Structure, Composition and Health of Whitebark Pine Ecosystems in California: a Statewide Assessment

Authors: Marc Meyer[a], Michèle Slaton[b], Shana Gross[c], Ramona Butz[d], and Carol Clark[b]

[a]USDA Forest Service, Region 5 Ecology Program, Southern Sierra Province, Bishop, CA 93514; marc.meyer@usda.gov

[b]USDA Forest Service, Region 5 Remote Sensing Laboratory, McClellan, CA 95652

[c]USDA Forest Service, Region 5 Ecology Program, Central Sierra Province, South Lake Tahoe, CA 96150

[d]USDA Forest Service, Region 5 Ecology Program, Northern California Province, Eureka, CA 95501 and Department of Forestry and Wildland Resources, Humboldt State University, Arcata, CA 95521

Abstract: Whitebark pine (*Pinus albicaulis*) forest ecosystems in California are diverse and unique, yet the status and condition of these ecosystems across the state are uncertain. Using a combination of geospatial and monitoring plot data, we assessed patterns in the structure, composition, and health of whitebark pine ecosystems on national forests throughout the state of California to evaluate potential signs of declining ecosystem integrity at subregional or statewide scales. We found whitebark pine ecosystems to be structurally, compositionally, and functionally distinct among subregions, with at least some evidence of declining ecological integrity and resilience in all five subregions of California. Whitebark pine forests in northern California exhibited signs of greater stand densification (Cascade-Klamath), encroachment by shade-tolerant conifer species (Cascade-Klamath and Warner Mountains), and tree mortality rates associated with mountain pine beetle outbreaks (Warner Mountains) than elsewhere in California. Whitebark pine stands in the Sierra Nevada displayed signs of greater crown loss (Southern Sierra), slightly higher tree mortality rates (Southern Sierra West), and stand densification (Central Sierra). In contrast to mountain pine beetle occurrence which was observed in scattered stands throughout the state (20% of the whitebark pine distribution in California based on aerial detection surveys and 2-3% of statewide monitoring plots), white pine blister rust activity was infrequent to rare in many parts of the state (0.01% based on aerial detection surveys and 0.9% of whitebark pine stems in monitoring plots) with greater frequencies of detection in the Cascade-Klamath and Central Sierra Nevada. Notwithstanding these negative signs, there are several indicators of resilience and adaptive capacity in California's whitebark pine forest ecosystems that are likely to contribute to future persistence of the species in the region (e.g., fire regime and fuel loading within reference conditions, sufficient or ample regeneration and cone production, low incidence of white pine blister rust, climate refugia distributed throughout region), particularly in the Sierra Nevada. Much of the state's whitebark pine ecosystems on national forestlands appear to be relatively healthy and intact compared to more northern latitudes, but active management may be required to build adaptive capacity in California's whitebark pine ecosystems with declining integrity.

Introduction

Whitebark pine is an important keystone and foundation species in high elevation montane ecosystems of western North America (Ellison et al. 2005, Tomback and Achuff 2010). In many parts of its range, whitebark pine is threatened by several interacting stressors, including an introduced fungal pathogen that causes white pine blister rust (*Cronartium ribicola*), outbreaks of mountain pine beetle (*Dendroctonus ponderosae*), a century of fire exclusion, and climate change (Keane et al. 2012, 2017). These stressors have led to widespread declines in whitebark pine throughout its range, resulting in the listing of whitebark pine as a candidate species under the US Endangered Species Act (US Fish and Wildlife Service 2011). In recent years, several management strategies have been developed to support whitebark pine restoration and conservation efforts at regional (focused on but not limited to U.S. Forest Service regions) and range-wide scales (e.g., Aubry et al. 2008, Keane et al. 2012) including one currently in progress for California. These strategies require sufficient region-specific data sources, including remote-sensed and field plot data, to effectively assess the current condition and trend of whitebark pine forest ecosystems at multiple spatial scales. Such information is essential for identifying regional restoration objectives and priorities for whitebark pine (Keane et al. 2012, Slaton et al. 2019).

Whitebark pine ecosystems in California represent a unique segment of the species' geographic range, yet relatively few studies have occurred in the region. Populations in the state occupy four distinct physiographic regions, including the Klamath Mountains, Southern Cascades, Basin and Range (e.g., Warner Mountains, Glass Mountains), and Sierra Nevada (Griffen and Critchfield 1976). In the Sierra Nevada, whitebark pine is a genetically distinct and contemporary refugial population (Richardson et al. 2002) that represents the southern range extent of the species (Arno and Huff 1990). In comparison with other regions, whitebark pine in California has been relatively less impacted by stressors such as white pine blister rust and mountain pine beetle outbreaks (Slaton et al. 2019a, Nesmith et al. 2019), although these stressors have become more apparent in recent years especially in more northern latitudes (e.g., Maloney et al. 2012, Millar et al. 2012, Jackson et al. 2019). Unlike more northern parts of the range (e.g., Rocky Mountains, Northern Cascades), whitebark pine communities in California may include foxtail pine (*P. balfouriana*), limber pine (*P. flexilis*), western white pine (*P. monticola*), Sierra juniper (*Juniperus grandis*), red fir (*Abies magnifica*), white fir (*A. concolor*), or Jeffrey pine (*P. jeffreyi*), and mixed stands of whitebark pine and Sierra lodgepole pine (*P. contorta* ssp. *murrayana*) are especially common throughout the region (Slaton et al. 2019a, Sawyer et al. 2009). Shade-tolerant subalpine species such as subalpine fir (*A. lasiocarpa*), Engelmann spruce (*Picea engelmannii*), and Douglas-fir (*Pseudotsuga menziesii*) which commonly co-occur with whitebark pine in more northern latitudes, are conspicuously absent in whitebark pine forests of California (Goeking and Izlar 2019), although mountain hemlock (*Tsuga mertensiana*) is a frequent associate of whitebark pine communities in the state (Sawyer et al. 2009). Natural fire regimes in Californian whitebark pine and other high elevation white pine forests may be notably different than other regions, with generally lower severity fire effects and possibly shorter fire return intervals evident in the Sierra Nevada than stands from more northern latitudes (Meyer and North 2019).

Despite this distinctiveness of California's whitebark pine forests, these ecosystems have received scant attention in the scientific literature until fairly recently (Slaton et al. 2019a). Plot-scale analyses of whitebark pine in California have often been limited in spatial extent to individual study sites (e.g., Meyer et al. 2016) or focused on specific management units such as national parks (e.g., Jackson et al. 2019, Nesmith et al. 2019), resulting in few subregional comparisons or larger scale analyses. Regional analyses of whitebark pine forests in California are largely lacking, although Slaton et al. (2019) examined subregional patterns in disturbance agents and stand densities in California's whitebark pine forests, and Millar et al. (2012) examined recent tree mortality patterns across the state using aerial detection survey data. Slaton et al. (2019) underscored the need to refine our understanding of stand structure and function across the state to inform management actions designed to retain integrity and resilience of whitebark pine ecosystems in California.

The purpose of our study was to evaluate broad patterns in the structure, composition, and health of whitebark pine forests in California, using a network of statewide monitoring plot data on national forest lands and geospatial data sources covering all land ownerships. Our evaluation focused on subregional and statewide patterns to examine large scale patterns in whitebark pine forests of California, which may provide the basis for future comparison with other regions outside the state. Lastly, we attempted to identify additional data and information gaps where they exist for the region, particularly on national forests (i.e., U.S. Forest Service Pacific Southwest Region). Our results evaluate the general status of whitebark pine in California, examine if there is evidence of declining integrity of whitebark pine forest ecosystems in the region, and inform the regional whitebark pine conservation strategy currently in development for California.

