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Ecological integrity of whitebark pine ecosystems in California's national forests

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Abstract

Whitebark pine (*Pinus albicaulis*) forest ecosystems in California are diverse and unique, yet their current status and condition are uncertain. Using a combination of geospatial and field 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. We found whitebark pine ecosystems to be structurally, compositionally, and functionally distinct among subregions of California, and all subregions displayed some evidence of declining ecological integrity. Whitebark pine forests in northern California exhibited signs of greater stand densification (Cascade–Klamath), potential encroachment by shade-tolerant conifer species (Cascade–Klamath and Warner Mountains), and increased tree mortality associated with mountain pine beetle outbreaks (Warner Mountains) than elsewhere in California. Whitebark pine stands in the Sierra Nevada showed signs of stand densification (central Sierra) and localized mountain pine beetle outbreaks (southern Sierra east). Notwithstanding these negative signs, much of the state's whitebark pine ecosystems on national forestlands appear to be relatively healthy and intact compared to more northern latitudes. Active management may be required to restore whitebark pine ecosystems on national forests in California with declining integrity, including stands experiencing substantial stand densification, encroachment by shade-tolerant conifers, and mountain pine beetle outbreaks.

Key words: whitebark pine, California, national forests, ecosystem integrity, mountain pine beetle, white pine blister rust

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 threatened species under the US Endangered Species Act (US Fish and Wildlife Service 2022). 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 for California (USDI and USDA 2020). These strategies require sufficient region-specific data sources, including remote sensing and field plot data, to effectively assess the current condition and future 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*a*).

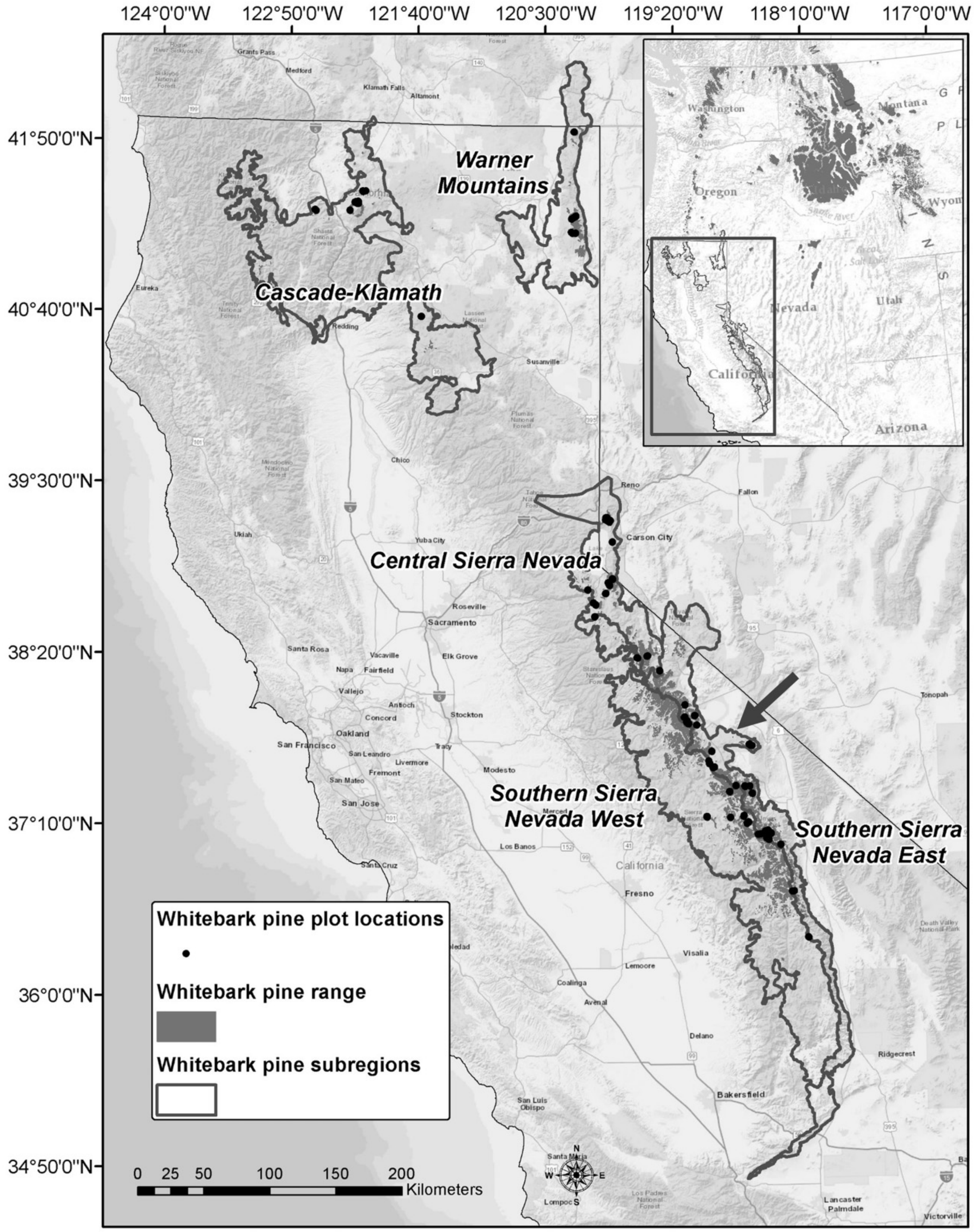
Whitebark pine ecosystems in California represent a unique segment of the species' geographic range, yet relatively few studies have occurred in the region. Populations in the state occupy four distinct physiographic regions, including the Klamath Mountains, Southern Cascades, Basin and Range (e.g., Warner Mountains and 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 (Nesmith et al. 2019; Slaton et al. 2019*a*; Jules et al. 2020), although these stressors have become more apparent in recent years, especially in more northern latitudes of the species' range (e.g., Maloney et al. 2012; Millar et al. 2012; Jackson et al. 2019). Whitebark pine communities in California often contain different species than other parts of the range (e.g., Rocky Mountains and Northern Cascades), including foxtail pine (*Pinus balfouriana*), limber pine (*Pinus flexilis*), western white pine (*Pinus monticola*), Sierra juniper (*Juniperus grandis*), red fir (*Abies magnifica*), white fir (*A. concolor*), or Jeffrey pine (*Pinus jeffreyi*) (Sawyer et al. 2009; Meyer and North 2019; Coppoletta et al. 2021). Mixed stands of whitebark pine and Sierra lodgepole pine (*Pinus contorta* ssp. *murrayana*) are especially common throughout the region (Slaton et al. 2019*a*; 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 2018), although mountain hemlock (*Tsuga mertensiana*) is a frequent associate of whitebark pine communities in parts of the state (Sawyer et al. 2009). Whitebark pine occurs as a dominant or codominant subalpine conifer at much higher elevations in California than elsewhere, often at elevations exceeding 2500 m in the southern Cascades and 3000 m in the Sierra Nevada (Arno and Hoff 1990). Additionally, above 3500 m elevation in the Sierra Nevada, whitebark pine often occurs in a broad, contiguous zone of monotypic, krummholz vegetation, especially on exposed sites near treeline, whereas this zone is narrower and more scattered in other parts of the range (Miller et al. 2020). Historical (i.e., pre-Euro-American colonization) fire regimes in Californian whitebark pine and other high elevation white pine forests may be notably different than elsewhere, 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), a pattern observed in other high elevation forest types in California (e.g., Merriam et al. 2022).

