



Widespread shifts in the demographic structure of subalpine forests in the Sierra Nevada, California, 1934 to 2007

Christopher R. Dolanc^{1*}, James H. Thorne² and Hugh D. Safford^{2,3}

¹Department of Plant Sciences and Ecology Graduate Group, University of California, Davis, CA 95616, USA, ²Department of Environmental Science and Policy, University of California, Davis, CA 95616, USA, ³USDA Forest Service, Pacific Southwest Region, Vallejo, CA 94592, USA

ABSTRACT

Aim Many climate-linked vegetation models predict major contraction of subalpine forests within the next 100 years, which would require a relatively rapid replacement of high-elevation species by lower-elevation species over large portions of subalpine forest. We tested this prediction by comparing empirical data from a historic data set with data collected from re-sampled sites from 2007–09.

Location Central Sierra Nevada, CA, USA, 2300–3400 m elevation.

Methods We re-sampled 139 undisturbed historical vegetation plots across 5500 km² originally sampled from 1929–34 in the subalpine zone of the Sierra Nevada, and compared historical with current forest structure and composition. We compared historic and modern climatic conditions using two high-elevation climate stations nearby.

Results Subalpine forests experienced a net increase in tree stem density of 30.4%, including a 63.3% increase in small trees. Six of eight tree species showed statistically significant increases in small tree density, including species with distributions at both the upper and lower boundaries of subalpine. Increases in small tree density were partly offset by a 20% decrease in large trees. These shifts were significant throughout the landscape of our study area. Modern stand composition was indistinguishable from historical composition. Daily minimum temperature (+ 1.2°C) and precipitation (+ 15–48%) both increased during the same period.

Main conclusions Warming temperatures plus steady to increasing precipitation have led to less stressful conditions for recruitment and survival of small trees, and are probably contributing to increased mortality of large trees. Tree abundance and composition in the subalpine has not changed in the direction predicted by vegetation models linked to future climate scenarios. Our results underline the fundamental role that moisture balance plays in structuring mediterranean-zone montane forests. Future shifts in vegetation composition and structure from these regions are likely to depend on interactions between water balance and disturbance factors like fire, insects and disease.

Keywords

California, climate change, composition shifts, demographic structure, forest, resampling, Sierra Nevada, subalpine, VTM, Wieslander.

*Correspondence: Christopher R. Dolanc, Department of Plant Sciences and Ecology Graduate Group, University of California, Davis, CA 95616, USA.
E-mail: crdolanc@ucdavis.edu

INTRODUCTION

Evidence of recent climate change is widespread (IPCC, 2007) and bioclimatic models based on current and projected trends have predicted significant loss of biodiversity (Sala *et al.*, 2000), range shifts (Loarie *et al.*, 2008) and novel and disappearing climates (Williams *et al.*, 2007). Unfortunately, most bioclimatic

models are not able to properly account for factors such as biological interactions, adaptation, dispersal limitation, disturbance and fine-scale habitat heterogeneity (Heikkinen *et al.*, 2006; Randin *et al.*, 2009; Dobrowski *et al.*, 2010), making them best applied as a first-draft, coarse estimation of climate effects on species ranges and biodiversity (Pearson & Dawson, 2003). There remains a great need for empirical data at regional and

local scales as a means to provide a more detailed and practical picture of current (and potentially future) species responses (Parmesan, 2006).

Most vegetation models linked to global warming scenarios predict that shrinking subalpine forests will be replaced by species from lower elevations that move upslope in response to warming (Guisan & Theurillat, 2001; Lenihan *et al.*, 2008), but is it safe to assume that species historically restricted to lower elevations will always out-compete and displace higher-elevation species? Even if this assumption is valid, most high-elevation conifers are extremely long-lived – many subalpine conifer species are known to attain ages in excess of 750–1000 years – and such species are famously slow to respond to climatic stimuli (Perkins & Swetnam, 1996; Grime, 2001). Adult trees in temperate forest ecosystems are hardly, if ever, at equilibrium with current climate (Svenning & Skov, 2004; Millar *et al.*, 2007b), and mature trees might be expected to survive future change for hundreds of years, depending on the strength of competition, the rate of climate warming, disturbances and potentially numerous unknown factors (Loehle, 1996).

Studies that resample historical data sets can quantify on-the-ground change and examine its relationship to spatiotemporal variance using a variety of regional or local variables. Results from these types of studies can be used to validate predictions of biotic response to future climates (Parmesan, 2006) and have the potential to reveal much more about how climate-driven responses of different species will manifest at more local scales (Beckage *et al.*, 2008; Moritz *et al.*, 2008). By providing insight into the trajectories of historical to current species demography, resampling studies also allow for more accurate projection of such changes into the future. This should help to identify areas that are more likely to experience climate-driven change, as well as which species or functional types are most or least susceptible to changes in climate (Dobrowski *et al.*, 2010). Such nuanced data should be more valuable to local land managers and conservationists than nebulous predictions of generalized ecosystem responses. Resampling historical field data also permits empirical assessment of temporal changes in ecological variables like phenology, species composition and distribution (Walther *et al.*, 2002; Parmesan, 2006). Recent US resampling studies assessing vegetation change over the last 25–80 years have documented marked increases in hardwood densities at a hardwood – conifer ecotone in Vermont (Beckage *et al.*, 2008); elevation increases for canopy trees in southern California (Kelly & Goulden, 2008) and shifting slope-aspect preferences for forest understorey herbs in southern Oregon (Damschen *et al.*, 2010). In all cases these trends have been at least partly ascribed to climate change.

The area occupied by subalpine and alpine vegetation in California is predicted by dynamic vegetation models to decrease substantially between now and the end of the 21st century (Lenihan *et al.*, 2008). This forecast represents the greatest areal reduction of any major vegetation type in California, and mapped projections show alpine and subalpine vegetation almost completely disappearing from the central and northern Sierra Nevada. Although the models behind these projections

incorporate mechanistic relationships between climate, fire and plant physiology, they mostly lack the capacity to predict species-specific responses. Idiosyncratic species-level responses to climate warming and interacting disturbances could compromise the accuracy of projections made at the level of physiognomic types (Peterson, 1998), especially where relatively few species dominate the type. For example, the recruitment of *Pinus albicaulis* (whitebark pine), a dominant subalpine tree throughout western North America, is heavily dependent on seed caching by Clark's nutcracker (*Nucifraga columbiana*) (Hutchins & Lanner, 1982) and the fate of whitebark pine is likely to be linked to that of the nutcracker. Also, tree species of the Sierra Nevada subalpine zone are differentially fire sensitive, and projected increases in fire activity are not likely to have a single, well-defined effect on the vegetation type as a whole. Dispersal ability also varies substantially among species, and should have a major effect on the ability of models to accurately forecast impacts of climate on vegetation (Dobrowski *et al.*, 2010).

