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Upward shifts in recruitment of high-elevation tree species in the northern Sierra Nevada, California

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We compared presence or absence of tree species recruitment in 381 recent random plots in the northern Sierra Nevada of California with 2160 Vegetation Type Map project plots of the 1930s. Of 12 tree species with adequate sample sizes for analysis, we found a significant upward elevation shift in recruitment in three species over this 80-year interval: red fir, western white pine, and mountain hemlock. A marginally significant upward shift was seen in lodgepole pine. All four species are higher elevation conifers in our study area. A few significant latitudinal shifts were also observed, but in a direction counter to the expectation of poleward shift. We believe this reversal is because more northerly latitudes in our study area have lower maximum elevations, whereas the more southerly latitudes have high mountains. One especially high-elevation species, mountain hemlock, became rare to lacking in the northern parts of our region, where the elevations at which it was formerly found may no longer be cool enough for the species. Because our measure of recruitment integrates over multiple years of seed germination and seedling and sapling survival, we believe these changes in small trees may reflect ongoing climatic changes in the Sierra Nevada, foreshadowing changes in plant communities and wildlife habitats.

Key words: Elevation shift, trees, conifers, latitude, climate change, *Abies magnifica*, *Pinus monticola*, *Tsuga mertensiana*, *Pinus contorta*, VTM

The Vegetation Type Map project of the 1920s and 1930s (VTM), headed by Albert Wieslander for the U.S. Forest Service, produced a vast store of data from tens of thousands of forest plots, representing a unique resource for judicious comparisons with past conditions (Wieslander 1935; Thorne et al. 2008; Dolanc et al. 2012, 2014a,b). A far-seeing effort by the Universities of California, Berkeley and Davis, has made the historical data readily available in digital and geospatial forms (Kelly et al. 2005, 2008; http://vtm.berkeley.edu).

When we began a long-term montane biodiversity monitoring project in 2009, we therefore planned our sampling to allow direct comparison with VTM data, such as by replicating VTM plot sizes and tree measurement categories. Our Ecoregional Biodiversity

Monitoring project (EBM, formerly Sierra Monitoring Project), now in its eighth year in the California Department of Fish and Wildlife (Department) North Central Region (NCR), uses a stratified random design to produce a scientifically valid sample of the Sierra Nevada landscape. The intent of our project is to establish a baseline and to test for trends in species, communities or habitats, and to relate those trends to environmental variables such as land use and climate change. The project was begun in the Department's Northern Region in 2002 (Furnas and Callas 2015) and later extended to the NCR, where we initiated the effort to compare with VTM data. Because the VTM project established certain vegetation baseline data in the 1930s, we have a unique opportunity to test for changes over an 80 year time interval, even while it is still too early for the EBM project to detect most gradual trends.

There is overwhelming evidence that average temperature has increased and is increasing globally (Rajaratnam et al. 2015), but to what extent has climate changed within our study area? Cordero et al. (2011) found that, statewide, California mean minimum (Tmin) and maximum (Tmax) temperatures have increased significantly since 1918; and at an increased rate since 1970. This was true in their Sierra Region (encompassing our EBM study area) especially for Tmin; changes in Tmax were not significant. In the Sierra Nevada, the change in Tmin was about + 0.6 deg C per 100 yrs, and was greatest in summer Tmin (June-July-August: +1.3 deg C per 100 yrs). East slope ("Northeast") increases were more pronounced (n=3 stations). Cordero et al. (2011) found long-term temperature changes in California consistent with greenhouse gas forcing. Declining snowpack in the northern Sierra Nevada including our EBM study area was described by Mote et al. (2005). These results are generally echoed by recent National Forest Service analyses for National Forests within our study area (Merriam et al. 2013, Meyer et al. 2013, Mallek et al. 2014), which also report declines in numbers of months with average Tmin below freezing.

Here we examine the question of whether comparing current with historical tree data shows any elevational changes in species distributions, as have been predicted and increasingly found to occur due to climate change (Beckage et al. 2008, Kelly and Goulden 2008, Kullman 2002, Lenoir et al. 2008). In order to test this question, we elected to examine a measure of recruitment of young trees into the forest, hypothesizing that this would be the first and most sensitive index of change for tree species (Kullman 2002). If climate change is causing habitable zones for montane tree species to move upward in elevation as has been predicted, we would expect upward shifts in recruitment over the 80-year interval between VTM and our study.