Despite this distinctiveness of California's whitebark pine forests, these ecosystems have received scant attention in the scientific literature until recently (Slaton et al. 2019*a*; Jules et al. 2020). Plot-scale analyses of whitebark pine in California have often been confined 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, Dudney et al. 2020), resulting in few subregional comparisons or larger scale analyses. Regional analyses of whitebark pine forests in California are limited to subregional patterns in disturbance agents and stand densities (Slaton et al. 2019*b*), white pine blister rust occurrence (Maloney 2011) and environmental correlations (Dunlap 2012), and recent tree mortality patterns based on aerial detection survey (ADS) data (Millar et al. 2012). Collectively, these studies suggest increasing signs of pathogens, insect outbreaks, and drought stress (the latter two stressors often associated with climate change) that may be negatively impacting the integrity of whitebark pine and other high elevation forest ecosystems in California (Meyer and North 2019; Coppoletta et al. 2021).

Ecosystem integrity is the state of an ecosystem whereby dominant structural and compositional components are similar to reference conditions (i.e., relatively undisturbed ecosystems that are within the historical range of variability, including both historical and contemporary reference information) and can sustain normal ecosystem functioning in response to perturbations and stressors (SER 2004; Palmer et al. 2016). Although the concept of ecological integrity has its limitations (e.g., applicability for highly altered ecosystems, incorporating climate change impacts), it does provide an operational framework for land managers to evaluate and monitor the condition and trend of targeted ecosystems (Wurtzebach and Schultz 2016). For whitebark pine ecosystems, signs of declining ecological integrity in whitebark pine ecosystems may include elevated mountain pine beetle and white pine blister rust occurrence, high climate exposure (i.e., degree of climatic change), and altered fire regimes (e.g., current fires burning too infrequently relative to the historical fire frequency) which has led to increased stand densification, landscape homogenization, encroachment by shade-tolerant conifers (e.g., mountain hemlock, fir species), and drought stress (Aubrey et al. 2008; Keane et al. 2012, 2017; Dolanc et al. 2013). Whitebark pine ecosystems that experience precipitous declines in ecological integrity can disrupt many fundamental ecological processes of high elevation landscapes (Ellison et al. 2005) and are often considered priority areas for forest restoration (Aubrey et al. 2008; Keane et al. 2012). In contrast, whitebark pine ecosystems with a high degree of ecological integrity exhibit structural (e.g., stand density) and functional (e.g., fire regime) elements within the historical range of variability (Keane et al. 2009, 2012). This includes a low incidence of insects and pathogens, sufficient natural regeneration dominated by whitebark pine, limited shade-tolerant conifer encroachment, a prevalence of low to moderate density stands across the landscape, and diverse seral and structural classes at landscape scales (including the presence of krummholz growth form at high elevations) (Tomback et al. 2001; Keane et al. 2012; Hansen et al. 2016). Additionally, whitebark pine and other forest ecosystems that are anticipated to maintain high integrity in response to climate change have limited climate exposure (i.e., lower degree of anticipated climatic change), ample climate refugia for persistence or expansion, and a high proportion of their geographic range within reserves or protected areas (e.g., wilderness, federal lands) that limit the effect of anthropogenic stressors (Swanston et al. 2012; Hansen et al. 2016; Keane et al. 2017).

The purpose of our study was to evaluate whether there are signs of declining integrity in whitebark pine forest ecosystems of California's national forests based on indicators of ecosystem structure, composition, and health (e.g., shade-tolerant conifer encroachment, elevated stand densities, and high levels of tree mortality due to insects and pathogens). We used a comprehensive network of field plot and geospatial data focused on national forest lands in California for our evaluation of whitebark pine ecosystem integrity. We evaluated current conditions and potential subregional differences in each indicator to investigate broader geographical patterns in ecological integrity and stressors in whitebark pine forests of California's national forests.