Our objective was to determine whether demographic and compositional changes have occurred in the last 75 years in undisturbed subalpine (> 2300 m elevation) conifer stands in the Sierra Nevada, CA, USA (Fig. 1). We re-sampled historical vegetation plots from the central Sierra Nevada to compare modern stand conditions with conditions about 75 years ago (see also Vankat, 2011). The historical data were from the USDA Forest Service's Vegetation Type Mapping (VTM) Project, which sampled and mapped vegetation across California from 1929–34 (Thorne *et al.*, 2008). Other researchers have re-sampled VTM plots to compare modern and historic conditions (e.g. Minnich *et al.*, 1995), but no study to date has re-sampled VTM plots with the specific purpose of examining differences that may be attributable to climate change. Our study took advantage of the many high-elevation VTM plots, where human disturbances common at low elevations are minimal, to examine changes in structure and composition of subalpine vegetation over the past 75 years. Given the magnitude of changes in air temperatures and snowpack that have already occurred over the last 50 years (Stewart *et al.*, 2005; Barnett *et al.*, 2008; Coats, 2010), we expected to find that projected future changes in subalpine forest structure and composition were already under way. Specifically, we hypothesized that composition of subalpine forest stands should be shifting to reflect greater proportional representation of tree species centred at lower elevations, and structure should be changing to reflect increasing densities of younger trees.

METHODS

Field methods and study area

VTM crews collected tree data in 2 chain × 1 chain (809 m²; 1/5 acre) plots, by species, 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). These size classes are referred to as (smallest to largest): size class 1 (SC1), size class 2 (SC2),

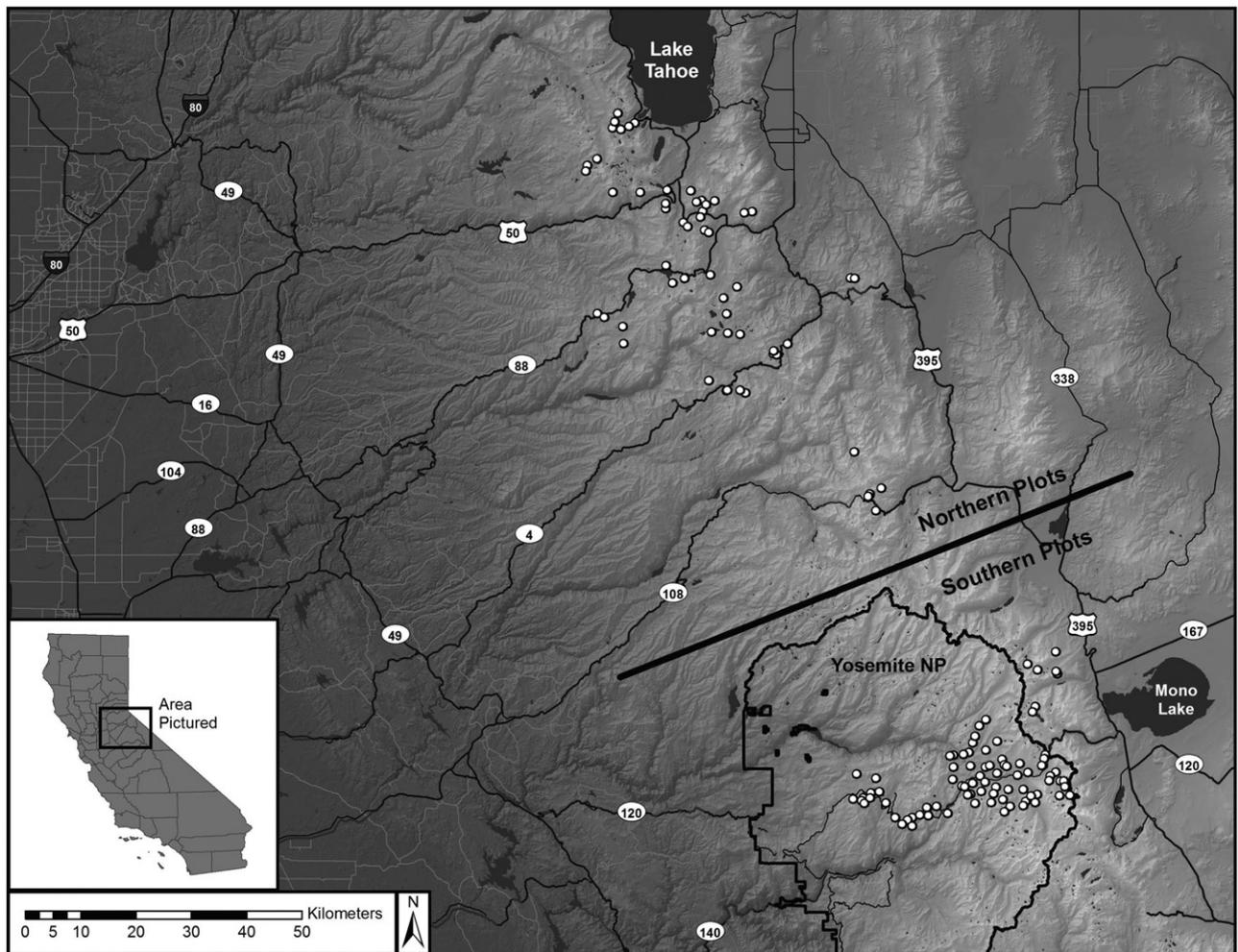


Figure 1 Map of the central Sierra Nevada, CA showing sites of the historic Vegetation Type Mapping (VTM) Project plots and re-sampled modern plots ($n = 139$; small circles). The entire study area encompasses approximately 5500 km² of subalpine forest (2300 m elevation up to the tree line). All revisited plots occur in minimally disturbed, wilderness areas within national parks and forests. Modern sampling of the sites occurred from 2007–09, approximately 75 years after original surveys. For analysis, plots were blocked by different groups: northern/southern plots (indicated by the solid black line), low/high elevation, cool/warm aspects and gentle/steep slopes.

size class 3 (SC3) and size class 4 (SC4). Data were also collected on herb and shrub cover, as well as site physical variables such as slope, aspect, elevation, soil depth and exposure. Plots were oriented perpendicular to the contour of the slope and along a cardinal direction in level areas. Plots were subjectively located, and intended to represent the vegetation of the map polygon in which they were situated. Details of the VTM sampling protocol can be found in the VTM field manual, accessible online (Wieslander *et al.*, 1933; <http://vtm.berkeley.edu/>). For concerns raised on using VTM plots as a historic reference, see Appendix S1 in Supporting Information.