Methods

Study region.—We focused on a nine-county area of the northern Sierra Nevada range, from Alpine and Calaveras County on the south to Butte and Plumas County in the north (Figure 1), and within the Sierra Nevada Ecoregion (USDA, http://www.fs.usda.gov/detail/r5/landmanagement/gis/?cid=STELPRDB5327836). Habitats above 914 m elevation (3000 feet) were considered.

VTM data.—We downloaded data from the VTM Project website (http://vtm.berkeley.edu/) and extracted plots that fell within our study region. VTM plot data in our region were mainly collected from 1934-1935. We accepted VTM plots without a digitally mapped latitude and longitude if the original datasheet cited an elevation and a township/range/section with a centroid within our study area (532 plots). We did not analyze treeless

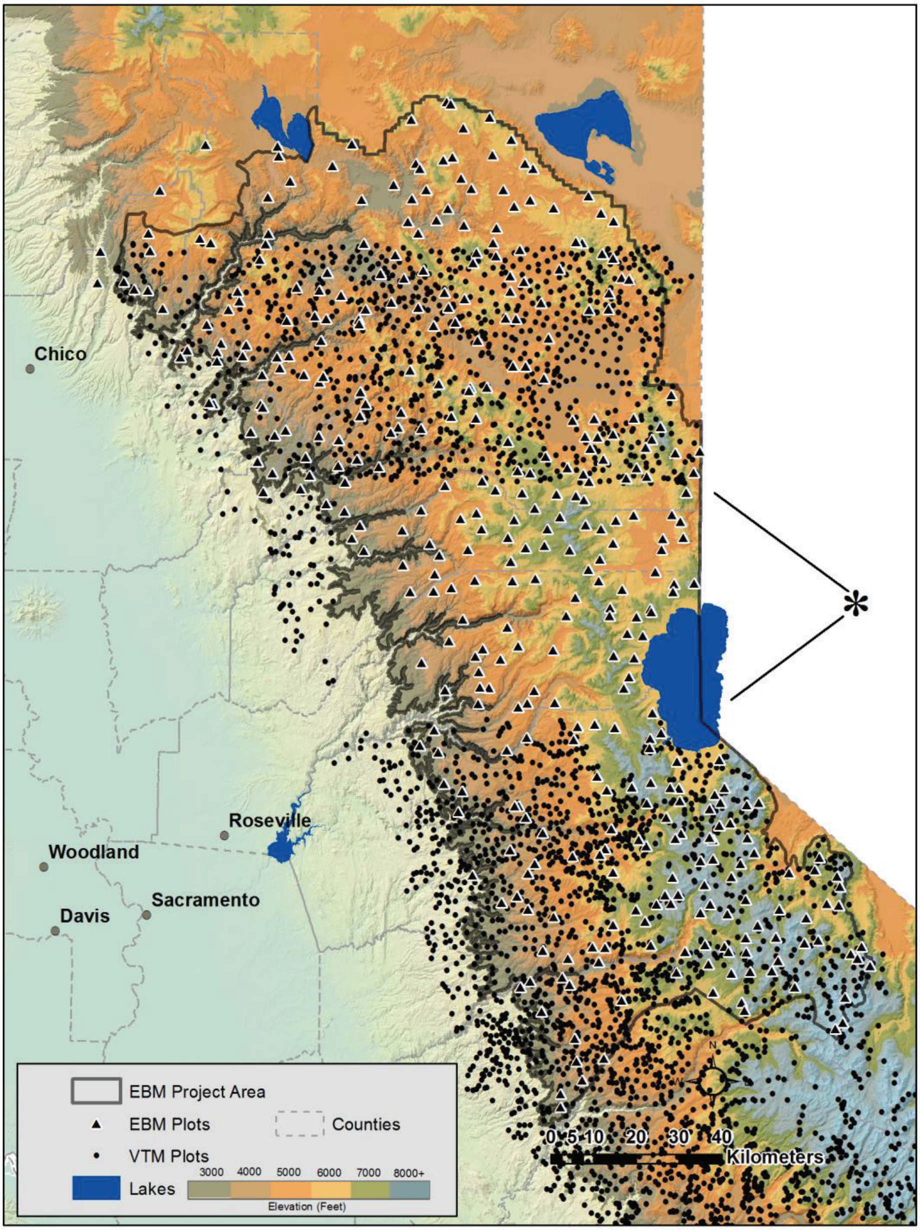

Figure 1 — Study area: the northern Sierra Nevada ecoregion, California, USA, above 914 m elevation (3000 feet). Lake Tahoe is at right-center. Black triangles show EBM sample points; small black dots show VTM plots. *The asterisk denotes an area where VTM data were available but not precisely mapped. We were able to incorporate 532 VTM plots from this area because it included elevations and township-range-section data from which we could accurately estimate latitude. A true gap in VTM data was present in the northernmost extent of the study area, from which VTM data have not been found. Elevation strata for EBM sampling are shown in color bands.

plots out of concern that the VTM project's commercial timber bent might have biased sampling of such plots. See Appendix I for additional discussion of error-checking and processing of VTM data.