Fig. 1. Map of whitebark pine geographic range, subregions of occurrence, and plot locations (244 total) in California. The Glass Mountains in the southern Sierra Nevada east subregion is indicated by the arrow. Whitebark pine range map in California is based on USDA Forest Service (2020a) and western North America (inset) range map is based on the National Whitebark Pine Restoration Plan (2019).



Methods

Study area and plot selection

Our study area included the entire geographic range of whitebark pine on National Forest system land within the state of California, including five major subregions identified and mapped in Slaton et al. (2019*a*) and USDA Forest Service (2020*a*): (1) Cascade and Klamath Mountains, (2) Warner Mountains, (3) central Sierra Nevada, (4) southern Sierra Nevada west, and (5) southern Sierra Nevada east (Fig. 1). We based these subregions on distinct physiographic units in California that represent major changes in biophysical features (i.e., geology, geomorphology, soils, and climate) and vegetation (Barbour et al. 2007; Graham and O'Geen 2016). 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 in the Great Basin province) and due to its proximity to and connectivity and biophysical similarity with the southern Sierra Nevada east (Fig. 1). Similarly, we combined the Cascade and Klamath Mountains (which are separate and distinct ranges) into one subregion, because of their proximity, connectivity, biophysical similarity, and our relatively small sample size per range.

Our dataset consisted of whitebark pine stands spatially delineated as polygons as described in USDA Forest Service (2020*a*), including a total of 12 926 polygons ranging from 0.01 to 1044 ha in size (Fig. S1). Though variable in size, each polygon represents a vegetation stand with relatively uniform topography and climate, as a result of the original process used to delineate them, which was based on a combination of Landsat-based classification and heads-up digitization (USDA Forest Service 2020a). We then selected topographic and climatic variables widely recognized as potential drivers of species' distributions, including that of whitebark pine: latitude, elevation, slope, topographic position, and potential evapotranspiration (PET). Latitude and elevation are correlated to precipitation and temperature at broad geographic scales, and slope, topographic position, and PET are generally related to incident radiation, temperature, and snow and moisture retention at the stand scale (Millar et al. 2012; Thorne et al. 2016; Cartwright 2019). We omitted other variables (e.g., temperature, precipitation, and aspect) that exhibited autocorrelation with our selected topographic and climate variables. We summarized values for each of the four selected variables (latitude, elevation, slope, topographic position, and PET) at the polygon level, binned these values into four classes of equal size, and used them to stratify sampling across the study area. We used a 30 m digital elevation model to create a raster for topographic position index (landscape concavity or elevation relative to the mean elevation of the surrounding landscape using ArcGIS 10.3 Topography Tools and a 500 m radius). We obtained PET (i.e., evaporative demand; PET; 270 m resolution) from the Basin Characterization Model (BCM) as modeled for years 2010–2039 under the A2 climate scenario (Flint and Flint 2014). The BCM dataset was selected for its good performance in mountainous terrain, and multi-year projected averages that encompassed our entire sample period (Flint et al. 2013). We categorized each variable into three classes (low, moderate, and high) to ensure field sampling would capture a wide range of environmental conditions, which resulted in 25 stratification units (two stratification units at high latitude and high PET did not occur in our study area and were dropped from further consideration). We then selected ten random polygons from each stratification group using the subset features tool in Geostatistical Analyst ArcGIS 10.1, giving all polygon sizes an equal probability of selection. When a stratification group contained less than 10 polygons (stratification groups 22, 23, 24, and 25), all polygons were selected. We randomly prioritized the order of sampling of these polygons within each stratification group.

As compared to an area-weighted approach, this method ensured that smaller stands, which may represent ecologically unique settings in species composition or biophysical environment, had an equal chance of being included in our field sampling. Our aim was to represent the broad ecological diversity of whitebark pine forests, rather than only emphasize the most common types. We chose to sample at least three polygons per stratification group, but accessibility constraints resulted in limited samples for some (stratification groups 2, 3, 5, 9, and 17; Table S1). Within each randomly selected polygon, we sampled two–five plots, with the first established at least 16.1 m (the plot radius length) beyond the initial whitebark pine encountered within the polygon. Inaccessible and exceptionally steep terrain typically precluded randomized plot placement, and we selected locations to be representative of the stand structure dominant within the polygon (i.e., we avoided areas with atypical slope breaks or shallow soils lacking vegetation cover for respective polygons and targeted the most common stand structural conditions). Each plot was separated by at least 50 m. In cases where whitebark pine was not found within a mapped polygon, we established plots in the closest site available. In some cases where neighboring sites were unavailable, we selected a new polygon from the stratification unit.

Field plot data collection

We surveyed whitebark pine stands in our study area primarily between June and September of 2016–2019 (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) and established an additional 205 plots with our stratified random sampling design; we did not detect a noticeable effect of plot size on measured stand variables. The larger plot size increased the utility of the dataset for validating and calibrating remote sensing products for planned future studies (Landsat satellite data are 30 m pixels) and increased the likelihood that plots included adequate stem numbers to accurately represent stand structural variability.

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 (personal communication, M. Slaton). The establishment process, time frame, data collected, and general stand conditions were the same for random and systematic plots as well as 0.05 and 0.08 ha plots (with the exception of time frame as noted above).

Our complete sampling strategy (random and systematic plots) 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

(Fig. 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 and much of the variation in biophysical variables we used to define our sampling strata (as supported by the higher number of strata in the Sierra Nevada). Most plots were 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%).

