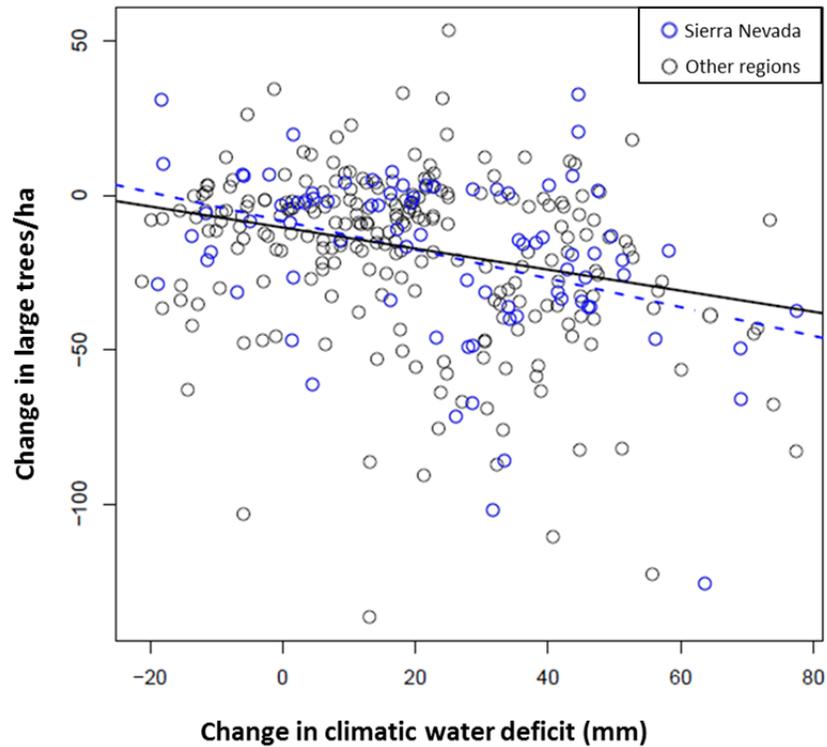
Supplemental Figure 4. Average changes in basal area for the 22 most common species in the joint VTM-FIA data between historical (1930's; VTM) and contemporary (2000's; FIA) forest surveys of California. Points represent values of basal area and 95% credible intervals (CRI) from plots across the full survey area (~120,000 km²) in each time period across California that were occupied by these taxa. Species are sorted in order of the value of change.



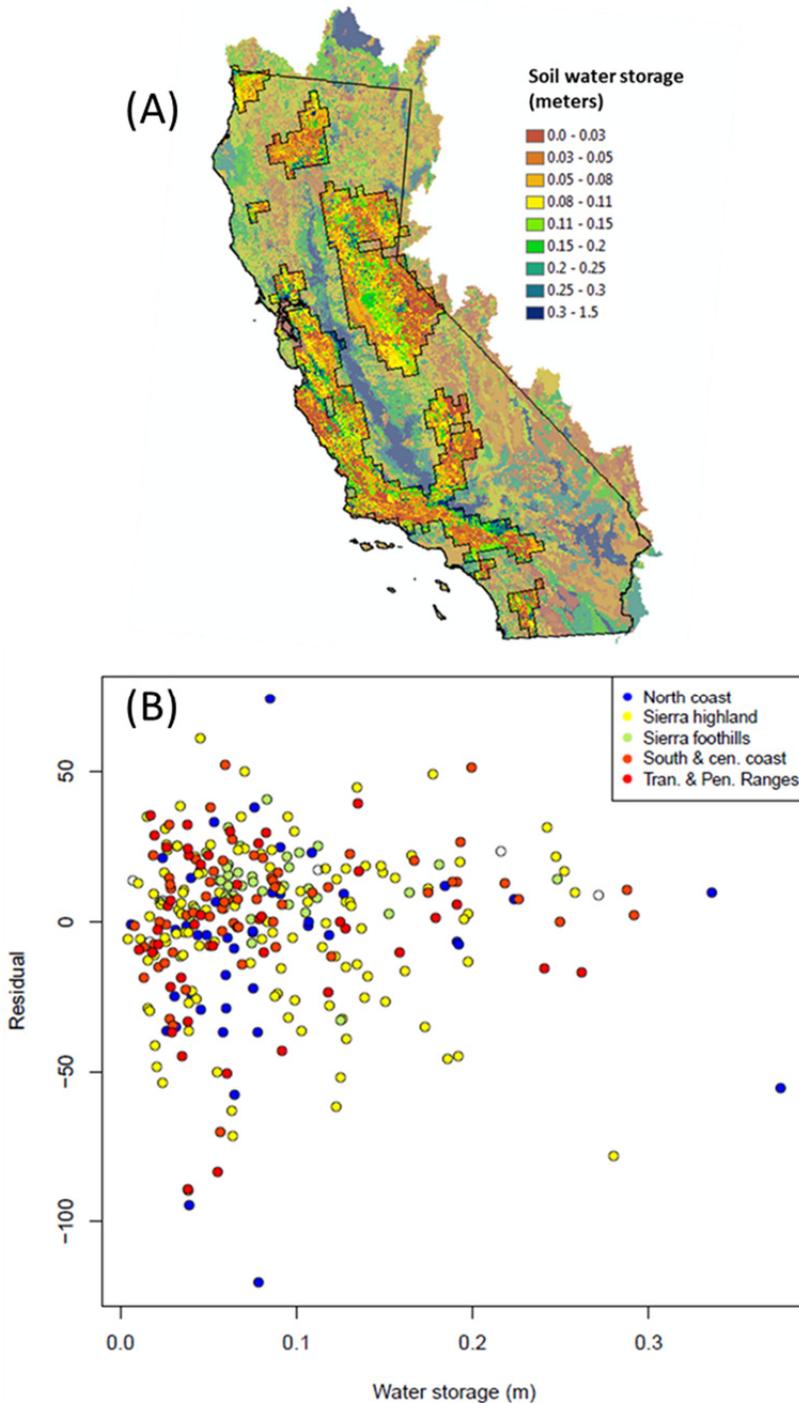
Supplemental Table 5. Due to potential uncertainty in models of climatic water deficit (CWD) for the Sierra Nevada ecoregions (foothill and highland), in combination with effects of land-use history in the Sierra Nevada such as fire and logging, we examined the effect of excluding the Sierra Nevada ecoregion on the relationship between large tree changes and CWD changes since the 1930's. Decline in large trees with increasing climate water deficit (CWD) is robust against removal of the Sierra Nevada ecoregion from analyses.

Data Included	Intercept	Slope	DF	P	R²
All data	-11.2	-0.407	311	< .0001	0.11
Excluding Sierra ecoregions	-10.2	-0.33	194	0.001	0.06
Only Sierra ecoregions	-14.95	-0.36	115	0.0003	0.09

Supplemental Figure 5. Decline in large trees with increasing climate water deficit (CWD) is robust against removal of the Sierra Nevada ecoregion from analyses. Black symbols correspond to regions outside of the Sierra Nevada. Blue symbols correspond to areas within the Sierra Nevada. See Table S-5 for model values.



Supplemental Figure 6. (A) Modeled soil water storage estimates for the VTM survey area (outlined and highlighted) and broader region over which CWD estimates were modeled. Soil water storage values were estimated from water content at field capacity minus wilting point multiplied by soil depth. For details see (Flint et al. 2013). (B) No pattern is observed when residuals from a linear regression (see Figure 3) of large tree density change and change in water deficit since the 1930's are plotted against estimates of soil water storage.



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