Methods

Study site and plot selection

Our study area included the entire geographic range of whitebark pine within the state of California, including five major subregions identified and mapped in Slaton et al. (2019a) and Slaton (2020): (1) Cascade and Klamath Mountains, (2) Warner Mountains, (3) central Sierra Nevada, (4) southern Sierra Nevada west, and (5) southern Sierra Nevada east (Figure *1*). We based these subregions on distinct physiographic units in California that represent major changes in geology, geomorphology, soils, and vegetation (Barbour et al. 2007, Graham and O'Geen 2016). As an exception, we further split the Sierra Nevada into three subregions to emphasize differences in precipitation and temperature gradients associated with recent tree mortality patterns and white pine blister rust incidence in California (Dunlap 2012, Young et al. 2017). We also included nine plots from the Glass Mountains in the southern Sierra Nevada east subregion as a matter of convenience (the Glass Mountains are located in the Great Basin province) and due to its proximity to and connectivity with the southern Sierra Nevada east. Similarly, we combined the Cascade and Klamath Mountains, which are separate and distinct ranges, into one region as a matter of convenience (there is a relatively small sample size per range) and due to their proximity and connectivity. Whitebark pine is commonly a dominant or codominant subalpine conifer throughout California, especially at elevations exceeding 2500 m in the southern Cascades and 3000 m in the Sierra Nevada (Arno and Hoff 1990). At lower elevations (2000–3000 m) within this zone, subalpine forests can be dominated by upright stands of whitebark pine, occurring with other subalpine conifers such as lodgepole pine, red fir, western white pine, mountain hemlock, limber pine, and foxtail pine (Meyer and North 2019, Coppoletta et al. in press). Above this zone, whitebark pine may occur as monotypic, krummholz vegetation, especially on exposed sites near treeline (generally above 3500 m in the Sierra Nevada). Our dataset consisted of whitebark stands spatially delineated as polygons as described in Slaton et al. (2019), including a total of 12,926 polygons ranging from 0.01 to 1044 ha in size. We used a 30 m digital elevation model to create a raster for topographic position index (TPI; elevation relative to the mean elevation of the surrounding landscape using ArcGIS 10.3 Topography Tools and a 500 m radius). We obtained potential evapotranspiration (i.e. evaporative demand; PET; 270 m resolution) from the Basin Characterization Model as modeled for years 2010-2039 under the A2 climate scenario (Flint and Flint 2014). We summarized mean latitude, TPI, and PET at the polygon level and stratified our sampling across the entire study area based on these three variables. We categorized each variable into three classes (low, moderate, high) for a total of 25 stratification units (two stratification units at high latitude and high potential evapotranspiration did not occur in our study area and were dropped from further consideration). We chose these strata to capture a wide range of environmental conditions in whitebark pine stands in national forests of California. Within each randomly selected polygon, we established plot locations at the first sign of whitebark pine encountered within the polygon, excluding areas located on inaccessible or exceptionally steep terrain. In cases where whitebark was not found within a mapped polygon, we established plots in the closest site available), or in some cases where neighboring sites were unavailable we selected a new polygon from the stratification unit. In addition to our random plots, we included 66 plots systematically established over elevational and latitudinal gradients in the southern Sierra Nevada East, Central Sierra, and Warner Mountains to capture a wider range of environmental variation described in a related study in progress by the US Forest Service Region 5 Remote Sensing Lab. This resulted in 25 plots established in the Cascade-Klamath, 22 plots in the Warner Mountains, 26 plots in the southern Sierra Nevada West, 59 plots in the Central Sierra Nevada, and 112 plots in the southern Sierra Nevada East, for a total of 244 sample plot locations across our study area (Figure *1*). We allocated greater sampling effort in the Sierra Nevada (81%), which accounts for approximately 91% of the area occupied by whitebark pine in California.

We surveyed whitebark pine stands in our study area primarily between June and September of 2016 to 2019 (in the Central Sierra, 2 plots were surveyed in 2013 and 17 plots were surveyed in 2014). We initially established a total of 39 circular plots (12.6 m radius; 0.05 ha) using a stratified random sampling design across several subregions of California. In 2019, we increased circular plot size to 16.1 m radius (0.08 ha) to address sampling objectives in a related study (Slaton et al. 2019b) and established an additional 205 plots with our stratified random sampling design. Within each plot, we recorded site attributes (e.g., slope, aspect, geographic coordinates), vegetation cover (ocular estimates of live and dead canopy cover, live shrub and herb cover, dominant understory species), ground cover (e.g., bare ground and rock cover), and stand variables (e.g., live and dead basal area). Within each plot, we also recorded the attributes of all trees ≥ 7.6 cm diameter at breast height (dbh, 1.37 m), including species, status (live or dead), dbh, number of stems per cluster (generally defined as ≤1 m of the base of a neighboring stem), percent live crown, presence of small (dbh, <7.6 cm) presumptive "clonal" stems arising from a cluster (i.e., often an underground branch extending more or less horizontally from a central point through "layering"), mountain pine beetle attack severity, years since beetle attack, cone abundance rating (0, 0 cones; 1, 1–10 cones; 2, 11–100 cones; 3, >100 cones), and evidence of other insects and pathogens (e.g., white pine blister rust). We estimated beetle attack severity for each tree based on Meyer et al. (2016): 0, no evidence of attack; 1, few pitch tubes; 2, moderate number of pitch tubes with limited spatial extent on bole; 3, many pitch tubes spread throughout bole. We identified small, whitebark pine clonal stems based on their immediate proximity to tree clusters (distance, <1 m), basal stem angle (directed more or less horizontally toward tree cluster), or evidence of physical underground connection to neighboring tree clusters. Within each plot, we recorded attributes of all seedlings (height, <1.37 m) and saplings (height, ≥1.37 m; dbh, <7.6 cm), including species, status (live or dead), estimated age class of seedlings (0-4 years age and ≥5 years age, based on whorl counts and bud scars), number of stems per cluster (defined as ≤10 cm of the base of a neighboring seedling or sapling stem), and evidence of insects or pathogens. We also recorded the density, proportional cover, maximum width, and height of all presumptive clonal and krummholz stems in each plot.

We sampled surface fuels in each plot using the planar-intercept method (Brown 1974) based on the following transect lengths: 3.3 m for 1- and 10-h fuels (0–0.64 and 0.65–2.54 cm in diameter), 7.6 m for 100-h fuels (2.55–7.62 cm), and 11.3 m for 1000-h fuels (i.e. coarse woody debris; >7.62 cm). We estimated litter and duff depth at two points and overall surface fuel depths at three points along four transects per plot, each oriented in separate cardinal direction (i.e., north, east, south, and west).

Analysis

We evaluated regional patterns in the land ownership, land designations, fire activity, and health of whitebark pine using geospatial data sources specific to California. We estimated the total mapped area of whitebark pine (Slaton 2020) occurring within specific land ownerships (e.g., national forests, national parks), land designations (wilderness, inventoried roadless areas, and research natural areas), and developed recreation sites (includes ski areas, campgrounds, and trailheads), accounting for areas of overlap (i.e., some research natural areas occur in wilderness) based on publically available data (USDA Forest Service 2020). We also estimated the total burned area since 1945 (75 years of data) within the mapped area of whitebark pine using the USFS Region 5 Fire Return Interval Departure data (Safford et al. 2015; excludes fires <4 ha), combining areas burned more than once in separate years to avoid double counting areas of overlap. We used USFS Aerial Detection Survey (ADS) data (US Forest Service 2019) to estimate the proportional area of mapped whitebark pine containing white pine blister rust and mountain pine beetle detections (2008-2019), incorporating all mortality agent classes (primary, secondary, or tertiary). ADS polygons represent forested areas of recent tree mortality delineated by aerial observers covering pre-determined flight paths, which may include opportunistic ground-based field surveys to verify mortality agents (US Forest Service 2019). Due to the irregularity of ground-based field surveys, many ADS mortality agents may be unverified in the field outside of aerial observations, leading to potential misidentifications. Additionally, ADS surveys with limited or inconsistent spatial coverage may fail to detect areas of recent tree mortality, which may result in the failure to detect insect or pathogen occurrence (i.e., false negatives), or may incorrectly assign mortality polygons to areas with non-lethal canopy loss (i.e., false positives) in whitebark pine stands (Slaton et al. in review).