Within the entire area of 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. 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 (defined as ≤1 m of the base of a neighboring stem), % live crown (i.e., compacted live crown), the 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 (up to 4 years based on degree of crown discoloration, dead needle and branch retention, and pitch tube condition), cone abundance rating (0, 0 cones; 1, 1–10 cones; 2, 11–100 cones; 3, >100 cones; representing current year cone production), and evidence of other insects and pathogens (recorded for live and dead trees). We distinguished high-elevation white pine species in subregions with overlapping distributions based on readily observable field characteristics (e.g., cone morphology, needle margin features, and bark coloration and pattern). We recorded the presence of white pine blister rust if a bole or branch contained aecia. During data analysis, we further identified white pine blister rust if at least two primary symptoms of infection were observed (i.e., cankers, branch swelling, conspicuous dead "flagged" branches, and gnawing of bark). We estimated mountain pine 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; and 3, many pitch tubes spread throughout bole. We calculated live and dead tree density and basal area based on full stem inventories of each plot. We estimated the proportion of whitebark pine tree crowns with crown loss (foliage browning or chlorotic needles) that we suspected was caused by moisture stress, insects, or pathogens as the proportion of dead (yellow, red, or gray), or dropped (missing, as evident from small branches without needles, or leaf-less fascicles remaining on stem) foliage relative to the total crown. We identified small, whitebark pine presumptive clonal stems based on their immediate proximity to tree clusters (distance, <1 m), basal stem angle (directed 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 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 a separate cardinal direction. 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 mean tree height approximately <3 m (maximum tree height <12 m) to estimate the proportion of plots characterized by krummholz. We selected these thresholds following inspection of plot photographs and testing numerous structural attribute summaries, with the purpose of facilitating summaries of two broad categories of plot structures, namely those generally characterized by krummholz mats or layers as opposed to upright trees. 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.

Geospatial data

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 (USDA Forest Service 2020*a*) occurring within specific land ownerships (e.g., national forests and 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 publicly available data (USDA Forest Service 2020*b*). 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 neighboring areas burned more than once in separate years to avoid double counting areas of overlap. We used USFS ADS data (USDA 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 predetermined flight paths, which may include opportunistic ground-based field surveys to verify mortality agents (USDA 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

Table 1. Primary indicators and evaluating evidence of declining and high ecological integrity in whitebark pine ecosystems on national forests in California.

Indicator of ecological integrity	Evaluating evidence
Declining ecological integrity	
Shade-tolerant conifer encroachment	This study; Dolanc et al. 2013, 2014; Jackson et al. 2019
Tree densification*	This study; Dolanc et al. 2013, 2014
Elevated mountain pine beetle activity	This study; Millar et al. 2012; Meyer et al. 2016
Increased white pine blister rust incidence	This study; Maloney 2011; Jackson et al. 2019; Nesmith et al. 2019; Dudney et al. 2020
High climate exposure*	Warwell et al. 2007; Thorne et al. 2016
High ecological integrity	
Low fire regime departure*	Safford and Van de Water 2014
Climate refugia present*	Warwell et al. 2007; Thorne et al. 2016
Sufficient small stem densities	This study
High percentage of range in protected areas	This study

*Evidence of tree densification, climate exposure, low fire regime departure, and climate refugia are also documented in studies summarized in Meyer and North (2019) and Coppoletta et al. (2021).

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 (M. Slaton, personal observation). Despite technical challenges with accurately mapping tree mortality, the ADS dataset is the corporate data product currently used for forest health reporting by national, state, and private entities, and it is frequently used to evaluate large scale patterns in tree mortality in California (e.g., Young et al. 2017).

Data analysis and evaluation criteria

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 occurrence based on the tally of all live stems ≥ 7.6 cm dbh in plots. Tree regeneration estimates included seedlings (<1.37 m height) and saplings (<7.6 cm dbh) but excluded small diameter (<7.6 cm dbh) presumptive clonal stems arising from a tree cluster. In comparison, small stems estimates included seedlings, saplings, and small diameter presumptive clonal stems. Unlike seedings and saplings, clonal stems (excluding krummholz) are oriented more horizontally, often structurally more homogeneous (i.e., similar size class distribution), and spatially associated with (i.e., arising from) mature stems within a cluster (Meyer et al. 2016, Slaton et al. 2019*b*). Both regeneration (i.e., product of sexual reproduction) and small stems (i.e., sexual reproduction and clonal generation) provide important insights in future forest recruitment patterns that influence the composition, structure, and resilience of whitebark pine stands.

Our evaluation criteria and corresponding evidence for whitebark pine ecosystem integrity were based on several important indicators (Table 1). We identified shade-tolerant conifers in whitebark pine forests of California (i.e., mountain hemlock, white fir, red fir, western hemlock, and noble fir) based on information summarized in Meyer and North (2019) and Coppoletta et al. (2021). Subregions with evidence of potential shade-tolerant conifer encroachment in whitebark pine stands had a high proportion (>50%) of shade-tolerant species by frequency or density in the smaller size classes (i.e., <7.6 cm diameter). We based tree density threshold values that exceeded the historical range of variation (HRV) on mean ± 2 standard deviations values summarized for Sierra Nevada and Cascade–Klamath subalpine stands in Meyer and North (2019) and Coppoletta et al. (2021), respectively. We used mean tree densities (live + dead) of high mortality stands (i.e., those experiencing mountain pine beetle outbreaks) documented in Meyer et al. (2016) as threshold values associated with elevated risk of mountain pine beetle attack in Sierra Nevada whitebark pine stands. We used ADS data to detect elevated mountain pine beetle activity and to characterize more frequent outbreak conditions across a subregion. Subregions with increased white pine blister rust incidence based on ADS or field plot data contained a higher relative frequency of white pine blister rust occurrence in whitebark pine compared to other subregions in California. We identified subregions of high climate exposure and climate refugia based on published climate model projections for whitebark pine in California and elsewhere, where range contraction was expected to exceed 90% (climate exposure) or whitebark pine is projected to persist as extensive and contiguous ecosystems within high-elevation landscapes (climate refugia) by the end of the 21st century. Low fire regime departure was indicative of whitebark pine ecosystems within a subregion where the current fire return interval and fire severity patterns were relatively similar to the historical reference (i.e., HRV) condition, especially compared to other lower-elevation forest types. We consulted agency guidance in revised land management plans for national forests in California to identify surface fuel load thresholds for high elevation stands (USDA 2022). We used whitebark pine reforestation guidelines in the western USA based generally on reference stands (i.e., Shoal et al. 2008; Keane et al. 2012, McCaughey et al. 2009) to establish a threshold density of regenerating whitebark pine (≥247 small stems/ha). We