VTM crews did not permanently mark their plots, making it impossible to precisely resample their plot boundaries. However, because the VTM crews placed their plots in areas of continuous, consistent vegetation cover, it is still possible to sample the stand containing each plot, effectively resampling the site. We navigated to the approximate locations of the original plots using GPS points derived from topographic maps on

which the VTM project recorded plot location. When on site, we used data recorded by the VTM crews on slope, aspect, elevation, tree species composition and forest structure to refine the final location of our modern plots.

Between 2007 and 2009, we re-sampled 139 historic VTM plots in the central Sierra Nevada, CA between Tioga Pass in Yosemite National Park (37.8° N latitude) and the Desolation Wilderness, west of Lake Tahoe (40.0° N; Fig. 1). Sampling was restricted to elevations above approximately 2300 m within undisturbed stands, to minimize the effect of exogenous factors like logging, grazing and human recreational uses. The plots occur in the subalpine zone of the Sierra Nevada, which is characterized by a short growing season (6–9 weeks) and precipitation ranging from 750–1250 mm, nearly all of which occurs in the winter. Soils are thin and derived mostly from granite (Fites-Kaufman *et al.*, 2007). The eight most common species in this zone are whitebark pine (*P. albicaulis*), lodgepole pine (*Pinus contorta* subs. *murrayana*), mountain hemlock (*Tsuga mertensiana*), western white

pine (*Pinus monticola*), red fir (*Abies magnifica*), Sierra juniper (*Juniperus occidentalis* var. *australis*), Jeffrey pine (*Pinus jeffreyi*) and white fir (*Abies concolor*). Of these, *P. albicaulis* and *T. mertensiana* have ranges restricted to the highest elevations of the subalpine zone, while *A. concolor*, *A. magnifica*, *J. occidentalis*, *P. jeffreyi* and are generally restricted to the lower subalpine and *P. contorta* can be found throughout, including at the tree line (see Appendix S2 for the typical structure of subalpine forests). *P. monticola* can be found throughout the subalpine, except at the highest elevations. For more information on the species and structure of these forests see Parker (1988), Potter (1998) and Fites-Kaufman *et al.* (2007). Sixty-four plots occur within the boundaries of Yosemite National Park and the remainder occur on US Forest Service land to the east and north: the Inyo, Stanislaus, Eldorado and Humboldt-Toiyabe National Forests (Fig. 1). Nearly all plots located on Forest Service land were in designated wilderness areas. Plots were 800 m² rectangular plots (10 m × 80 m), with the long axis oriented parallel to the hillslope. Plots were located on slopes that have a consistent slope angle along the length of the plot axis, to match the slope and aspect recorded in VTM plots. Neither VTM nor modern plots were slope-corrected. Universal Transverse Mercator (UTM) coordinates, elevation, aspect, slope and physical and environmental factors were recorded. Diameter at breast height (d.b.h.) was taken, by species, for every live or dead stem > 1 cm d.b.h.

Analyses

To evaluate changes in composition, relative basal area and relative density were determined for each species, then averaged together to get an 'importance value' for each species for all sites (Barbour *et al.*, 1999). These calculations were made for both VTM and modern data and compared.

To facilitate direct comparisons of stand structure, stem diameters (d.b.h.) from modern plots were binned into the four diameter categories (SC1 to SC4) used by the VTM program (see Table 1). Analyses were carried out on the number of stems per plot in historic versus modern plots using a generalized linear mixed-effects model (GLMM) with plot as a random factor and a Poisson distribution. Analyses were performed using the lmer procedure in R version 10.1 (R Development Core Team, 2009). Since VTM plots were slightly larger (809 vs. 800 m²), we divided the number of stems in VTM plots by 1.01125 (which is 809/800). Data for both modern and VTM plots are presented as densities in terms of stems per plot.

Three comparisons of modern versus VTM tree data were made: (1) all species combined, all sites; (2) all species combined, grouped by different site types; and (3) each species, all sites. For (1), all 139 plots were considered, with all species combined. For (2), all species were combined but plots were grouped into four pairs of different geographic and topographic variables, to examine whether trends observed for (1) varied by site type. Group pairs were the following: northern (all plots north of Yosemite region; $n = 57$) versus southern (plots in Yosemite National Park and vicinity; $n = 82$), with the centroid of each cluster separated by approximately 100 km (Fig. 1); low-

elevation plots (2293–2638 m; $n = 69$) versus high-elevation (2639–3395 m, $n = 70$), divided arbitrarily to place similar plot numbers in each category; warm plots (south-east through west aspects; $n = 61$) versus cool (north-west through east aspects; $n = 78$); and gentle slope ($\leq 30\%$ grade, including level plots; $n = 84$) versus steep slope plots ($> 30\%$ grade; $n = 53$), $> 30\%$ being a typical US federal agency definition of 'steep'. For (3), analysis of all plots by each of the eight species was made. The sample size remained the same ($n = 139$) regardless of how many plots the individual species were present in. This approach is supported by a Poisson distribution and enables the design to be balanced.

To determine how the climate of our study area has changed since the early 20th century, we downloaded publicly available data from the Tahoe City, CA (<http://www.wrcc.dri.edu/cgi-bin/cliMAIN.pl?ca8758>) and Huntington Lake, CA <http://www.wrcc.dri.edu/cgi-bin/cliMAIN.pl?ca4176> weather stations. The Tahoe City station (1899 m elevation) lies about 20 km north of the northernmost plot in our study area; the Huntington Lake station (2140 m elevation) is approximately 45 km south of our southernmost plot. These stations have the two longest weather records of all high-elevation stations in the Sierra Nevada. For each station, we calculated means in annual minimum temperature (ATmin), annual maximum temperature (ATmax) and annual precipitation (APrec), for the 30-year period from 1916 to 1945 (Time1) and the 30-year period from 1976 to 2005 (Time2). In addition, we calculated the same variables for the subalpine potential growing season of July to October for each 30-year period, resulting in growing season minimum temperature (GSTmin), growing season maximum temperature (GSTmax) and growing season precipitation (GSPrec). Change in each variable was calculated by subtracting Time1 from Time2.