EBM sampling.—Plots for sampling for our EBM project were randomly generated in a geographic information system (GIS), in equal numbers within 6 elevation strata across the study region (914-1218 m, 1219-1523 m, 1524-1828 m, 1829-2133 m, 2134-2438 m, and above 2438 m) (3000-3999, 4000-4999, 5000-5999, 6000-6999, 7000-7999, and 8000+ feet). Plots were constrained to be 1) terrestrial, i.e., not in water, 2) non-urban, 3) more than 100 m from a road, and 4) not within an area of less than 10 hectares "islanded" by surrounding roads. We also rejected potential plots with slopes steeper than 35 degrees or requiring more than five hours hiking time to complete. Subsequent random plots were rejected if they fell within a Forest Inventory and Analysis (FIA) (Bechtold and Patterson 2005) 5.26-km hexagon containing a previously selected plot, or within 400 m of a previous plot in a different hexagon: this resulted in some spatial dispersion of plots (Figure 1).

The present analysis includes EBM plots sampled during 2009-2015. The majority of land ownership in our study region is public – mainly US Forest Service – and ultimately the great majority of our plots were on public lands. In practice, we found it necessary to eliminate or randomly relocate a handful of plots that were too close to residences or other development, or inaccessible due to private property restrictions. Field protocols included a procedure for offsetting such plots in a manner that would result in an unbiased plot location.

At each random plot location, we recorded all trees to species and in size categories within a 0.0809 ha plot (circular in EBM, equal in area to 0.2-acre rectangular plots in VTM). Our EBM plot locations broadly sampled the region from which we selected VTM plot data (Figure 1). For comparison with the VTM plots, we omitted 14 treeless EBM plots with no burn history within 35 years of the time of sampling from analysis. Data from our EBM sampling are freely available on the CDFW website, "BIOS" geographic database (http://www.dfg.ca.gov/biogeodata/bios/).

Data analysis.— To assess recruitment of trees, we used the10-30 cm, "extra-small" size category (4-11-inch in VTM, diameter at breast height [dbh]) as an index of recruitment into the plot over the recent past. In some instances a tree less than 30.5 cm dbh in the Sierra Nevada may be more than 75 years old (FEIS 2013, USDA-FS 1990), but in most cases an extra-small tree in the present was recruited to that size category sometime after the period of VTM sampling. On the other hand, a tree of this size can be a few decades old, so our use of extra-small trees as an index of recruitment integrates conditions affecting seed germination and survival and growth of seedlings and saplings over multiple seasons.

For valid comparison with the VTM data, we sought a recruitment variable that would be insensitive to possible biases. For example, we might suspect that VTM field workers tended to select plots "representative" of vegetation types, or tended (perhaps unconsciously) to select more open or more mature plots. We elected to use simple presence of at least one "extra-small" (10-30 cm) stem of a species as our response variable, reasoning that the presence or absence of one small tree would be unlikely to have influenced VTM workers in selecting or avoiding a plot. This rudimentary variable will still be sensitive to distributional shifts over time, especially into areas where the species was not recruiting previously or loss of recruitment from areas where it formerly occurred.

For each tree species, we compared the project means (VTM vs. EBM) of elevation of plots where extra-small stems were present, testing for statistical significance by t-test. Tests for latitude shifts were conducted similarly. We used Welch's t-test for comparison of samples with unequal variances for all comparisons because unequal variances were evident in some tests (Levene 1960, Zimmerman 2004). Since our working hypothesis was that tree species distributions might be shifting upward, we applied a one-tailed significance test. We also tested for latitudinal shifts, but since changes in climate across latitude may be more complex (such as possible spatially varying precipitation changes: Merriam et al. 2013, Mallek et al. 2014), we applied a two-tailed test.