Table 2. Percent of whitebark pine distribution among California's subregions (all land ownerships) and % of distribution within a subregion with signs of mountain pine beetle, white pine blister rust, and fire occurrence based on geospatial and aerial detection survey data (national forest lands only). The total number of installed field plots for each subregion is provided in the last column.

Subregion	Whitebark pine distribution (%)*	Mountain pine beetle (%)†	White pine blister rust (%)†	Wildland fire (%)‡	Number of field plots
Cascades–Klamath	2 (8)	44	0	0.9	25
Warner Mountains	7 (0)	75	0	3.9	22
Central Sierra	12 (0)	14	0.1	0.6	59
Southern Sierra—West	40 (71)	16	0	0.1	26
Southern Sierra—East	39 (0)	22	0	0.7	112
Total (statewide)	100 (29)	26	0.02	0.9	244

*Percent of the total statewide area (all land ownerships) of whitebark pine attributed to each subregion. The % of whitebark pine distribution attributed to other lands besides national forests (i.e., national parks) within a subregion is provided in parentheses.

†Based on aerial detection survey data (2008–2019).

‡Based on fire return interval departure geospatial data (1945–2019).

arbitrarily considered subregions with a majority (>50%) of plots exceeding this threshold value to have sufficient natural regeneration indicative of resilient whitebark pine ecosystems with relatively high ecological integrity. We identified protected areas based on wilderness and inventoried roadless area boundaries or federal land ownerships.

Results

Statewide indicators based on geospatial data

Approximately 91% of whitebark pine in California (all land ownerships) occurs in the Sierra Nevada (79% occurs in the southern Sierra Nevada), with relatively smaller and more isolated populations occurring in the Cascade–Klamath and Warner Mountains (Table 2). Seventy-one % of the distribution of whitebark pine in California occurs on National Forest lands, with the remaining 29% on National Park Service lands primarily in the Southern Sierra west (Table S2); only 0.09 ha (<0.001%) 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 roadless areas (13% excluding overlap with wilderness), and research natural areas (0.5%) (Table S3). 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 2004). Developed recreation sites occur in approximately 1.5% of whitebark stands, with nearly all of these sites (98%) located in four developed ski areas (i.e., Heavenly, Mammoth Mountain, June Mountain, and Mount Rose).

Between 2008 and 2019, ADSs detected mountain pine beetle related tree mortality in 26% of whitebark pine stands on national forests in California (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 located within national forests of California (0.01% of the statewide range), with all records located in the central Sierra subregion (recorded in 2015 and 2016). Seventy-six % of these hectares also contained records of mountain pine beetle activity. Over the past 75 years, 1296 ha of whitebark pine in the state's national forests has burned (<1% of the statewide range), and < 1% of burned whitebark pine stands have experienced two fires during this period.

Field plot indicators: species composition

Whitebark pine plots were located in high elevation sites across all subregions of California's national forests, generally between 2400 and 3150 m elevation (Table S4). Statewide, approximately 40% (range: 33%–46%) of field plots with forest cover (excludes plots lacking stems classified as trees) 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 species associated with whitebark pine, in order of relative frequency, included lodgepole pine, white fir, western white pine, red fir, and mountain hemlock (Table 3); 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 (*Populus tremuloides*), foxtail pine, limber pine, ponderosa pine (*Pinus ponderosa*), western hemlock (*Tsuga heterophylla*), Sierra juniper, and curlleaf 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 and 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 Nevada and Cascade–Klamath only.

Table 3. Percent frequency of tree species associated with whitebark pine stands among California's subregions based on field plot data*.

Subregion	Lodgepole pine	White fir	Western white pine	Red fir	Mountain hemlock	Jeffrey pine	Aspen	Foxtail pine	Limber pine†	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
Southern Sierra—West	62	0	5	0	0	0	0	5	0	0	0
Southern 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

*Species with < 1% statewide occurrence were not included (i.e., curl-leaf mountain mahogany, Sierra juniper).
†67% of limber pine occurrences in the southern Sierra east were in the Glass Mountains.

Table 4. Frequency of occurrence of small stems (includes seedlings, saplings, and presumptive clonal stems < 7.6 cm dbh) by species group* within stand inventory plots and percentage of plots containing small whitebark pine stems only within whitebark pine stands by subregion.

Subregion	Whitebark pine (%)	Shade tolerant species (%)†	Other pines (%)‡	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

*Does not include aspen (occurs in 3% of plots), Sierra juniper (2%), and curl-leaf mountain mahogany (<1%).
†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%).
‡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.