We computed plot-based summary statistics for whitebark pine for each subregion in California and for the entire state (representing national forestlands only). We calculated the frequency of tree species composition based on the tally of all live stems ≥7.6 cm dbh in plots. Tree regeneration estimates included seedlings (<1.37 m height), saplings (<7.6 cm dbh), and small diameter (<7.6 cm dbh) presumptive clonal stems arising from a tree cluster. We based tree density threshold values that exceeded the natural range of variation (NRV) on mean ± 2 standard deviations values summarized for Sierra Nevada subalpine stands in Meyer and North (2019) and Coppoletta et al. (in press). We identified shade-tolerant conifers in whitebark pine forests of California (e.g., mountain hemlock, red fir) based on information summarized in Meyer and North (2019) and Coppoletta et al. (in press). We based tree density threshold values associated with elevated risk of mountain pine beetle attack in Sierra Nevada whitebark pine stands on mean tree densities (live + dead) of high mortality stands in Meyer et al. (2016). We counted the number of plots with either krummholz whitebark pine trees (≥1 stem; characterized by curved or twisted stems, typically parallel to and touching the ground surface for at least a portion of its length) or ≥20 regeneration (seedlings and saplings) stems and a maximum tree height of 12 m to estimate the proportion of plots with krummholz whitebark pine stems. We selected these thresholds because they generally characterized plots as dominated by krummholz mats and layers as opposed to upright trees, following inspection of plot photographs and testing numerous structural attribute summaries. Within each plot, we used the presence of fire scars on one or more trees and naturally charred coarse woody debris as evidence of past fire activity, and the deposition of massive rocks and woody debris and presence of tree breakage or uprooting in runout zones as evidence of past avalanche activity.

Results

Statewide indicators based on geospatial data

Approximately 91% of whitebark pine in California occurs in the Sierra Nevada (79% occurs in the Southern Sierra Nevada), with relatively smaller and more isolated populations occurring in the Cascades-Klamath and Warner Mountains (Table *1*). Seventy-one percent of the distribution of whitebark pine in California occurs on National Forest lands, with the remaining 29% on National Park Service lands (*Supplemental Tables*, Table *14*); only 0.09 ha of whitebark pine stands in the state were located on private or state lands or lands administered by another federal agency. The vast majority (94%) of California whitebark pine occupies protected areas with limited management opportunities including wilderness (81%), inventoried and roadless areas[1] (13% excluding overlap with wilderness), and research natural areas (0.5%) (*Supplemental Tables*, Table *15*). Of the three research natural areas that contain whitebark pine in California, only the Harvey Monroe Hall research natural area in the Southern Sierra East (one of the first established research natural areas in California) was designated specifically to protect whitebark pine and other mixed subalpine forests as target elements (Cheng et al. 2004). Developed recreation sites occur in approximately 1.5% of whitebark stands, with the vast majority of these sites (98%) located in four developed ski areas (i.e., Alpine Meadows, Mount Rose, June Mountain, and Mammoth Mountain).

Between 2008 and 2018, aerial surveys in California detected mountain pine beetle related tree mortality in 20% of whitebark pine stands throughout the state (Table *2*). Mountain pine beetle-related mortality occurred in all subregions, but was most prevalent in the Warner Mountains. Since 2008, aerial surveys detected 17 ha of white pine blister rust in whitebark pine stands of California (0.01% of the statewide range), with all records located in the Central Sierra subregion (recorded in 2015 and 2016). Seventy-six percent of these hectares also contained records of mountain pine beetle activity. Over the past 75 years, 1222 ha of whitebark pine in the state has burned (<1% of the statewide range). Only 9 of these hectares experienced two fires during this period, with nearly all (91%) located in the Southern Sierra West subregion.

Monitoring plot indicators: species composition

Whitebark pine plots were located in high elevation sites across all subregions of California, generally between 2400 and 3150 m elevation (Table *3*). Most plots were mostly located on moderately steep slopes on all aspects, including north-facing slopes (32%), south-facing slopes (28%), west-facing slopes (21%), and east-facing slopes (18%). Approximately forty percent (range: 33-46%) of monitoring plots (total with live trees = 222) contained whitebark pine trees exclusively, and 75% of plots (range: 65-86%) were dominated by whitebark pine (≥50% of trees were whitebark pine). The most common tree

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[1] Estimate includes Inventoried Roadless Area class 1B (areas where road construction and reconstruction is prohibited) and class 1C (areas where road construction and reconstruction are not prohibited). All class 1C areas that are within the geographic range of whitebark pine in California have limited or no road access and are unlikely to experience road construction or reconstruction in the near future.

species associated with whitebark pine included (in order of relative frequency) lodgepole pine, white fir, western white pine, red fir, and mountain hemlock (Table *4*); 94% of lodgepole pine occurrences and 100% of western white pine occurrences were from the Sierra Nevada, 63% of white fir occurrences were from the Warner Mountains, and 60% of red fir occurrences were from the Cascade-Klamath. Less common associates included Jeffrey pine, aspen, foxtail pine, limber pine, ponderosa pine, western hemlock (*Tsuga heterophylla*), Sierra juniper, and curl-leaf mountain mahogany (*Cercocarpus ledifolius*). Noble fir (*Abies procera*) regeneration was also detected in a single plot in the Cascade-Klamath. Whitebark pine stands included greater frequencies of lower montane species (i.e., white fir, ponderosa pine) in the Warner Mountains, more upper montane species (i.e., red fir, Jeffrey pine) in the Cascade-Klamath, and greater frequencies of lodgepole pine and western white pine in the Sierra Nevada. Mountain hemlock and limber pine were detected in plots from the Sierra Nevada but were absent from plots in other subregions. Foxtail pine was detected in plots from the Southern Sierra and Cascade-Klamath only.

Whitebark pine small stems (includes seedlings, saplings, and clonal stems <7.6 cm dbh) occurred in 100% of plots in all subregions except the Cascade-Klamath and Warner Mountains (Table 5). Shade-tolerant regeneration occurrence was highest in the Cascade-Klamath and Warner Mountains and lowest in the Sierra Nevada. Small stems of other pines (especially lodgepole pine but excluding whitebark pine) were generally higher in the Sierra Nevada than other subregions, and 41% of plots statewide recorded whitebark pine small stems exclusively (i.e., no other tree species present with stems <7.6 cm dbh). Small stem densities were highest in the Southern Sierra East and Cascade-Klamath, and 74% of plots exceeded 300 small stems per ha statewide (Table *6*). Only a single plot (0.4% of total) lacked small stems of any species. The mean proportional density of whitebark pine tree small stems ranged from 26 to 93% across subregions, with the lowest mean values recorded in the Warner Mountains and Cascade-Klamath where a greater proportion of shade-tolerant small stems occurred (67 and 58%, respectively). Other pine species (65% attributed to lodgepole pine) contributed a lower relative proportion of small stems in California's whitebark pine stands (Table *6*), contributing ≥50% of small stems in only 6% of plots statewide. Shade-tolerant species comprised the majority (≥50%) of small stems in 36% of plots in the Warner Mountains and Cascade-Klamath, but virtually no plots in the Sierra Nevada had small stems dominated by shade-tolerant species (Table 5). The highest and lowest small stem densities of whitebark pine occurred in the Southern Sierra East and Warner Mountains, respectively (Supplemental; Table *16*). Statewide, 96% of clonal stems, 50% of seedlings, and 70% of saplings were attributed to whitebark pine. Whitebark small stem densities were abundant in all subregions, except the Warner Mountains (low densities of whitebark pine regeneration and clonal stems) and the Cascade-Klamath (low clonal stems; may be a consequence of differences in the identification of clonal stems among subregions, resulting in an undercount of clonal stems in the Cascade-Klamath).