Results

Elevation shift.—We were able to compare data on 381 recent EBM plots with 2160 historical VTM plots. Both EBM and VTM sampled broadly across forested elevations (Figure 1). Plots in the recent EBM study averaged slightly higher in elevation than VTM plots (+28 m), due to more equal stratification across elevation zones (Figure 2a), but this difference was not statistically significant (t = 1.01, 2-tailed, P > 0.30). Note that more plots were sampled than contained recruitment of any individual tree species, therefore slightly differing total plot distribution across elevations between EBM and VTM time periods is

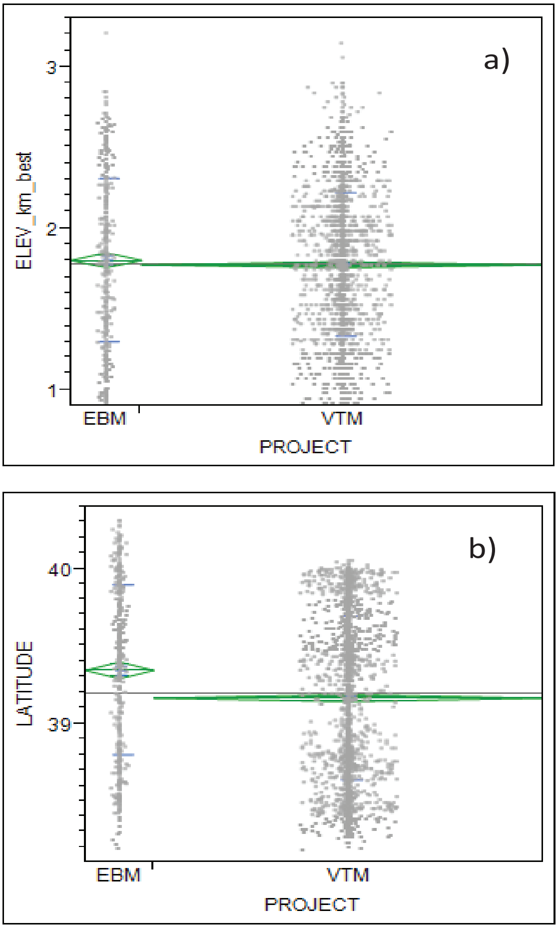

Figure 2 — a) Elevation distribution of plots sampled, VTM and EBM (elevation in km; "best" means datasheet-reported elevations were used for VTM and 10-m digital GIS elevations for EBM; gray points represent plot elevations jittered around the vertical project line; green diamonds center on the mean, extend to the upper and lower confidence limits of the mean, and have width proportional to sample size). EBM plots averaged 28 m higher than VTM; this difference was not significant (P > 0 .30). Both projects broadly sampled across northern Sierra Nevada elevations; b) Latitudinal distribution of plots sampled, VTM and EBM (latitude in degrees north; symbols as above). VTM data from north of 40° remain missing within our study area (Kelly et al. 2005); EBM samples ranged significantly further north (P < 0.0001).

unlikely to constrain the average elevation of plots with recruitment, discussed below.

Three of 12 tree species with adequate sample sizes for analysis showed significant upward shifts in elevation of recruitment between the 1930s and recent sampling: red fir (*Abies magnifica*), western white pine (*Pinus monticola*), and mountain hemlock (*Tsuga mertensiana*) ($t = 4.49, 2.78, 3.68$, respectively, all $P < 0.005$ one-tailed; Figure 3). The average elevation of plots with mountain hemlock recruitment shifted upward by 119 m, red fir by 147 m, and western white pine by 112 m. In addition, a fourth species, lodgepole pine, showed a suggestive upward trend ($t = 1.45$, $P = 0.075$ one-tailed; Figure 3d), with an average upward shift in recruitment of 75 m. These four coniferous species are the highest-elevation common species in our study (EBM median elevations of occurrence, all stem sizes included: red fir 2310 m, western white pine 2450 m, mountain hemlock 2600 m, lodgepole pine 2390 m).