Within small stem classes (includes seedlings, saplings, and clonal stems < 7.6 cm dbh), shade-tolerant conifers had the highest occurrence and relative density in the Cascade–Klamath and Warner Mountains and lowest in the Sierra Nevada (Table 4; Fig. 2). The proportion of plots where shade-tolerant conifers dominated (i.e., >50% of stems by density) also was greatest in the Cascade–Klamath and Warner Mountains (36% of plots in both subregions) compared to the Sierra Nevada (≤3% of plots). Small stems of other pines (excluding whitebark pine; 65% attributed to lodgepole pine) were generally higher in the Sierra Nevada than other subregions and had relatively low proportional density statewide. A total of 79% of small stems were attributed to seedlings and saplings statewide (range: 70%–93% by subregion). Small stem densities were highest in the southern Sierra east and Cascade–Klamath, and 66% of plots exceeded 247 small stems per ha statewide (Fig. 2; Table S5). Only a single plot (0.4% of total) lacked small stems of any conifer species. Statewide, 96% of clonal stems, 50% of seedlings, and 70% of saplings were attributed to whitebark pine. Whitebark pine 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 stem densities) (Table S5).

Field plot indicators: stand health and structure

Sign of mountain pine beetle, white pine blister rust, and recent fire activity was infrequently encountered within field plots (Table 5). At the subregional scale, the percentage of whitebark pine trees attacked by mountain pine beetle ranged from 1.7% to 2.9%, with the highest percentage in the Warner Mountains. At the state level (all subregions combined), approximately 2% of plots contained signs of elevated mountain pine beetle activity (>25% of trees attacked) primarily between 2016 and 2019 (2% of observations were from 2014), and attacked trees averaged 12 cm in diameter (range: 8–30 cm). 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. 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 Nevada. Only 0.8% of plots representing two locations in the southern Sierra Nevada 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 (Table 5). Seventy-six % 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 6). A greater percentage of plots in the Cascade–Klamath and the central Sierra contained tree densities that exceeded the upper limit of HRV for subalpine forest stands

Fig. 2. Mean ± standard error small stem densities (No./ha, includes seedlings, saplings, and presumptive clonal stems <7.6 cm dbh) and their proportional representation by species group (provided in Table 4) among subregions of California. See Table S5 for densities of whitebark pine small stems by size and structure class.

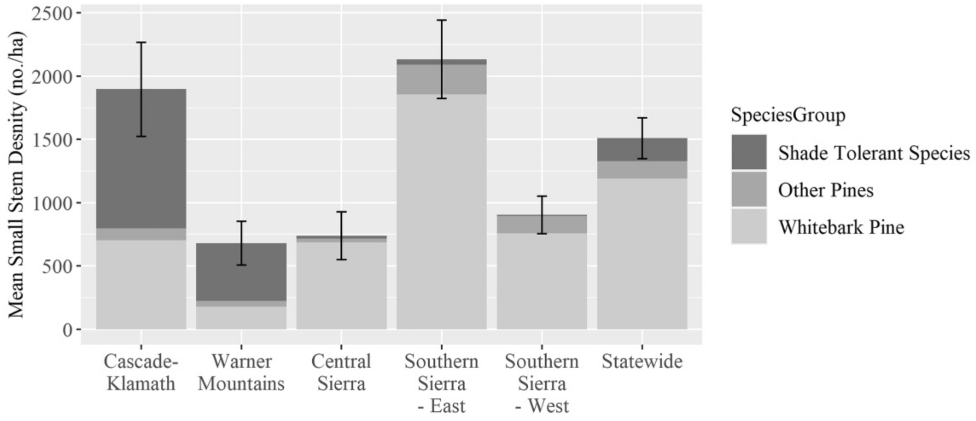


Table 5. Mean ± standard error percentage of whitebark pine trees exhibiting signs of mountain pine beetle attack or white pine blister rust, percentage of trees (all species ≥ 7.6 cm dbh included) that recently died (≤7 years), and percentage of plots showing signs of prior fire activity based on field plots only.

	Whitebark pine trees (%)			Plots (%)
Subregion	Mountain pine beetle	White pine blister rust	Recent tree mortality	Wildland fire
Cascade–Klamath	1.7 ± 1.3	3.2 ± 3.2	3.9 ± 1.8	0
Warner Mountains	2.9 ± 1.5	0	5.8 ± 2.7	12
Central Sierra	1.7 ± 0.7	2.3 ± 1.4	4.1 ± 1.3	2
Southern Sierra—West	2.3 ± 1.3	0	6.1 ± 2.0	18
Southern Sierra—East	2.0 ± 0.6	0	4.5 ± 1.0	8
Statewide	2.0 ± 0.4	0.9 ± 0.5	4.6 ± 0.7	7

Table 6. Mean ± standard error tree (≥7.6 cm diameter at breast height (dbh)) density, basal area, canopy cover, diameter, live crown, and crown loss among subregions of California.

	All tree species included			Whitebark pine trees only			
Subregion	Density (No./ha)	Basal area (m^2/ha)	Canopy cover (%)	Mean dbh (cm)	Live crown (%)	Crown loss (%)	Trees with cones (%)
Cascade–Klamath	842 ± 139	35.5 ± 5.6	23 ± 4	18.8 ± 1.5	69 ± 6	3 ± 3	43 ± 5
Warner Mountains	220 ± 43	16.9 ± 4.7	28 ± 6	18.2 ± 1.6	62 ± 6	1 ± 6	48 ± 9
Central Sierra	576 ± 67	23.0 ± 2.6	22 ± 2	19.8 ± 1.0	60 ± 3	6 ± 2	11 ± 3
Southern Sierra—West	208 ± 79	10.8 ± 2.6	18 ± 2	18.3 ± 0.8	58 ± 3	9 ± 3	30 ± 6
Southern Sierra—East	311 ± 28	17.8 ± 1.9	25 ± 2	17.1 ± 1.1	61 ± 2	7 ± 1	22 ± 3
Statewide	417 ± 30	20.2 ± 1.4	24 ± 1	18.2 ± 0.5	61 ± 1	6 ± 1	25 ± 2