Keeley (2004) noted that high spatial heterogeneity in vegetation could make plot-by-plot statistical comparisons between historical and re-sampled modern plots tenuous, where the precise location of the original samples cannot be determined. We went to great efforts to locate VTM plot locations on the ground, using mapped locations and VTM descriptions of elevation, slope, aspect, forest type and forest structure. Although it is likely that many of our plots fell outside of the exact footprint of the original VTM plot, we are confident that the great majority (if not all) of our samples were located in the same forest stand as the VTM plots. Evidence for this comes from the large snag (> 60.9 cm d.b.h.) data we collected in our plots. When large snag density is added to live large tree (> 60.9 cm d.b.h.; SC3 and SC4) density in the re-samples, the resulting value is approximately equal to large live tree density in the original VTM plots (4.47 vs. 4.86 trees/plot, modern versus VTM; means not significantly different). This not only suggests that we were sampling from the same stand (or at least a very similar stand), but that tree mortality accounts for the temporal change in large tree density between the original VTM sample and modern samples. In accordance with Keeley (2004), our study covers a large area (5500 km²), with a large number of re-sampled plots ($n = 139$) and we draw conclusions based on aggregated, not individual plots.

Table 1 Summary statistics and *P*-values (generalized linear mixed model) for all species combined and each of the eight species in the study in modern versus historic Vegetation Type Mapping (VTM) Project plots. Each analysis was carried out on all plots ($n = 139$) on stem density per plot for each of four size classes: SC1 (10.2–30.4 cm diameter); SC2 (30.5–60.9 cm); SC3 (61.0–91.3 cm); SC4 (≥ 91.4 cm). Statistically significant results appear in bold.

	SC1 10.2–30.4 cm	SC2 30.5–60.9 cm	SC3 61.0–91.3 cm	SC4 ≥ 91.4 cm
All species combined				
VTM (ave. no. of stems/plot)	12.96	8.07	3.30	1.49
Modern (ave. no. of stems/plot)	21.18	8.69	2.60	1.20
Δ Stems/plot	8.22	0.62	– 0.70	– 0.29
% Change	+ 63.3	+ 7.7	– 21.1	– 19.1
<i>P</i> -value (GLMM)	< 0.001	0.055	< 0.001	0.051
<i>Abies concolor</i>				
VTM (ave. no. of stems/plot)	0.28	0.07	0.09	0.05
Modern (ave. no. of stems/plot)	0.51	0.24	0.07	0.04
Δ Stems/plot	0.23	0.17	– 0.02	– 0.01
% Change	+ 79.5	+ 233.7	– 15.7	– 29.9
<i>P</i> -value (GLMM)	0.003	0.001	0.698	0.591
<i>Abies magnifica</i>				
VTM (ave. no. of stems/plot)	1.66	1.17	0.94	0.59
Modern (ave. no. of stems/plot)	3.16	1.41	0.75	0.51
Δ Stems/plot	1.50	0.24	– 0.19	– 0.08
% Change	+ 90.5	+ 20.1	– 20.3	– 13.4
<i>P</i> -value (GLMM)	< 0.001	0.071	0.072	0.131
<i>Pinus jeffreyi</i>				
VTM (ave. no. of stems/plot)	0.12	0.18	0.25	0.18
Modern (ave. no. of stems/plot)	0.30	0.17	0.17	0.12
Δ Stems/plot	0.18	– 0.01	– 0.08	– 0.06
% Change	+ 149.8	– 2.9	– 33.5	– 31.9
<i>P</i> -value (GLMM)	0.003	0.970	0.139	0.045
<i>Pinus monticola</i>				
VTM (ave. no. of stems/plot)	0.63	0.41	0.42	0.26
Modern (ave. no. of stems/plot)	0.74	0.35	0.21	0.24
Δ Stems/plot	0.11	– 0.06	– 0.21	– 0.02
% Change	+ 17.0	– 16.3	– 50.2	– 7.4
<i>P</i> -value (GLMM)	0.295	0.396	0.004	0.618
<i>Juniperus occidentalis</i>				
VTM (ave. no. of stems/plot)	0.40	0.28	0.15	0.13
Modern (ave. no. of stems/plot)	0.47	0.25	0.19	0.15
Δ Stems/plot	0.07	– 0.04	– 0.04	0.02
% Change	+ 17.3	– 11.8	– 27.8	+ 17.8
<i>P</i> -value (GLMM)	0.389	0.690	0.359	0.856
<i>Pinus contorta</i>				
VTM (ave. no. of stems/plot)	5.27	4.12	1.03	0.08
Modern (ave. no. of stems/plot)	8.94	3.85	0.86	0.08
Δ Stems/plot	3.67	– 0.27	– 0.17	0.00
% Change	+ 69.5	– 6.6	– 16.3	+ 2.9
<i>P</i> -value (GLMM)	< 0.001	0.289	0.161	0.983
<i>Tsuga mertensiana</i>				
VTM (ave. no. of stems/plot)	2.41	1.33	0.38	0.07
Modern (ave. no. of stems/plot)	3.48	1.49	0.37	0.05
Δ Stems/plot	1.07	0.16	– 0.01	– 0.02
% Change	+ 44.4	+ 11.9	– 4.4	– 26.3
<i>P</i> -value (GLMM)	< 0.001	0.271	0.822	0.830
<i>Pinus albicaulis</i>				
VTM (ave. no. of stems/plot)	2.19	0.51	0.04	0.00
Modern (ave. no. of stems/plot)	3.58	0.94	0.07	0.01
Δ Stems/plot	1.39	0.43	0.03	0.01
% Change	+ 63.5	+ 86.5	+ 68.5	n.a.
<i>P</i> -value (GLMM)	< 0.001	< 0.001	0.348	n.a.

GLMM, generalized linear mixed-effects model; n.a., not applicable.

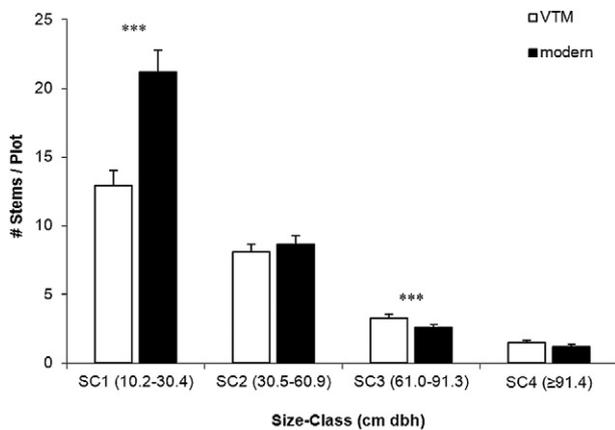


Figure 2 Comparison of historic [Vegetation Type Mapping (VTM) Project plots; clear bars] and 'Modern' plots for stem density per plot + SE for all species combined for all 139 plots, aggregated by the four diameter size-classes used by the VTM Project (SC1, 10.2–30.4 cm diameter; SC2, 30.5–60.9 cm; SC3, 61.0–91.3; SC4, ≥ 91.4 cm). Statistically significant differences are indicated by *** $P < 0.001$.