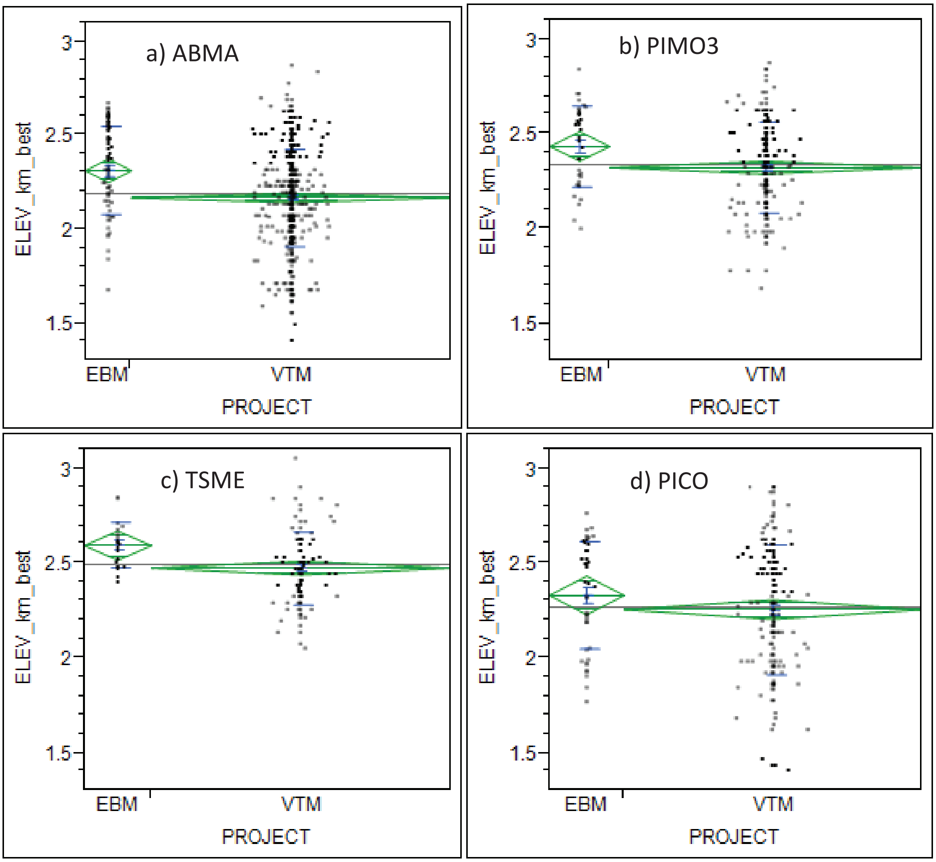

Figure 3—Elevation distribution of historical (VTM) and recent (EBM) plots containing recruitment of four high-elevation conifers: a) red fir (*Abies magnifica*), b) western white pine (*Pinus monticola*), c) mountain hemlock (*Tsuga mertensiana*), and, d) lodgepole pine (*Pinus contorta*). Points represent individual plots; green diamonds center on the mean and extend to its 95% confidence limits. Differences between EBM and VTM are significant for red fir ($P < 0.0001$), western white pine ($P = 0.0038$), and mountain hemlock ($P = 0.0003$); and are marginally significant for lodgepole pine ($P = 0.0755$) (Welch's t-test, all one-tailed).

For these four high-elevation conifers with significant or suggestive upward shifts in recruitment, evidence was primarily for a loss at lower elevations and upward redistribution of recruitment in middle elevations, with lesser or no expansion of recruitment at higher elevations (Table 1; Figure 3). Minimum and maximum elevations are suggestive of the same trends (Figure 3), although minima and maxima are subject to more sampling variation and are affected by sample size, which was smaller for EBM than VTM.

Table 1.—Historic versus recent elevations at lower and upper percentiles of elevation distribution of recruitment, for four high-elevation conifer species in the northern Sierra Nevada, California, USA. Entries show VTM / EBM elevations and the change, in meters (e.g., the lower 10th percentile elevation of red fir recruitment plots in VTM was 1829 m / in EBM was 1980 m, a change of +151 m). All four species lost more distribution at lower elevations than they gained at the highest elevations.

	Percentile			
Species	10%	25%	75%	90%
Red fir	1829/1980 +151	2012/2145 +133	2332/2529 +197	2499/2601 +102
Western white pine	1990/2136 +146	2134/2244 +110	2499/2602 +103	2621/2684 +63
Mountain hemlock	2225/2436 +211	2316/2477 +161	2598/2675 +77	2743/2798 +55
Lodgepole pine	1835/1929 +94	1981/2045 +64	2530/2577 +47	2682/2638 -44

The remaining eight species did not show significant upward change in elevation of recruitment between time periods (white fir–*Abies concolor*; incense cedar–*Calocedrus decurrens*; sugar pine–*Pinus lambertiana*; Jeffrey pine–*P. jeffreyi*; Ponderosa pine–*P. ponderosa*; Douglas fir–*Pseudotsuga menziesii*; canyon live oak–*Quercus chrysolepis*, black oak–*Q. kelloggii*). Power to detect change may have been less for these species other than white fir because the lower portion of their elevation ranges was not sampled by this study–they extend below the 914 m elevation sampling boundary. As was seen for the four highest-elevation conifer species, the lower elevation range margin may be important in reflecting elevation shifts.