Monitoring plot indicators: stand health and structure

At the subregional scale, the percentage of whitebark pine trees attacked by mountain pine beetle ranged from 0.9 to 6.7%, with the highest percentage in the Warner Mountains (Table 7). At the state level, approximately 2% of plots contained signs of elevated mountain pine beetle activity (>25% of trees attacked). White pine blister rust was observed in low frequencies in the Cascade-Klamath and Central Sierra but was not detected in plots from other subregions of California (Table 7). Evidence of recent fire was detected in 7% of whitebark pine plots statewide, with most records of fire from the Warner Mountains and Southern Sierra (Table 7). Only 0.8% of plots representing two locations in the Southern Sierra West exhibited signs of prior avalanche activity. The mean percentage of trees that recently died (≤ 7 years; 75% were whitebark pine) ranged from 4 to 6% among subregions of California, resulting in an estimated (crude) mean tree mortality rate of 0.56 to 0.87% per year across subregions of California (Table *8*). Tree mortality rates tended to be higher in the Warner Mountains and Southern Sierra West, but mean snag densities were greatest in the Cascade-Klamath and Central Sierra. Seventy-six percent of recently dead trees of all species and 74% of recently dead whitebark pine trees were associated with mountain pine beetle activity, and 10% of these trees exhibited signs of white pine blister rust.

Tree densities were generally higher in the Cascade-Klamath and Central Sierra subregions of California, but elsewhere tree densities averaged between 208 and 311 trees per ha (Table *9*). A greater percentage of plots in the Cascade-Klamath and the Central Sierra contained tree densities that exceeded the upper limit of NRV for subalpine forest stands or exceeded whitebark pine stand densities associated with elevated mountain pine beetle activity (Table *10*). In the Warner Mountains and Southern Sierra, 10-21% of plots exceeded NRV for tree density and 0-10% of plots contained tree densities associated with elevated risk of mountain pine beetle attack. Mean basal area was generally higher in the Cascade-Klamath, with most other subregions averaging between 11 and 23 m^2/ha (Table *9*). Canopy cover, whitebark pine tree diameter, and whitebark pine live crown (compacted) were generally similar among all five subregions of California. Whitebark pine crown loss was generally 4 to 5 times greater in the Sierra Nevada than the northern California subregions (Cascade-Klamath, Warner Mountains). In most subregions, the percentage of whitebark pine trees containing cones averaged approximately 20-30%, with the exception of the Warner Mountains where an average of 44% of whitebark pine trees contained cones (Table *9*). Among whitebark pine trees with cones present, 71% contained few cones (1-10 total), 27% contained many cones (11-100 total), and 2% contained numerous cones (>100 total). Small stems of whitebark pine plots were composed primarily of tree regeneration (seedlings and saplings) in all subregions, except the Southern Sierra East (Supplemental; Table *16*). The density and cover of short-statured (generally <3 m height) whitebark pine tree clusters attributed to clonal and krummholz stems were greater in the Sierra Nevada than the Cascade-Klamath and Warner Mountains (Table *11*). The greatest percentage of plots containing krummholz whitebark pine stems were located in the Southern Sierra.

Understory shrub and herb cover varied in whitebark pine stands (subregional mean range: 4-24% and 3-24%, respectively), with generally higher shrub cover observed in the Cascade-Klamath than other subregions (Supplemental; Table *17*. Common understory shrub species included big sagebrush (*Artemisia tridentata*), mountain gooseberry (*Ribes montigenum*), wax currant (*R. cereum*), and mountain snowberry (*Symphoricarpos rotudifolius*). Surface ground cover was mostly attributed to litter (mean ± SE: 43 ± 2%), rock (37 ± 2%), and bare ground (11 ± 2%), with very little coarse woody debris (2 ± 1%) observed across all subregions. Litter depth averaged 3 cm across the state. Surface fuel loading varied substantially among plots within a subregion, although median values (<6 tons per acre) indicated relatively low surface fuel loads in most plots (Supplemental; Table *18*). Sporadic heavy surface fuel loads (mostly in the form of coarse woody debris, or 1000+ hour fuels) were encountered within a subset of plots in all thoroughly-sampled subregions (excludes Cascade-Klamath), with 36% of plots statewide (range: 31-44%) exceeding 15 tons per acre and maximum surface fuel loading ranging from 188 to 455 tons per acre.

Discussion

Whitebark pine forest ecosystems in California vary considerably in structure, composition, and health and occupy five distinct subregions in the state (see Figures 2 through 6 in *Supplemental Tables and Figures*). Approximately 79% of this distribution is restricted to the Southern Sierra Nevada, where whitebark pine frequently occurs at exceptionally high elevations (>3000 m) in moderately-sloped landscapes with granitic-based soils. Across the state, whitebark pine occurs exclusively on federal lands, including a dozen national forests and three national parks, and the vast majority of these lands are within protected areas (e.g., wilderness, inventoried roadless areas) where management opportunities for whitebark pine stands are limited. A small proportion (1.5%) of the distribution of whitebark pine in California does occur in developed ski areas, where unique management and educational opportunities are available for improving the adaptive capacity of whitebark pine stands.

There are several initial signs of declining ecological integrity within whitebark pine stands in all subregions of California based on our assessment of aerial survey and plot data (Table *12*). Shade-tolerant conifer encroachment (particularly from red fir, mountain hemlock, and white fir) is evident in whitebark pine stands of the Cascade-Klamath and Warner Mountains. Tree densification is also apparent in stands of the Cascade-Klamath, Central Sierra, and elsewhere in California. Such areas could be affected by long-term fire exclusion and considered a priority for management actions to restore stand composition, reduce stand densities, and improve ecological resilience and integrity. The Warner Mountains are noteworthy for elevated levels of mountain pine beetle-related tree mortality in whitebark pine stands (primarily occurring in 2007-2010), a pattern documented in this study and Millar et al. (2012) using aerial detection survey data; our plot data was not effective at capturing mountain pine beetle occurrence at the larger subregional scale. In the coming decades, whitebark pine stands in the Warner Mountains may convert to a montane mixed conifer forest type or possibly semiarid shrublands (e.g., sagebrush steppe) considering the low observed densities of whitebark pine regeneration and relatively abundant white fir or, in a few cases, ponderosa pine regeneration. Interestingly, whitebark pine ecosystems in the Warner Mountains have higher estimated levels of fire occurrence (4-12%) than other subregions over the past several decades, but actual fire frequency may be underestimated throughout California (especially using geospatial data) because many high elevation fires are relatively small (<1 ha) and undocumented in statewide fire history data (e.g., Safford et al. 2015).

Signs of greater white pine blister rust activity in whitebark pine stands of the Cascade-Klamath and Central Sierra are corroborated by other recent surveys in these subregions (e.g., Maloney et al. 2011, 2012; Jackson et al. 2019), although our plot and aerial detection survey data failed to detect this introduced pathogen in the Southern Sierra West where it was documented to occur at low frequencies by Maloney et al. (2011) and Nesmith et al. (2019). These results support the observation of increased white pine blister rust incidence in areas of greater relative humidity and wetter climates associated with more northern latitudes in California (Dunlap 2012). Our observation of increased tree canopy loss in whitebark pine trees of the southern Sierra Nevada has been documented in stands dominated by whitebark pine, foxtail pine (Nesmith et al. 2019), and red fir (Meyer et al. 2019) in the southern Sierra Nevada, and may be indicative of elevated moisture stress associated with climate change and recent drought. The combination of these stressors (i.e., hotter droughts) resulted in exceptionally high tree mortality rates in montane forests of the southern Sierra Nevada (Young et al. 2017, Stephenson et al. 2018) including subalpine forests (Brodrick and Asner 2017). These recent trends of increasing tree mortality rates associated with climate change and drought are consistent with climate envelope models that project major losses in suitable habitat for California's whitebark pine and other subalpine forest ecosystems by the end of the 21st century (Meyer and North 2019, Coppoletta et al. in press).