RESULTS

Contrary to our first hypothesis, stand composition has changed very little since the original VTM sampling (1929–34). Of the eight species sampled, *P. albicaulis* exhibited the greatest increase in importance (+ 1.9%), while *P. monticola* showed the greatest decrease (– 1.7%). Other species responses fell between these two extremes, but none of the shifts were statistically significant. The relative dominance by different species was unchanged. No tree species absent in the VTM plots moved up in elevation to be counted in our resample, and no tree species sampled in the VTM plots dropped out.

In agreement with our second hypothesis, the overall density of stems per plot for the smallest size class (SC1, 10.2–30.4 cm d.b.h.) was significantly higher in modern plots than historical (VTM) plots, representing a 63.3% increase over historical conditions and an average of eight more stems per plot (Fig. 2, Table 1). Density in SC2 (30.5–60.9 cm d.b.h.) was not significantly different between modern and historical samples. For the larger trees (SC3, 61.0–91.3 and SC4, ≥ 91.4 cm d.b.h.), tree densities were lower in modern plots (decreases of 21.1% and 19.1%, respectively), but only the SC3 decrease was statistically significant while SC4 was marginally significant (Fig. 2; combining SC3 and SC4 also gave a significant decrease). For all size classes combined, tree density was 30.4% higher in modern plots.

Overall, the trends described above hold for different groups of physical variables: latitude, elevation, aspect and slope (Fig. 3, Appendix S3). All eight groups had significantly higher tree densities in modern plots for SC1. Seven of eight groups also showed significantly lower densities in SC3 and four of eight exhibited significant decreases for SC4. For SC2, the northern plots showed a significant increase while the southern plots decreased significantly (Fig. 3, Appendix S3).

All eight species sampled exhibited an increase in stem density over historic levels in SC1, representing increases ranging from 16–147% over historic levels (Fig. 4, Table 1). Densities were significantly higher for six of the eight species sampled: *A. concolor*, *A. magnifica*, *P. jeffreyi*, *P. contorta*, *T. mertensiana* and *P. albicaulis*. Increased densities were statistically significant for higher-elevation species (*T. mertensiana* and *P. albicaulis*), lower-elevation species (*A. concolor* and *P. jeffreyi*) and elevation generalists (*P. contorta*). For SC2, two species, *A. concolor* and *P. albicaulis*, showed significantly higher densities in modern plots.

In general, as with the combined species analysis, both SC3 and SC4 showed decreases in stem densities in modern plots, but with fewer statistical differences. *Pinus monticola* had significantly lower densities in modern plots for SC3 and *P. jeffreyi* showed significantly lower densities for SC4 (Fig. 4, Table 1).

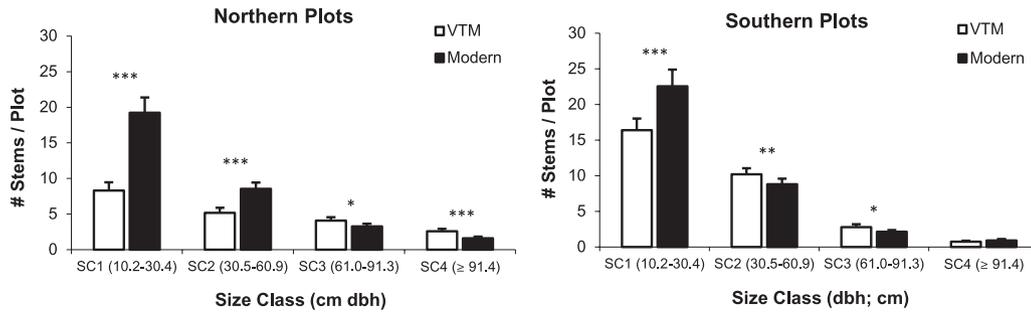
When dead and live large trees (> 60.9 cm d.b.h.) are pooled in the modern plot data, large tree densities in the modern re-samples are not significantly different from large (live) tree densities in the VTM plots (4.47 vs. 4.86 trees/plot, modern versus VTM, $t = 1.164$, $P = 0.246$). The density of large dead trees ('snags') in the modern re-samples shows a weak positive correlation with the density of very small trees (< 10 cm diameter; $r = 0.221$, $P = 0.01$).

Annual and growing season mean temperature and precipitation increased from the early to the late 20th century (Time1 to Time2; Table 2). At Tahoe City, ATmin increased by 1.27°C, ATmax increased by 0.47°C and APrec rose by 112.5 mm, an increase of 15.3%. At this station, GSTmin increased by 1.22°C, GSTmax decreased by 0.22°C and GSPrec increased by 18.03 mm (+ 27.7%). Of these, ATmin, ATmax and GSTmin were all statistically significant changes (Table 2). At the Huntington Lake station, ATmin increased by 1.49°C, ATmax increased by 0.46°C and precipitation increased by 360.9 mm, or + 47.8%. GSTmin increased by 0.42°C, GSTmax increased by 0.28 and GSPrec increased by 30.2 (+ 41.5%). The increases in ATmin and APrec were statistically significant (Table 2) at the Huntington Lake station.