Latitude shift.—VTM data from the northern portion of our study area have never been found (Kelly et al. 2005, Dolanc et al. 2014), whereas EBM did sample at latitudes north of 40° (Figure 2b). Omitting EBM samples north of 40° latitude from analysis, EBM samples averaged 0.07° (6.7 km) poleward of the VTM mean latitude, a small but significant difference ($t = 2.36$, $P < 0.02$ two-tailed). If anything, this might be expected to predispose results toward finding recent northward shifts of species. Working with the same subset of the data (truncated to ≤40°; $n = 333$ EBM, 2160 VTM), we found a variety of patterns including both northward and southward shifts. These results will be addressed in more detail separately; but notably, the same three species with significant upward elevation shifts also showed significant *southward* shifts in latitude (mean latitude difference EBM-VTM: red fir, -0.14°, $t = 2.34$, $P = 0.022$; western white pine, -0.15°, $t= 2.14$, $P = 0.037$; mountain hemlock, -0.22°, t = 3.01, P = 0.004, all tests two-tailed).

We believe these southerly recruitment shifts by species which have also displayed upward elevation shifts result from the fact that more northerly latitudes have lower maximum elevations and thus warmer temperatures than the southern portions of our study area (Figure 1). Consequently, if recruitment of these species is tracking changing temperatures to higher, cooler elevations, areas where recruitment may be found are more rapidly lost in the northern portions of our study area than in the south.

For example, a substantial zone of distribution of mountain hemlock below 2380 m was completely absent during the EBM sample period (Figure 3c), which was also expressed as a significant loss of latitudinal distribution (Figure 4). A remaining outpost of mountain hemlock recruitment at approximately 39.4° (Figure 4) corresponds to higher-elevation areas of Nevada County. North of Nevada County, elevations in excess of 2400 m (7880 ft) are rare, relatively low (none over 2700 m), and small in areal extent. Consequently, cool, high elevation refugia for species like the mountain hemlock are limited in number and extent within our study region north of Nevada County.

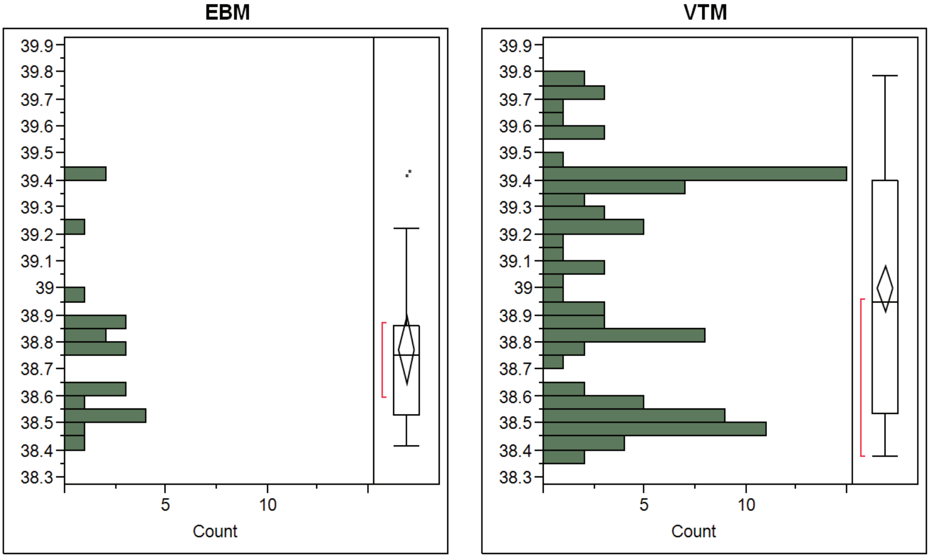

Figure 4 — Latitude in degrees north versus number of plots containing one or more “extra-small” (10-30-cm dbh) mountain hemlock stem (*Tsuga mertensiana*): EBM, n = 22; VTM, n = 100. There has been a noticeable reduction of distribution of the species northward of 39° latitude in our study area.

Discussion

Northern Sierra Nevada tree species that shifted upward in this study were all higher elevation species – they are the four highest-occurring species that we recorded with any frequency. Whitebark pine (*Pinus albicaulis*) does occur at even higher median elevation but was not well enough represented in the data to analyze. All four species that shifted in our analysis also prefer cool microhabitats within our region, as indicated by their preference for more northeasterly as opposed to southerly slope aspects (this study: unpublished data). All are conifers, as are all more common tree species in the Sierra Nevada above 2000 m.