Despite some early signs of declining integrity, California's whitebark pine ecosystems also are showing indications of ecological resilience and adaptive capacity (Table *13*). Across the state, whitebark pine stands occur largely in protected areas, exhibit low natural fire regime departure and surface fuel loading, contain sufficient regeneration densities (i.e., mean whitebark pine regeneration densities are generally within or exceeding NRV for subalpine stands and include a mixture of young seedlings, older seedlings, and saplings) and cone production, and possess numerous clonal stems and krummholz tree clusters to potentially buffer stands from interacting stressors. Whitebark pine ecosystems in the Sierra Nevada also exhibit other indications of resilience and adaptive capacity, such as the presence of high-elevation climate refugia (i.e., extensive and contiguous area of high-elevation subalpine and alpine landscapes) that will likely increase the likelihood of persistence by the end of the 21st century (Warwell et al. 2007, Roberts and Hamann 2016, Meyer and North 2019). Additionally, Sierra Nevada whitebark pine forest ecosystems appear to be less impacted by stand densification and potential type conversion to shade-tolerant species that are likely due, at least in part, to a century of fire exclusion in the Cascade-Klamath and Warner Mountains. From a range-wide standpoint, whitebark pine ecosystems in California and especially the Sierra Nevada may be relatively healthier and more resilient to the combined impacts of mountain pine beetle outbreaks, white pine blister rust, altered fire regimes, and climate change than more northern parts of the species' range (e.g., Rocky Mountains, Pacific Northwest), where the impacts of these stressors have been much more severe and widespread (Keane et al. 2012, 2017). However, more direct comparisons among regions over time would be required to further elucidate regional differences in whitebark pine ecosystem health, structure, and composition.

Management Recommendations

Our study has several implications for the management of whitebark pine forest ecosystems on national forests and elsewhere in California. First, our results suggest that whitebark pine stands in the northern part of the state (i.e., Warner Mountains, Cascade-Klamath) are in greater need of restoration actions to reduce stand densities, especially of shade-tolerant species, to improve ecosystem integrity. Importantly, "seral whitebark pine sites" (more productive sites where whitebark pine undergoes successional replacement by shade-tolerant conifers especially in the absence of fire; *sensu* Keane et al. 2012) could be targeted for treatment in northern California and elsewhere in the state where whitebark pine tree regeneration is inadequately represented. Similarly, mixed forest stands containing but not dominated by whitebark pine (e.g., mixed whitebark pine-mountain hemlock stands) may also be targeted for management actions that enhance whitebark pine regeneration and promote the species at a landscape scale (Goeking et al. 2019). Second, many whitebark pine forests in California, particularly in the Southern Sierra Nevada, currently exhibit high ecosystem integrity and adaptive capacity. Management actions in the Sierra Nevada may ideally target seral whitebark pine sites (where they exist), mixed stands containing whitebark pine, and areas of high human impact (e.g., ski areas) where they exist. Lastly, regional and statewide inventory and monitoring efforts are clearly essential in tracking the future health and status of California's whitebark pine stands. Current US Forest Service and National Park Service monitoring efforts in California, in addition to academic research, provide much needed information on current conditions and future trends in whitebark pine forest ecosystems, such as tree mortality and recruitment rates, stand structure and composition, and activity of mortality agents. Monitoring partnership efforts, such as Slaton et al. (2019), will prove critical in assessing whitebark pine condition and trend across administrative boundaries. Additionally, regional effectiveness monitoring and research of forest management actions (e.g., Retzlaff et al. 2019) and focused monitoring in stands with significant mortality (e.g., Meyer et al. 2016) will aid in the development of effective restoration and adaptation approaches in California's whitebark pine forest ecosystems.

Future Monitoring and Research

Based on our assessment and other related work (e.g., Slaton et al. 2019a), there are a number of lingering questions that could be addressed in future whitebark pine monitoring and research efforts in California. These include:

- Are restoration treatments effective in restoring whitebark pine within seral whitebark pine sites or lower-elevation mixed stands where whitebark pine is dominated by other conifer species?
- What is the current condition of whitebark pine stands in high-use recreation sites, such as ski areas and day use areas, and what opportunities exist for their management?
- Do wildfires managed for resource objectives (i.e., unplanned ignitions that are primarily managed to benefit ecosystems and other valued resources and assets) have a positive effect on whitebark pine stands?
- What are the pre-Euro-American settlement fire return intervals in whitebark pine stands of California, and are fire regime characteristics (e.g., fire frequency, fire severity) changing over time?
- Can a restoration prioritization approach for whitebark pine be developed using indicators of ecological integrity?
- Based on monitoring data, where are climate refugia for whitebark pine in California at regional, subregional, and landscape scales? Does the Southern Sierra Nevada represent a climate refugium for the species in California?
- How do whitebark pine ecosystems in the Sierra Nevada differ from those in the Great Basin of California (e.g., Glass Mountains, Sweetwater Mountains) and elsewhere (e.g., Nevada, Idaho)?
- What are the long-term (i.e., decadal) trends in whitebark pine ecosystem integrity and resilience?

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Table 1. Area and percent of whitebark pine distribution in California's subregions. The percentage column displays the percent of the total statewide area of whitebark pine in each subregion.

Subregion	Whitebark Pine Area (ha)	% of Statewide Area
Cascades-Klamath	3,356	2
Warner Mountains	10,044	7
Central Sierra	16,611	12
Southern Sierra - West	57,632	40
Southern Sierra - East	55,086	39
Total	142,729	100

Table 2. Area and percent of whitebark pine distribution within a subregion with mountain pine beetle and white pine blister rust associated tree mortality (based on 2008-2019 aerial detection surveys) and fire occurrence (based on FRID[2] geospatial data).

	Mountain Pine Beetle		White Pine Blister Rust		Wildland Fire	
Subregion	Area (ha)	% of Subregion	Area (ha)	% of Subregion	Area (ha)	% of Subregion
Cascades-Klamath	1,407	42	0	0	28	0.8
Warner Mountains	7,560	75	0	0	389	3.9
Central Sierra	2,287	14	17	0.1	107	0.6
Southern Sierra - West	5,059	9	0	0	327	0.6
Southern Sierra - East	12,400	23	0	0	371	0.7
Statewide	28,743	20	17	0.01	1222	0.9

Table 3. Mean ± SE topographic attributes of whitebark pine plots among subregions of California.

Subregion	Elevation (m)[3]	Slope (%)	Primary Parent Material
Cascades-Klamath	2401 ± 22	31 ± 3	Volcanic, Granitic[4]
Warner Mountains	2424 ± 50	28 ± 3	Volcanic (residuum weathered over basalt)
Central Sierra	2873 ± 17	30 ± 2	Granitic
Southern Sierra - West	3132 ± 21	29 ± 3	Granitic
Southern Sierra - East	3107 ± 22	27 ± 2	Granitic, Volcanic[5]
Statewide	2898 ± 22	26 ± 1	—

[2] Fire Return Interval Departure (Safford et al. 2015)

[3] The minimum elevation whitebark pine plot was 1976 m (Warner Mountains) and maximum elevation plot was 3529 m (Southern Sierra East).

[4] Some whitebark pine ecosystems in the Klamath Mountains occur on serpentine soils.

[5] Volcanic parent material occurs primarily in the Mammoth and June Lakes area and Glass Mountains.

Table 4. Percent frequency of tree species associated with whitebark pine stands in California by subregion and statewide (based on monitoring plots). Species with <1% statewide occurrence were not included (i.e., curl-leaf mountain mahogany, Sierra juniper).

Subregion	Lodgepole pine	White fir	Western white pine	Red fir	Mountain hemlock	Jeffrey pine	Aspen	Foxtail pine	Limber pine[6]	Ponderosa pine	Western hemlock
Cascade-Klamath	21	8	0	42	0	13	0	8	0	0	13
Warner Mountains	0	50	0	0	0	0	5	0	0	15	0
Central Sierra	30	2	16	4	11	5	0	0	2	0	0
S. Sierra - West	62	0	5	0	0	0	0	5	0	0	0
S. Sierra - East	48	4	6	4	8	3	5	1	4	0	0
Statewide	37	8	7	7	6	4	3	2	2	1	1

Table 5. Frequency of occurrence of small stems (includes seedlings, saplings, and presumptive clonal stems <7.6 cm dbh) by species group[7] and percentage of plots containing small whitebark pine stems only within whitebark pine stands by subregion.