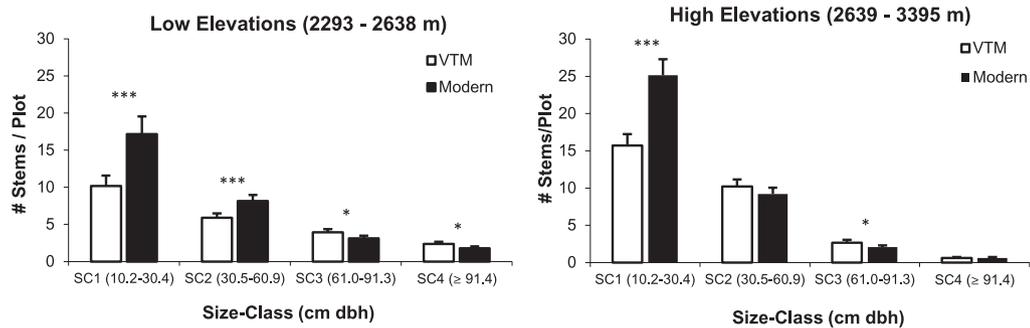
DISCUSSION

Over the last 80 years, stem density of small trees has significantly increased for most of the conifer species native to the subalpine region of the central Sierra Nevada. Density of small trees increased across the entire landscape of our study area, including both low- and high-elevation bands, warm and cool aspects, and steep and gentle slopes. Although forest stand structure has become more strongly skewed toward younger size classes during the past 75 years, the relative abundances of the different tree species have not changed appreciably and there is no evidence of lower-elevation species replacing higher-elevation species. Other sources have documented a general infilling or densification of high-elevation forests (Vankat & Major, 1978; Vale, 1987; Taylor, 1995; Gruell, 2001), but, to our knowledge, our findings represent the first resampling-based

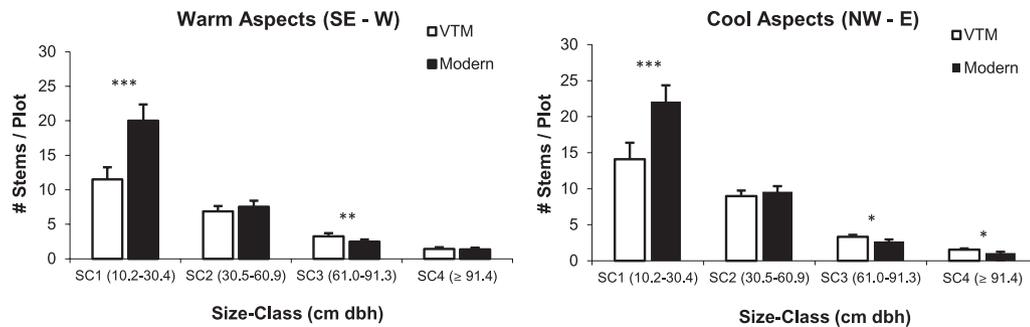
(a) North vs. South



(b) Low vs. High Elevations



(c) Warm vs. Cool Aspects



(d) Gentle vs. Steep Slopes

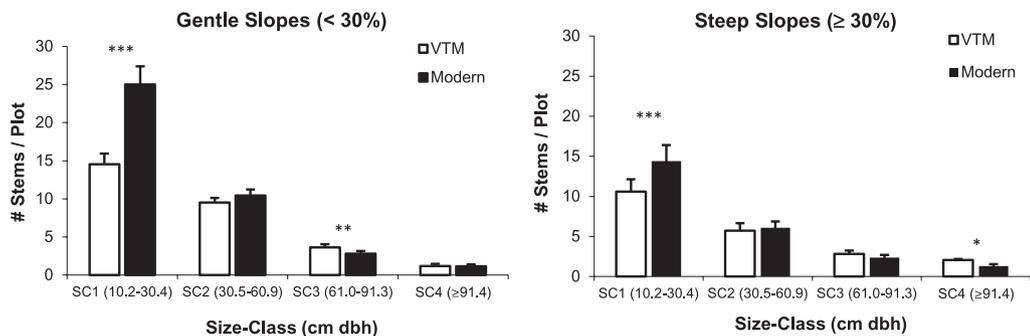


Figure 3 Comparison of historic [Vegetation Type Mapping (VTM) Project plots; clear bars] and ‘Modern’ plots for stem density per plot + SE for four different categories of site physical variables: (a) latitude, north versus south; (b) elevation, low (2293–2638 m) versus high (2639–3395 m); (c) aspect, warm (SE – W) versus cool (NW – E); and (d) slope, gentle ($\leq 30\%$) versus steep ($> 30\%$), aggregated by the four diameter size classes used by VTM crews (SC1, 10.2–30.4 cm diameter; SC2, 30.5–60.9 cm; SC3, 61.0–91.3; SC4, ≥ 91.4 cm). Statistically significant differences are indicated by * $0.01 < P < 0.05$; ** $0.001 < P \leq 0.01$; and *** $P < 0.001$.

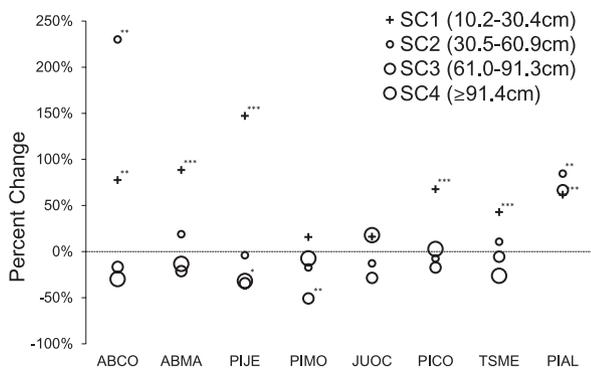


Figure 4 Percentage change of stem abundance (number of stems/plot), from historic [Vegetation Type Mapping (VTM)] plots to modern plots for each of the eight conifer species sampled: ABCO (*Abies concolor*), ABMA (*Abies magnifica*), PIJE (*Pinus jeffreyi*), PIMO (*Pinus monticola*), JUOC (*Juniperus occidentalis* var. *australis*), PICO (*Pinus contorta* subsp. *murrayana*), TSME (*Tsuga mertensiana*), and PIAL (*Pinus albicaulis*). Species are listed approximately in order of elevational distribution, from lower to higher. The four diameter size classes are indicated by numbers. Statistically significant differences (between historic and modern stem densities) are indicated by * $0.01 < P < 0.05$; ** $0.001 < P \leq 0.01$; and *** $P < 0.001$.

empirical evidence of widespread, multiple-species increases in density of young trees.

Our data confirm that densities of trees of larger size classes in Sierra Nevada subalpine forests have generally decreased. This pattern has been described for Yosemite National Park (Lutz *et al.*, 2009) and for forests throughout the west (van Mantgem *et al.*, 2009); however, our study explicitly accounts for the 'lost' trees – they represent mortality and are present in the modern plots as dead snags. The decrease in large tree density we measured was substantial across species, but only statistically significant for two of them: *P. jeffreyi* and *P. monticola*. In a study of old growth forests across the western USA, van Mantgem *et al.* (2009) found that over approximately the last two decades species of the genus *Pinus* had experienced higher mortality rates than species of any other conifer genus they measured. Similarly, in our study, *Tsuga* experienced relatively low rates of mortality. Lutz *et al.* (2009), comparing Yosemite National Park VTM plots with an independent modern inventory, found that four of six *Pinus* species had undergone significant decreases in large tree density.