This report of upward shift of higher-elevation tree recruitment across a large region is one of relatively few studies to date documenting such shifts by tree species across large spatial scales. Lenoir et al. (2008) reported 41 significant upward shifts among 171 forest plant species from six mountain ranges in western Europe. Woody species were less likely to show a significant shift, but one coniferous (*Abies alba*) and six deciduous tree species were identified as shifting up; one deciduous tree species shifted down (*Quercus pubescens*) (Lenoir et al. 2008 including supplemental online materials). The longer life-spans and survival capacity of woody plants and particularly trees seem likely to make detection of overall-population changes more difficult. Recruitment or mortality may respond more quickly to environmental changes. Examining establishment in former snowfields, invasion of meadows, branch growth, and upright stem development in high-elevation Sierra Nevada conifers, including western white pine and lodgepole pine, Millar et al. (2004) found these ecological responses were broadly correlated with increases in minimum temperature. Van Mantgem, Lutz, Stephenson and others (van Mantgem et al. 2009, Lutz et al. 2009) have reported large-scale observations of increased tree mortality rates, apparently in response to rising temperatures and increasing water deficits. Lutz et al. (2009) and McIntyre et al. (2015) found declines in large-diameter trees since the VTM surveys, correlated with changes in water availability due to warming climate. For *Pinus jeffreyi*, *P. lambertiana*, and *P. ponderosa*, the decline of large trees was greatest in lower elevation habitats of their ranges within Yosemite National Park (centered 50 km south of our study region; Lutz et al. 2009). Thorne et al. (2008) and McIntyre et al. (2015) found large-scale shifts in vegetation types including tree dominance in the Sierra Nevada since the VTM project. They concluded that some conifers were losing low and mid-elevation distribution or abundance and being replaced by oaks.

Several studies of smaller areas have shown trees' upward shifts or other plant species trends consistent with warming climate. Kullman (2002) found a shift in recruitment across elevation and +120 to +375 m increases over a 50-year interval in the upslope range margins of five tree taxa in southern Sweden. Along an elevation transect established in 1964 in the northeastern USA (Green Mountains, Vermont), Beckage et al. (2008), reported upward elevation changes of several conifer and hardwood tree species. Kelly and Goulden (2008) revisited precise sites in Deep Canyon, Santa Rosa Mountains, California, USA and found upward shifts of white fir (*Abies concolor*) and other species over a 30-year interval. Species and community shift over a 57-year interval since Whittaker's (1960) classic study, toward plants more typical of warmer, drier conditions, was described by Damschen et al. (2010). Lutz et al. (2010) modeled past, present, and future climatic water deficit and judged western white pine (*P. monticola*) and mountain hemlock (*T. mertensiana*) – two of the species showing significant upward shift in recruitment in our study – most likely to be affected by climate change in Yosemite National Park, just south of our study region.

Despite multiple examples and rich results in the literature from such studies, trends over time are minimally resolved by examining only a single, albeit 80-year, interval; yet those are the data available to us. In the future, we anticipate expanding this study in multiple ways, not the least of which is continued EBM sampling to detect trends within the continuously sampled EBM record, now approaching its 8th year of sampling in NCR and a 15-year continuous record in CDFW Northern Region (Furnas and Callas 2015).

While VTM data were collected for the specific purpose of supporting a vegetation mapping effort and were not a rigorously randomized sample of forest conditions of the time, like many researchers before us we have found the scope, intensity and consistency of the VTM sampling presents opportunities for careful comparisons with current datasets. We believe concerns about the potential for sampling bias in the VTM data must be addressed (Keeley 2004, Bouldin 2009); therefore we chose a conservative metric – presence of at least one “extra-small” size tree – as our test measure for changes in recruitment. Another reason we believe our analysis is robust to possible bias in VTM sampling is that the test of interest is not of the main effect of the project period (mean VTM recruitment presence vs. mean EBM recruitment presence) but of the interaction between project period and elevation: namely, difference in the elevation distribution of recruitment between VTM and EBM samples. We might well suspect that VTM crews consciously or unconsciously tended to select plots with more mature trees, likely to support fewer extra-small trees [though Dolanc et al. (2014a) reported comparable spread of tree density across VTM and FIA plots]. However, to produce the requisite interaction effect, any bias of VTM sampling would have had to differ at different elevations. For example, for a VTM bias to explain our analysis results, one would have to posit stronger VTM bias against including extra-small trees at higher elevations than at lower elevations, for western white pines, mountain hemlocks, and red firs but not for white fir or other species. We consider such a strained bias hypothesis to be unrealistic; the data are more simply explained by true elevation shifts by a few species.