(63% and 43%, respectively) or exceeded whitebark pine stand densities associated with elevated mountain pine beetle activity (46% and 27%, respectively) (Table 7). In contrast, only 10%–20% of plots in the Warner Mountains and southern Sierra Nevada exceeded HRV for tree density and 0%–10% of these plots contained tree densities associated with elevated risk of mountain pine beetle attack (Table 7). Mean basal area was generally higher in the Cascade–Klamath, with most other subregions averaging between 11 and 23 m^2/ha (Table 6). 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 (due to multiple stressors) was generally greater in the Sierra Nevada than the northern California subregions (Cascade–Klamath and Warner Mountains). In most subregions, the percentage of whitebark pine trees containing cones averaged approximately 20%–50%, except for the Central Sierra where an average of 11% of whitebark pine trees contained cones (Table 6). 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 recorded in whitebark pine plots were composed primarily of tree regeneration (seedlings and saplings)

Table 7. Percentage of plots with tree (≥7.6 cm diameter at breast height (dbh)) densities exceeding the upper limit of the historical range of variation (HRV; >432 trees/ha) and with tree densities associated with elevated risk of insect attack (>881 trees/ha)*.

Subregion	Plots exceeding HRV 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	34	14

*Tree density values are based on Meyer and North (2019) and Coppoletta et al. (2021) for HRV and Meyer et al. (2016) for elevated risk of mountain pine beetle attack.

in all subregions except the southern Sierra east, and young whitebark pine seedlings were relatively abundant in all subregions except the Warner Mountains and central Sierra (Table S5). The density and cover of short-statured (generally <3 m height) whitebark pine tree clusters attributed to presumptive clonal and krummholz stems were greater in the Sierra Nevada than the Cascade–Klamath and Warner Mountains (Table S6). The greatest percentage of plots dominated by krummholz whitebark pine were in the southern Sierra Nevada west.

Understory shrub and herb cover varied in whitebark pine stands (subregional mean range: 2%–24% and 3%–24%, respectively), with generally higher shrub cover observed in the Cascade–Klamath and Warner Mountains than other subregions (Table S7). 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: 46 ± 2%), rock (39 ± 2%), and bare ground (12 ± 2%), with very little coarse woody debris (2 ± 1%) observed across all subregions. Surface fuel loading varied substantially among plots within a subregion, although median values (<13 Mg/ha) indicated relatively low surface fuel loads in most plots (Table S8). Sporadic heavy surface fuel loads (mostly in the form of coarse woody debris, or 1000+ h 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 33.6 Mg/ha and maximum surface fuel loading ranging from 422 to 1021 Mg/ha.

Discussion

Whitebark pine forest ecosystems in California vary considerably in structure, composition, and health and occupy five distinct subregions in the state. 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 almost exclusively on federal lands, including a dozen national forests and four 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 ecological integrity 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 geospatial and field plot data and other information sources (Table 8). Potential for 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. This is consistent with recent studies documenting an increase in small diameter shade-tolerant conifers in whitebark pine and other subalpine forests of the Sierra Nevada (Dolanc et al. 2013, 2014) and the Cascade Range (Coppoletta et al. 2021). Similarly, the relative prevalence of lodgepole pine (generally considered relatively shade-intolerant; Arno and Hoff 1990) in whitebark pine stands of the Sierra Nevada may indicate encroachment as found by Slaton et al. (2019*b*), because lodgepole pine has increased in recent decades in the Sierra Nevada (Dolanc et al. 2013) and has the potential to colonize and replace whitebark pine stands over time (e.g., Jackson and Faller 1973). Tree densification (relative to HRV) is apparent in stands of the Cascade–Klamath, central Sierra, and elsewhere in California, consistent with previous assessments of subalpine forests (Meyer et al. 2019; Coppoletta et al. 2021). Such areas could be affected by long-term fire exclusion and climate change and are considered a priority for management actions to restore stand composition, reduce stand densities, and improve ecosystem integrity. However, it is likely that many whitebark pine stands in more exposed, lower productivity, and higher elevation sites (e.g., krummholz stands) naturally contain (i.e., within HRV) relatively high small stem densities of whitebark pine, indicative of environmental site controls that favor clonal sprouting instead of large diameter tree development. Nonetheless, stands with disproportionately few small diameter whitebark pine stems, relative to shade-tolerant conifer species (especially in the Warner Mountains), is likely evidence of declining integrity in whitebark pine stands.

The Warner Mountains are noteworthy for elevated levels of mountain pine beetle-related tree mortality in whitebark

Table 8. Indications of declining and high ecological integrity in whitebark pine ecosystems among California's subregions.

	Declining ecological integrity					High ecological integrity			
Subregion	Shade-tolerant encroachment	Tree densification	Increased MPB activity*	White pine blister rust*	High climate exposure	Low fire regime departure	Climate refugia present	Sufficient small stem densities†	High percent of range in protected areas
Cascade–Klamath	×	×	×	×	×	✓		✓	✓
Warner Mountains	×		×		×	✓			✓
Central Sierra		×		×	×	✓		✓	✓
Southern Sierra—West					×	✓	✓	✓	✓
Southern Sierra—East			×		×	✓	✓	✓	✓

*Increased mountain pine beetle (MPB) activity is based primarily on aerial detection survey data and is characterized by more frequent outbreak conditions across the subregion. White pine blister rust refers to the relative frequency of occurrence in whitebark pine compared to other regions in California.