Subregion	Whitebark Pine (%)	Shade Tolerant Species (%)[8]	Other Pines (%)[9]	Whitebark Pine Only (%)
Cascade-Klamath	96	60	32	28
Warner Mountains	86	41	14	45
Central Sierra	100	19	37	53
Southern Sierra – West	100	15	81	15
Southern Sierra - East	100	11	51	42
Statewide	98	21	45	41

[6] 67% of limber pine occurrences in the southern Sierra east were located in the Glass Mountains.
[7] Does not include aspen (occurs in 3% of plots), Sierra juniper (2%), and curl-leaf mountain mahogany (<1%).
[8] Shade tolerant species and their statewide frequency include red fir (9%), mountain hemlock (7%), white fir (6%), western hemlock (0.4%), and noble fir (0.4%).
[9] Other pines column (and statewide frequency) includes lodgepole pine (36%), western white pine (7%), Jeffrey pine (5%), limber pine (3%), foxtail pine (2%), and ponderosa pine (2%) but excludes whitebark pine.

Table 6. Mean ± SE small stem densities (no./ha, includes seedlings, saplings, and presumptive clonal stems <7.6 cm dbh), proportional density by species group, and frequency of plots dominated by shade tolerant species among subregions of California. See table 4 for the list of shade tolerant and other pine species. See Table 16 (Supplemental) for densities of whitebark pine small stems.

Subregion	Total Density (no/ha)[a]	Whitebark Pine (%)	Shade Tolerant Species (%)	Other Pines (%)	Shade Tolerant Species Dominant (%)[b]
Cascade-Klamath	1896 ± 372	37	58	2	36
Warner Mountains	679 ± 172	26	67	2	36
Central Sierra	738 ± 190	93	3	4	2
Southern Sierra - West	903 ± 149	84	1	14	0
Southern Sierra - East	2133 ± 310	87	2	4	3
Statewide	1509 ± 161	79	12	4	9

[a] 79% of small stems are attributed to seedlings and saplings statewide (range: 70-93% by subregion).
[b] Percentage of plots where small stems of shade-tolerant species ≥50% of total tree regeneration in the plot.

Table 7. Percentage of whitebark pine trees exhibiting signs of mountain pine beetle attack or white pine blister rust and percentage of plots showing signs of prior fire activity based on monitoring plots only.

Subregion	Mountain Pine Beetle (%)	White Pine Blister Rust (%)	Wildland Fire (%)
Cascade-Klamath	1.7 ± 1.3	3.2 ± 3.2	0
Warner Mountains	2.9 ± 1.3	0	12
Central Sierra	1.7 ± 0.7	2.3 ± 1.4	2
Southern Sierra – West	2.6 ± 1.5	0	18
Southern Sierra - East	2.0 ± 0.6	0	8
Statewide	2.0 ± 0.4	0.9 ± 0.5	7

Table 8. Mean + SE percentage of trees (all species ≥7.6 cm dbh included) that recently died (≤7 years), estimated tree mortality rate, and density of all dead trees (i.e., snags) among subregions of California.

Subregion	Recent Tree Mortality (%)	Estimated Tree Mortality Rate (%/yr)[a]	Snag Density (no/ha)
Cascade-Klamath	3.9 ± 1.8	0.56 ± 0.25	36 ± 14
Warner Mountains	5.8 ± 2.7	0.82 ± 0.39	10 ± 4
Central Sierra	4.1 ± 1.3	0.58 ± 0.18	19 ± 10
Southern Sierra - West	6.1 ± 2.0	0.87 ± 0.29	7 ± 5
Southern Sierra - East	4.5 ± 1.0	0.65 ± 0.14	11 ± 3
Statewide	4.6 ± 0.7	0.66 ± 0.09	15 ± 3

[a] Tree mortality rates are based on forest inventories conducted at a single point in time and represent crude estimates of the actual tree mortality rates due to errors in time since death estimation and other factors.

Table 9. Mean ± SE tree (≥7.6 cm dbh) density, basal area, diameter, canopy cover, compacted live crown, and crown loss among subregions of California. Tree diameter, compacted live crown, crown loss, and trees with cones are based on whitebark pine trees only.

Subregion	Density (no/ha)	Basal Area (m^2/ha)[10]	Mean DBH (cm)	Canopy Cvr (%)	Compacted Crown (%)	Crown Loss (%)	Trees w/ Cones (%)
Cascade-Klamath	842 ± 139	35.5 ± 5.6	18.8 ± 1.5	23 ± 4	69 ± 6	3 ± 3	25 ± 6
Warner Mountains	220 ± 43	16.9 ± 4.7	18.2 ± 1.6	29 ± 6	62 ± 6	1 ± 6	44 ± 8
Central Sierra	576 ± 67	23.0 ± 2.6	19.8 ± 1.0	22 ± 2	61 ± 3	6 ± 2	27 ± 4
Southern Sierra - West	208 ± 79	10.8 ± 2.6	18.3 ± 0.8	17 ± 2	59 ± 3	9 ± 3	22 ± 7
Southern Sierra - East	311 ± 28	17.8 ± 1.9	17.1 ± 1.1	25 ± 2	61 ± 2	7 ± 1	20 ± 3
Statewide	417 ± 30	20.2 ± 1.4	18.2 ± 0.5	24 ± 1	61 ± 1	6 ± 1	25 ± 2

Table 10. Percentage of plots with tree (≥7.6 cm dbh) densities exceeding the upper limit of the natural range of variation (NRV; >429 trees/ha) and with tree densities associated with elevated insect risk (>881 trees/ha)[11].

Subregion	% Plots Exceeding NRV for Tree Density	% Plots at Elevated Risk of Insect Attack
Cascade-Klamath	63	46
Warner Mountains	20	0
Central Sierra	43	27
Southern Sierra - West	10	10
Southern Sierra - East	31	4
Statewide	27	14

Table 11. Mean ± SE density and total percent cover of whitebark pine presumptive clonal and krummholz stems (generally <3 m height) among subregions of California.

Subregion	Clonal and Krummholz Stem Density (no./ha)	Total Cover of Clonal and Krummholz Stems (%)	Plots Containing Krummholz Stems (%)
Cascade-Klamath	27.8 ± 7.5	2.2 ± 0.7	8
Warner Mountains	23.2 ± 3.6	1.3 ± 0.3	0
Central Sierra	71.6 ± 21.3	5.7 ± 1.3	6
Southern Sierra - West	43.5 ± 10.1	6.2 ± 1.1	59
Southern Sierra - East	44.0 ± 3.8	7.7 ± 1.0	13
Statewide	46.4 ± 4.7	6.3 ± 0.6	13

[10] Basal area values ranged from 0.1-99.5 m^2/ha in the Cascade-Klamath, 0.1-83.6 m^2/ha in the Warner Mountains, and 0.1-135.5 m2/ha in the Sierra Nevada subregions.
[11] Tree density values are based on Meyer and North (2019) and Coppoletta et al. (in press) for NRV and Meyer et al. (2016) for elevated risk of mountain pine beetle attack.

Table 12. Primary signs of declining ecological integrity and stressors in whitebark pine ecosystems of California. Column headings in italics can be directly manipulated by land management actions and may reflect increased fire exclusion over the past century.

Subregion	***Shade-tolerant Encroachment***	***Tree Densification***	**Increased Tree Mortality**	**Increased MPB Activity**[12]	**White Pine Blister Rust**	**Greater Crown Loss**	**High Climate Exposure**[13]
Cascade-Klamath	X	X		X	X		X
Warner Mountains	X		X	X			X
Central Sierra		X			X		X
Southern Sierra - West			X			X	X
Southern Sierra - East				(X)[14]		X	X

[12] Increased mountain pine beetle (MPB) activity is based primarily on aerial detection survey data and includes more frequent outbreak conditions across the subregion.

[13] Climate exposure is based on studies summarized in Meyer and North (2019) and Coppoletta et al. (in press) for whitebark pine and subalpine forests in the later 21st century.

[14] Some areas of recent mountain pine beetle outbreaks and associated whitebark pine mortality have been documented in the Southern Sierra East by Millar et al. (2012) and Meyer et al. (2016).

Table 13. Indicators of ecological integrity and adaptive capacity in whitebark pine ecosystems among subregions of California.