We find climate change in the Sierra Nevada to be a leading contender among possible causes for the significant elevation shifts we documented. The large spatial scale of our study implies a large-scale effect like climate change. Of the three species most affected, all are higher-elevation species, and western white pine and mountain hemlock were both identified by Lutz et al. (2010) as species at risk from climate change at their lower elevation margin. In a Bayesian logistic regression distribution-modeling study, Bell et al. (2014) found that projected change in climatic envelopes for high-elevation conifers, including lodgepole pine, are likely to result in substantial loss and upward shift of habitable area. Climate in our study area has been measurably changing, resulting in fewer freezing days, lower snowpack, earlier snowmelt, warmer nighttime temperatures, and greater water-deficit values (Cordero et al. 2011, Lutz et al. 2010), especially at low to middle elevations. At high elevations there may be some tendency to increased precipitation (Mallek et al. 2014) and warmer temperatures may yet be below freezing at night, creating opportunities for upslope establishment by some higher elevation tree species (Millar et al. 2004, Dolanc et al. 2013).

Fire and logging are two other often-discussed catalysts of forest change in the Sierra Nevada (Dolanc et al. 2014b, McIntyre et al. 2015, Naficy et al. 2010). Because they occur in patchworks, they appear less likely to cause clear patterns over very large scales, though they may do so on average. While beyond the scope of this paper, we did amass data on fire and logging history for our plots which will be analyzed elsewhere. Particularly at the elevations and in the habitats occupied by western white pine and mountain hemlock, fire and harvest are relatively less frequent than at lower elevations (Caprio and Swetnam 1995, Skinner and Chang 1996) – for example, we found no history of fire in mountain hemlock plots. Within our study area at higher elevations there are substantial areas of designated wilderness where no logging may occur. Thus even where forest-stand effects of timber harvest and fire are expected to have been weak, we observed upward shifts of high-elevation tree species. Schwartz et al. (2015) reported increasing frequency of fire over time at higher elevations in the Sierra Nevada, suggesting that the limited effects of fire within the highest portions of our study area may expand over time. Whether increased fire frequency would facilitate or impede tree elevation shifts remains to be seen and is likely to be species-specific.

Coniferous trees in the Sierra Nevada are major establishers of habitats and habitat types, and produce seed that is food for numerous species of mammals and birds (Mayer and Laudenslayer 1988). Our results suggest that, with trees moving up, stands of vegetation forming habitats will move up as well, with a range of implications for multiple wildlife species. Well developed habitats will take time to establish on cool, rocky slopes. Another widely appreciated aspect of such upward shifts is that there is less area available at higher elevations – because mountains are roughly cone-shaped – therefore subalpine habitats and the wildlife they support are likely to be confined to reduced and fragmented areas over time (Dullinger et al. 2012, Bell et al. 2014).

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APPENDIX I

While the VTM database compiled online is a uniquely valuable resource, users should examine the data carefully for errors before drawing conclusions from it. Here we catalog some edits we found necessary.

Incorrect codes (or, regional differences in the codes that VTM allowed that were not preserved in the historical information available to the University of California VTM Project):

VTM code	Nominal code species	Likely species intended in our study area	Comments, per our study area
Ld	incense cedar (*Calocedrus (Libocedrus) decurrens*): also I, IC	tan oak (*Lithocarpus densiflora*): codes Lde, T	Ld code co-occurs in data with I code, suggesting Ld used for Lde
R	coast redwood (*Sequoia sempervirens*)	red fir (*Abies magnifica*): code R1	Coast redwood does not occur. Elevation and data notations confirm red fir. We interpreted R as a code for red fir where a tree was indicated.
SP	Bishop pine (*Pinus muricata*)	sugar pine (*Pinus lambertiana*): code S	Bishop pine does not occur. Data notations and elevations consistent with sugar pine. We interpreted SP as sugar pine.
W	Interior live oak (*Quercus wislizeni*)	white fir (*Abies concolor*): code W1	Elevation and notations suggest white fir. We did not include these occurrences in our analysis.

Incense cedar and tan oak were not analyzed, in part due to these ambiguities. We did not analyze potential shifts of interior live-oak because a complete absence in recent sampling (0/381) and 57/2160 samples in VTM suggested miscoding in the VTM data that we could not resolve.

We used verbatim elevations reported by VTM surveyors for VTM plots rather than digital elevations derived from estimated latitude and longitude in a GIS. A regression analysis showed no substantial deviation of VTM elevation estimates from the digitized estimates, and we found occasional errors in the GIS locations. For EBM, we used digital elevations (10-m resolution) calculated using geographic positioning system (GPS) averaged waypoints obtained in the field and compared with pre-planned plot locations.