Taken together, our recruitment and mortality results present a picture of how subalpine forest stand structure in the Sierra Nevada is changing. Compared to the early 1930s, subalpine conifer stands are denser overall, with many more small trees and fewer large trees, yet with little difference in relative tree species abundance. These patterns hold across almost all geographic and physiographic clines. This pattern of nearly ubiquitous change is indicative of a factor or factors that are operating with strong influence and at regional, rather than stand-level, scale.

Possible causal factors

Structural changes in low- to mid-elevation forests of the Sierra Nevada are often attributed to 20th century fire suppression (McKelvey & Busse, 1996; North *et al.*, 2009). However, higher-elevation subalpine forests (more accurately called woodland) of the Sierra Nevada are sparse and open-canopied, with shallow fuel beds and frequent rock outcrops that restrict the frequency and severity of fire (van Wagtendonk & Fites-Kaufman, 2006; Fites-Kaufman *et al.*, 2007; Appendix S2). Natural fire return intervals in Sierra Nevada subalpine forests have been estimated at hundreds of years, and landscape fire rotations at thousands to tens of thousands of years (van Wagtendonk & Fites-Kaufman, 2006). Human efforts at fire suppression within the subalpine zone (which are already relaxed due to wildland fire use policies in many wilderness areas, as well as the great distances to human population centres) have had little to no effect on forest composition or structure, as these efforts began only 75–100 years ago, a much shorter time period than the natural mean fire-free period in Sierra Nevada subalpine forests. As a result, unlike forests where human fire suppression has caused major shifts in fire regime, modern recent fires in high-elevation forests of the Sierra Nevada are burning well within the historical range of variation for fire severity (Miller & Safford, 2008).

Changing concentrations in atmospheric gases potentially affect tree growth and recruitment success, and thus stand densities. Carbon dioxide (CO_2) fertilization was originally thought to have sizeable effects on the growth of subalpine conifers (Lamarche *et al.*, 1984) but the equivocal results of studies researching the effects of CO_2 on high-elevation tree growth (Graumlich, 1991; Tang *et al.*, 1999) make it unlikely to account for the widespread shifts reported here. Nitrogen (N) deposition is also a potential factor, but high site to site variability of N pollution based on proximity to downslope fertilization sources (Fenn *et al.*, 2003) makes it unlikely to be responsible for the widespread consistent trends reported here. Also, as with CO_2 , it has so far been difficult to demonstrate an effect of N deposition on growth in the field (Saurer *et al.*, 2004).

Historically, the most prevalent anthropogenic disturbance in the high Sierra Nevada was grazing, in particular by sheep in mountain meadows (Kinney, 1996; Menke *et al.*, 1996). Sheep grazing was halted around 1900 in National Parks and slowly abated on Forest Service land throughout the 20th century (Menke *et al.*, 1996). Our study did not include plots from meadows, but rather from sparsely vegetated and rocky sites with little to no cover of palatable forage. Historic grazing and/or subsequent recovery are unlikely to be major drivers of trends in tree structure from upland locations such as in our study.

Climate change

Climate data indicate that our study area has warmed and experienced slightly increased precipitation since the first half of the 20th century. As with many other parts of the globe, the night-

Table 2 Change in climate from 1916–45 (Time1) to 1976–2005 (Time2) for two long-term climate stations at the north and south ends of the study area.

Climate station	ATmin (°C)	ATmax (°C)	APrec (mm)	GSTmin (°C)	GSTmax (°C)	GSPrec (mm)
Tahoe City, CA	+1.27***	+0.47*	+112.33	+1.22***	−0.22	+18.03
Huntington Lake, CA	+1.49***	+0.46	+360.93***	+0.42	+0.28	+30.17

The Tahoe City station (north) is located at 39°10.0′ N, 120°9.0′ W; 1899 m elevation. The Huntington Lake station (south) is located at 37°13.76′ N, 119°14.63′ W; 2140 m elevation. Data presented are the differences (Time2 – Time1) and represent means during their respective periods for annual minimum temperature (ATmin), annual maximum temperature (ATmax), annual precipitation (APrec), growing season minimum temperature (GSTmin), growing season maximum temperature (GSTmax) and growing season precipitation (GSPrec). Growing season is July to October. Statistical differences were tested using a *t*-test; significant results are indicated by *0.01 < *P* < 0.05; ****P* < 0.001.

time lows (daily minima) in our study area have risen more than the daytime highs, with both annual and growing season minima considerably higher in Time2 (1976–2005) than Time1 (1916–45; Table 2). Precipitation is also higher in Time2 at both stations, especially at Huntington Lake, where both annual and growing season precipitation have increased by more than 40%. These trends are corroborated by aggregated climate data from the entire Sierra Nevada region (see Appendices S4 & S5). Measurement of snow (e.g. snow depth, snow water equivalent, snowfall) is prone to high variability and does not have as complete a record as temperature and precipitation. However, sources indicate that in western North America snowpack is declining (Mote *et al.*, 2005), the proportion of rain to snow is increasing (Knowles *et al.*, 2006) and snowpack is melting sooner (Stewart *et al.*, 2005). For the Lake Tahoe Basin, the percentage of precipitation falling as snow decreased from > 50% in 1910 to c. 35% in 2010 (Coats, 2010). From 1960 to 2010, the date of snowmelt in the Tahoe Basin moved earlier in the season by 0.4 days/year, resulting in an average snow-free date about 2 weeks earlier now than it was 50 years ago (Coats, 2010).

Changes in climate should be expected to have strong effects on high-elevation ecosystems, where abiotic factors (as opposed to biotic factors such as competition) more directly shape plant distribution and vegetation structure (Grime, 2001). In addition, climate change should be expected to affect vegetation of a region such as our study area more evenly than other exogenous factors. Temperature and precipitation are known to have both direct and indirect effects on the structure and distribution of subalpine conifers. In California's Mediterranean climate, the principal limiting factors for tree establishment are deep snow cover in the spring and low soil moisture in the summer (Peterson, 1998), both of which are controlled by a temperature – precipitation interaction. Temperature has a direct positive impact on growth by increasing nutrient uptake and photosynthesis but can negatively affect growth indirectly by driving up evapotranspiration, resulting in more limited available moisture (Korner, 2003). Precipitation can positively affect growth directly by improving moisture availability, especially during the growing season, but it can also limit growth and recruitment of smaller trees via deep, long-lasting snow (Lloyd & Graumlich, 1997). Numerous subalpine tree species demonstrate tempera-

ture limitations at their high-elevation range limit and moisture limitations at their low-elevation limit (e.g. Lamarche, 1974; Peterson, 1998; Salzer *et al.*, 2009). Historically, the length of the growing season in the subalpine zone of the Sierra Nevada was 6–9 weeks, with almost all precipitation occurring during the winter (Fites-Kaufman *et al.*, 2007). However, increased temperatures and steady to increased annual and growing-season precipitation have lengthened the growing season and probably ameliorated conditions during the dry season. Such improvement in growing conditions seems a likely explanation for the generalized increase in abundance of small trees that we observed.