Relevant Subregions	**Indicator(s) of Ecological Integrity and Resilience**
Statewide	High percentage of range in protected areas and federal land ownership
Statewide	Low natural fire regime departure (e.g., low FRID condition class)[15] and surface fuel loading generally within reference conditions[16]
Statewide[17]	Whitebark pine regeneration and clonal stems present in sufficient densities and mature trees producing cones[18]
Statewide	Krummholz growth form (low susceptibility to mountain pine beetle) and short-statured whitebark pine clusters common at high elevations
Warner Mountains, Southern Sierra	Current low incidence or absence of white pine blister rust in whitebark pine and low potential for rapid spread with climate change
All Sierra Nevada subregions	Seral whitebark pine sites with shade-tolerant conifer encroachment are uncommon to rare
Southern Sierra, Klamath	Other high elevation white pines present and provide ecological redundancy[19]
Southern Sierra	High elevation climate refugia are distributed throughout subregion(s)[20]

[15] Fire regime departure information is summarized in Meyer and North (2019) and Coppoletta et al. (in press).

[16] Historical reference values for surface fuel loading in whitebark pine stands are based on similar high elevation stands in the Sierra Nevada as documented by Taylor et al. (2014).

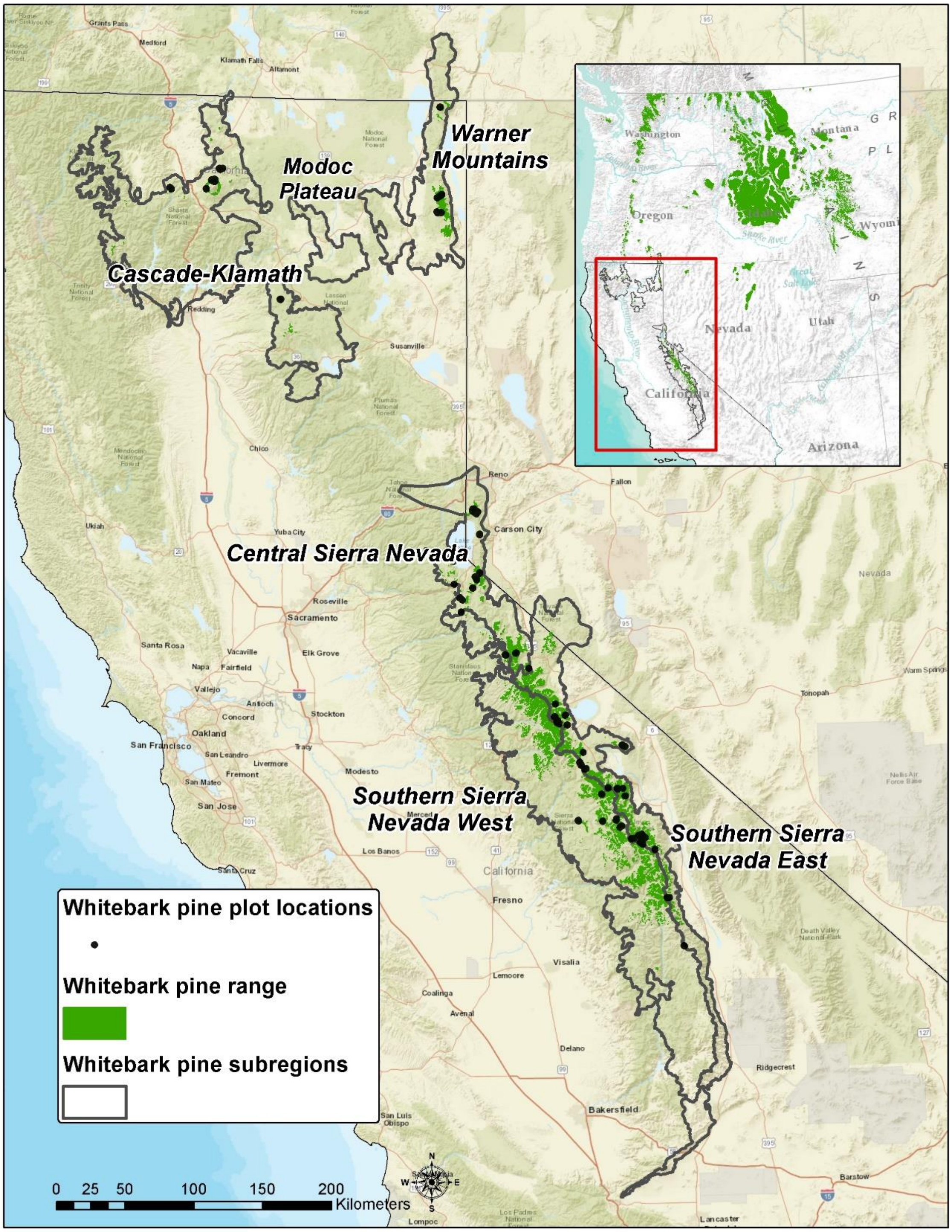
[17] As exceptions, whitebark pine regeneration densities in the Warner Mountains and clonal stem densities in the Cascade-Klamath are low relative to other subregions (the latter may be a sampling artifact; see Results section).

[18] Sufficient densities of small stems (regeneration + clonal stems) are based on whether subregional estimates are within or exceed NRV for tree density. Whitebark pine regeneration densities in the Warner Mountains are near the low end of NRV.

[19] Other high elevation white pine species include foxtail pine, limber pine, and western white pine.

[20] Based on climate projections for whitebark pine by Warwell et al. (2007), Roberts and Hamann (2016) and other sources summarized in Meyer and North (2019) and Coppoletta et al. (in press).

Figure 1. Map of whitebark pine geographic range, subregions of occurrence, and plot locations (244 total) in California[21].



[21] The Modoc Plateau shown in the map contained a single polygon of whitebark pine that has not been verified, but is suspected to be unoccupied by the species. Whitebark pine range map in California is based on Slaton (2020) and western North America (inset map) is based on The National Whitebark Pine Restoration Plan (2019).

Supplemental Tables and Figures

Table 14. Area and percent of whitebark pine distribution by management unit in California.

Management Unit	Area (ha)	%
Eldorado NF	332	0.2
Humboldt-Toiyabe NF	19534	13.6
Inyo NF	47872	33.4
Klamath NF	632	0.4
Lake Tahoe Basin Management Unit	5630	3.9
Lassen NF	301	0.2
Modoc NF	10009	7.0
Sequoia NF	92	0.1
Shasta-Trinity NF	2167	1.5
Sierra NF	14122	9.9
Stanislaus NF	1323	0.9
Tahoe NF	2	<0.1
Total NFS lands	**102017**	**71.2**
Lassen Volcanic NP	143	0.1
Sequoia and Kings Canyon NPs	18794	13.1
Yosemite NP	22206	15.5
Total NPS lands	**41143**	**28.7**

Table 15. Area and percent of whitebark pine distribution in protected areas of California.

Protected Area	**Area (ha)**	**%**
Lassen Volcanic NP Wilderness[22]	67	0.05
Sequoia and Kings Canyon NPs Wilderness[16]	18794	13.03
Yosemite NP Wilderness[16]	22171	15.37
Ansel Adams Wilderness	7553	5.24
Carson-Iceberg Wilderness	4012	2.78
Desolation Wilderness	712	0.49
Dinkey Lakes Wilderness	17	0.01
Emigrant Wilderness	58	0.04
Golden Trout Wilderness	125	0.09
Hoover Wilderness	12689	8.80
John Muir Wilderness	39426	27.33
Marble Mountain Wilderness	26	0.02
Mokelumne Wilderness	293	0.20
Monarch Wilderness	24	0.02
Mt. Rose Wilderness	448	0.31
Mt. Shasta Wilderness	1922	1.33
Owens River Headwaters Wilderness	1804	1.25
Russian Wilderness	4	0.00
South Sierra Wilderness	18	0.01
South Warner Wilderness	5812	4.03
Thousand Lakes Wilderness	295	0.20
Trinity Alps Wilderness	81	0.06
Harvey Monroe Hall Research Natural Area	553	0.38
Red Butte - Red Fir Ridge Research Natural Area	19	0.01
Sentinel Meadow Research Natural Area	191	0.13
Inventoried Roadless Area 1B[23]	12848	8.91
Inventoried Roadless Area 1C[17]	14310	9.92

[22] 99.7% of the area occupied by whitebark pine in California's national parks are in wilderness.
[23] Inventoried Roadless Area class 1B includes areas where road construction and reconstruction is prohibited, and class 1C includes areas where road construction and reconstruction are not prohibited.

Table 16. Mean ± SE whitebark pine young seedlings (<5 years old), all seedlings, saplings, total regeneration (seedling + sapling), and presumptive clonal stem densities (no./ha) and percentage of plots containing ≥250 small whitebark pine stems per ha among subregions of California.

Subregion	Young Seedlings	All Seedlings	Saplings	Seedlings & Saplings	Clonal Stems[24]	% Plots with ≥250 small stems/ha
Cascade-Klamath	190 ± 76	509 ± 128	172 ± 55	681 ± 147	21 ± 12 (3%)	68
Warner Mountains	14 ± 6	72 ± 22	56 ± 14	128 ± 32	51 ± 15 (28%)	23
Central Sierra	27 ± 8	147 ± 34	302 ± 115	449 ± 123	235 ± 73 (34%)	51
Southern Sierra – West	122 ± 30	162 ± 33	316 ± 67	478 ± 89	284 ± 84 (37%)	69
Southern Sierra - East	242 ± 41	442 ± 68	383 ± 45	826 ± 105	1035 ± 226 (56%)	78
Statewide	151 ± 21	315 ± 37	305 ± 36	620 ± 61	569 ± 109 (48%)	64

Table 17. Mean ± SE shrub and herb cover in whitebark pine plots among subregions of California.

Subregion	Shrub Cover (%)	Herb Cover (%)
Cascades-Klamath	24 ± 1	3 ± 5
Warner Mountains	17 ± 1	24 ± 4
Central Sierra	5 ± 1	7 ± 2
Southern Sierra - West	10 ± 1	18 ± 4
Southern Sierra - East	4 ± 1	12 ± 1
Statewide	9 ± 1	12 ± 1

[24] Percentage of small stems that are presumptive clonal stems (not regeneration) are included in parentheses.

Table 18. Mean ± SE surface fuel loading (tons/acre) in whitebark pine plots among subregions of California. Cascade-Klamath is not included due to an inadequate sample size of fuel transects in this subregion.

Subregion	1-hr	10-hr	100-hr	Total Surface Fuel Load[25]	Fuel Depth (cm)
Warner Mountains	0.072 ± 0.023	0.018 ± 0.003	0.014 ± 0.004	43.6 ± 14.6 (3.9)	4.6 ± 0.7
Central Sierra	0.037 ± 0.005	0.018 ± 0.003	0.010 ± 0.002	36.4 ± 9.4 (5.8)	4.2 ± 0.8
Southern Sierra - West	0.021 ± 0.010	0.012 ± 0.004	0.007 ± 0.002	54.7 ± 27.6 (0.3)	2.6 ± 0.6
Southern Sierra - East	0.045 ± 0.004	0.020 ± 0.002	0.006 ± 0.001	33.8 ± 7.3 (4.3)	2.9 ± 0.2
Statewide	0.044 ± 0.004	0.019 ± 0.002	0.008 ± 0.001	38.0 ± 5.8 (4.3)	3.4 ± 0.2

[25] Median values are in parentheses.

Figure 2. Krummholz and non-krummholz whitebark pine ecosystems in the Cascade-Klamath subregion (Shasta-Trinity National Forest). Note the high density of shade-tolerant conifer species in the right panel.

Figure 3. Open canopy (top panel) and closed canopy (bottom panel) whitebark pine stands in the Warner Mountains (Modoc National Forest). The bottom panel shows a seral whitebark pine site where whitebark pine is being replaced by white fir through forest succession in the absence of fire.

Figure 4. Whitebark pine stands in the Central Sierra Nevada. The left panel shows a pure, relatively open whitebark pine stand on the Eldorado National Forest. The right panel shows a whitebark pine stand with mountain hemlock regeneration on the Lake Tahoe Basin Management Unit.

Figure 5. Whitebark pine stands in the Southern Sierra West (Sierra National Forest), including recent tree mortality in the foreground of the upper panel.

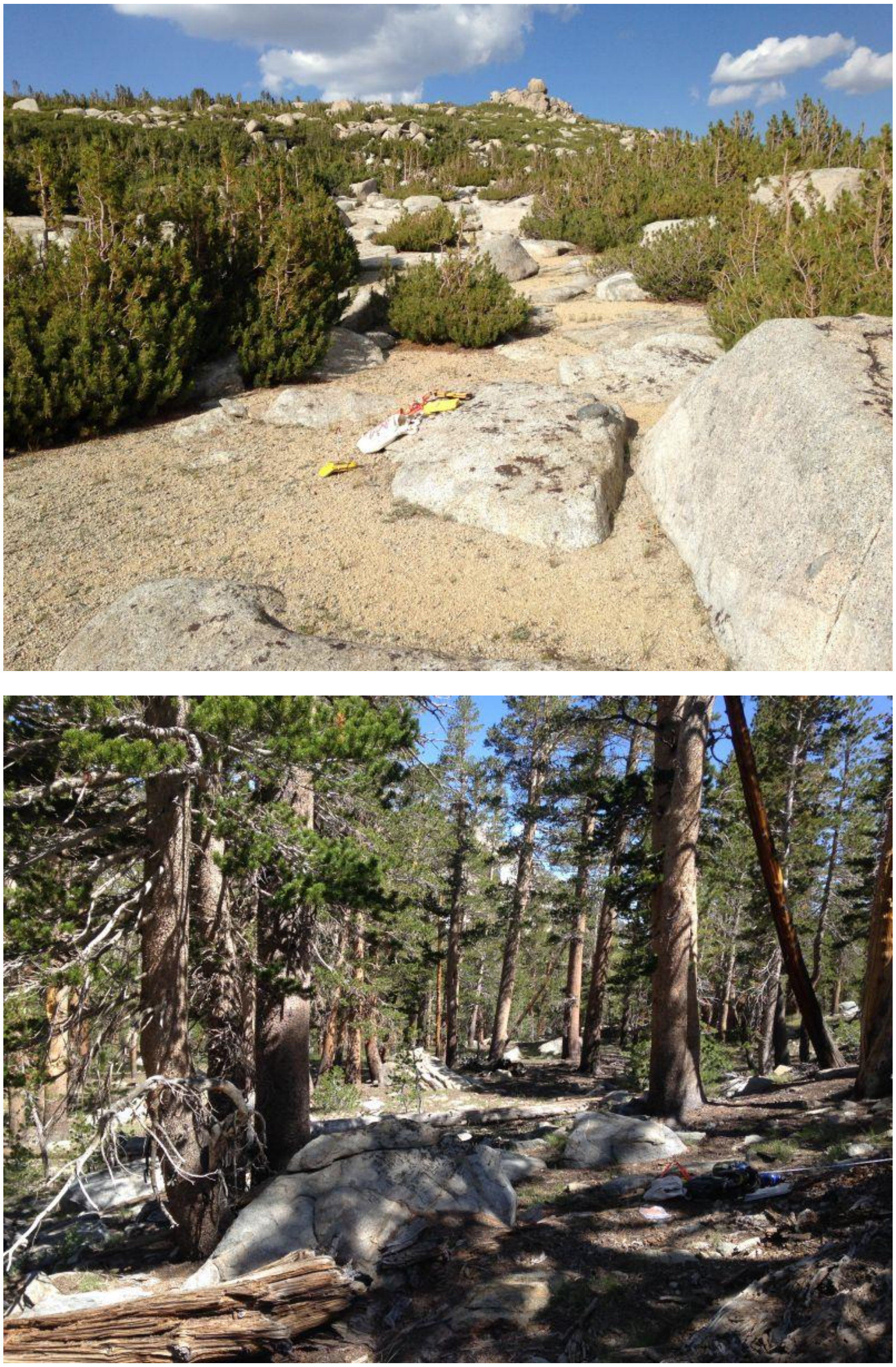


Figure 6. Whitebark pine stands in the Southern Sierra East (Inyo National Forest), including krummholz (upper panel) and non-krummholz (bottom panel) structural types. The bottom panel shows a mixed lodgepole pine-whitebark pine stand that is common in many parts of the Sierra Nevada.