Decreased density of large trees in Sierra Nevada subalpine forests over the last 75 years is also consistent with observed climate change. It has been shown that higher temperatures shorten the time to drought-induced mortality of trees (Adams *et al.*, 2009), and warming temperatures can increase the susceptibility of trees to pathogen and insect attack (Allen *et al.*, 2010). Increasing rates of tree mortality have been attributed to warming – drought interactions for conifer forests in Yosemite National Park (Guarin & Taylor, 2005) and for multiple sites in old-growth forest throughout the western USA, including high-elevation (> 2000 m) stands (van Mantgem & Stephenson, 2007; van Mantgem *et al.*, 2009). van Mantgem *et al.* (2009) found increased mortality rates for both young and old trees, and Smith *et al.* (2005) similarly found high mortality across tree size classes. Our study also found decreasing densities of large trees over time, but small tree densities in our system are increasing, and our seedling and sapling data (not analysed here) show that tree recruitment is currently outpacing mortality. It seems probable that these opposing trends are interrelated. Studies done in lower-elevation forests in the Sierra Nevada have found a strong correlation between small tree density and large tree mortality (Guarin & Taylor, 2005). Our study was done at higher elevations in relatively open stands where competition for resources is presumably less intense. We did find that small tree density was negatively correlated with large snag density, but the relationship was weak. Whatever the case, whether large tree mortality in the subalpine zone is driven primarily by density-independent or density-dependent factors, it seems unavoidable that climate change will play an increasingly fundamental role.

Implications for the future

Current climate warming trends are thought to pose a significant threat to high-elevation vegetation (Lenihan *et al.*, 2008). However, our data show that warming over the last 75 years has not caused appreciable change in tree species composition in the subalpine forests of the Sierra Nevada. Instead, warming, coupled with steady or increasing precipitation, has enhanced survival and/or recruitment of younger trees of all species. Overall, species appear to be recruiting in proportions more or less commensurate with their canopy abundances. Although young tree densities are increasing for species whose elevational range is mostly below the subalpine zone (e.g. *A. concolor*, *P. jeffreyi*), higher-elevation species are keeping pace.

Is it possible to reconcile our observations with the prediction that subalpine forests will shrink substantially in extent over the next century? We may be witnessing a lag effect, where lower-elevation species may eventually move upslope and displace higher-elevation species, but this process may take many decades to centuries to play out. Currently, mortality rates in older trees (as estimated by temporal changes in density) in the subalpine forests we sampled are not higher for high-elevation versus low-elevation species, so this sort of process is not yet evident.

Subalpine conifer species are mostly long-lived stress-tolerators, and mature individuals may be able to endure significant environmental change. Such forest ecosystems may require large-scale disturbance (i.e. the death/removal of tree biomass) to provoke major changes in canopy dominance. Fires are currently infrequent in the Sierra Nevada subalpine zone, but linked climate – vegetation models predict increases in fire frequency and intensity as temperatures continue to warm (Lenihan *et al.*, 2008). Most high-elevation conifers are poorly adapted to fire, and changing fire regimes may benefit fire-adapted lower-elevation species like *P. jeffreyi*.

Other disturbance factors like insect outbreaks and disease could also have important influences on the future composition and geographic extent of subalpine forests. Warming temperatures and increasing drought stress have been implicated in massive outbreaks of pine beetles (*Dendroctonus* spp.) across western North America, with high rates of mortality recorded for *P. contorta* and *P. albicaulis* (Kurz *et al.*, 2008; Logan *et al.*, 2010). Both of these species occur in Sierra Nevada subalpine forests, but pine beetle mortality is not yet a major ecological factor in our study system. Likewise, white pine blister rust (*Cronartium ribicola*) has significantly increased mortality of *P. albicaulis* at many locations throughout the western US mountains (Tomback & Achuff, 2010). This pathogen is present in our study area and infected individuals of both *P. albicaulis* and *P. monticola* have been confirmed; however, to date, impacts in the Sierra Nevada remain minimal (Maloney, 2011). Spread of the disease may be at least partly limited by the cold and dry climate of this region (Maloney, 2011) but increasing growing seasons could facilitate spread. Increased prevalence of either *Dendroctonus* or *Cronartium* could eventually tip the scales in favour of widespread vegetation shifts.

We should expect similar mechanisms of response to climate change in other mediterranean and semi-arid mountain ranges world-wide, where growing season has historically been severely moisture-limited. In these environments, future trends in forest structure and distribution are likely to depend heavily on the degree to which precipitation changes. If precipitation increases, at least during the growing season, rising temperatures should increase tree growth rates, recruitment and/or survival of younger trees. However, rising temperatures coupled with unchanged or decreased precipitation could lead to widespread mortality (Millar *et al.*, 2007a) and might be expected to differentially affect species (Lutz *et al.*, 2010). The effects of ecological disturbances linked directly or indirectly to these climatological factors may be the ultimate arbiters of the outcome of climate change in the subalpine zone.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site.

Appendix S1 Using vegetation type mapping data as a historic reference.

Appendix S2 Figure showing photographs of four typical sub-alpine stands in the Sierra Nevada.

Appendix S3 Generalized linear mixed model results for the difference in stem abundance for all species combined by four

size classes for modern versus historic plots for four different pairs of site types.

Appendix S4 Temperature trends for the Sierra Nevada region from 1895–2010.

Appendix S5 Precipitation trend for the Sierra Nevada region from 1895–2010.

BIOSKETCHES

Chris Dolanc is a PhD candidate at the University of California, Davis. His research interests are in forest ecology, particularly stand dynamics and factors affecting distribution.

James Thorne is a landscape ecologist with a focus on integrating historic trends with projected futures to inform sustainable resource management.

Hugh Safford works in science application to resource management, principally in the fields of disturbance ecology, forest ecology and climate change.

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