†Sufficient densities of small stems (regeneration + presumptive clonal stems) are described in the Methods section. Small stem densities were marginally higher than this threshold in the Central Sierra.

pine stands (primarily occurring in 2007–2010), a pattern documented in this study and Millar et al. (2012) using ADS data. In contrast, our plot data were not effective at capturing mountain pine beetle occurrence at the larger subregional scale, likely because our plot sampling occurred a decade after the 2007–2010 mountain pine beetle outbreak event. In the coming decades, some 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 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 (<4 ha; Meyer and North 2019; Coppoletta et al. 2021) and undocumented in statewide fire history data (Safford and Van de Water 2014).

Signs of greater white pine blister rust activity in whitebark pine stands of the Cascade–Klamath and central Sierra observed in our study are corroborated by other recent surveys in these subregions (e.g., Maloney 2011; Maloney et al. 2012; Jackson et al. 2019; Dudney et al. 2020), possibly owing to latitudinal gradients in moisture in California (Dunlap 2012). However, ADSs and our plot surveys failed to detect this introduced pathogen in the southern Sierra west where it was documented to occur at low frequencies by Maloney (2011), Maloney et al. (2012), Nesmith et al. (2019), and Dudney et al. (2020). Additionally, our plot inventories in the central Sierra detected white pine blister rust at a frequency 10–15 times lower than Maloney (2011) and Maloney et al. (2012). This could be due to differences in the sampling methodology (e.g., larger size of plots in prior studies) and plot selection criteria (e.g., plot stratification factors and minimal tree density requirements for sampling) between studies, as well as the difficulty in detecting rusts and other localized pathogens from distant, aerial observations. Our observation of marginally higher crown loss in whitebark pine trees of the southern Sierra Nevada has been documented in red fir stands in the southern Sierra Nevada (Meyer et al. 2019) and may be indicative of increased moisture stress associated with climate change and recent drought; although a different pattern (i.e., increased crown loss following years of high precipitation) was observed by Nesmith et al. (2019) in whitebark pine and foxtail pine of the southern Sierra Nevada. 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 (Thorne et al. 2016; Meyer and North 2019; Coppoletta et al. 2021).

Understory vegetation cover and surface fuel loads in whitebark pine stands were broadly within the HRV or other targeted conditions for California, with some exceptions. Statewide estimates of understory (i.e., collective shrub and herbaceous plant) cover averaged 21%, which was similar to historical estimates of understory cover in the Sierra Nevada (24 ± 31% cover; Meyer and North 2019) and the Cascade–Klamath (range is 0%–65% but generally less than 25% cover in drier sites; Coppoletta et al. 2021). This suggests that secondary host species for white pine blister rust (e.g., *Ribes* spp. and *Castilleja* spp.) have not substantially increased over the past century in whitebark pine stands of California. Similarly, surface litter depth in whitebark pine stands of the Sierra Nevada (range of averages: 2.6–3.4 cm) were generally similar to or slightly higher than historical estimates (1.9 ± 2.4 cm), and surface fuel loads were mostly (64% statewide) within agency-defined thresholds (<33.6 Mg/ha), although some exceptionally high values (>100 Mg/ha) occurred in all subregions. These results suggest that most whitebark pine stands in the California have relatively low surface fuels that, when coupled with lower tree densities, contribute to reduced wildfire severity. However, whitebark pine stands with elevated surface fuels, possibly associated with recent tree mortality events, may be at elevated risk of large and severe wildfires under a warming climate (Keane et al. 2017, 2022).

Despite some early signs of declining integrity, California's whitebark pine ecosystems also are showing indications of ecological integrity (Table 8). Across the state, whitebark pine stands occur largely in protected areas, exhibit relatively low fire regime departure and surface fuel loading, contain sufficient regeneration densities (i.e., mean whitebark pine regeneration densities are generally within or exceeding whitebark pine reforestation guidelines for the western United States and include a mixture of young seedlings, older seedlings, and saplings), show a moderate level of cone production (with ≥ 20% of trees producing cones in a particular year of sampling), and possess numerous clonal stems and krummholz tree clusters that contribute to spatial variation in stand structure (e.g., non-krummholz clonal stems are more clustered around mature stems than regeneration). Whitebark pine ecosystems in the Sierra Nevada also exhibit other indications of ecological integrity, such as the presence of high-elevation climate refugia that could 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 and 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.

A major limitation of our study is that our plot network was designed to represent national forest lands in California but excluded national park lands, creating a spatial gap in our summary of whitebark pine stand structure, composition, and health, particularly in the southern Sierra west. In addition, although our study design was stratified by geographic and environmental variables, accessibility also constrained the sampling design, leading to further underrepresentation of sampling plots in the southern Sierra west (relative to the total potential sampling area). Stand conditions for national parks in California, including the southern Sierra west were thoroughly documented by Nesmith et al. (2019), Jackson et al. (2019), and Dudney et al. (2020) and were more broadly described throughout the state by Slaton et al. (2019*b*). Despite our limited sample size for that subregion, many of our plot-scale results of whitebark pine stand structure, composition, and health on national forest lands are consistent with these prior studies.

Potential inaccuracies in our field surveys and available remote sensing data pertaining to mortality agents and fire activity also may have influenced our study results. Signs and symptoms of white pine blister rust on older dead trees (>2 years dead) (J. Nesmith, personal communication), and evidence of fire activity from older (>20 years) low severity fires (M. Meyer, personal observation) can often be indistinct, which can lead to underestimates of white pine blister rust and fire occurrence, respectively, in our sampled stands. Although ADS data provide reasonable estimates of tree injury and mortality and insect and disease occurrence at larger spatial scales (e.g., landscape), estimates at finer spatial scales are imprecise (Slaton et al. 2021), and detection rates for indistinct mortality agents are potentially inaccurate even at broader spatial scales (Coleman et al. 2018). Aerial survey detection of white pine blister rust in whitebark pine of California was exceptionally low (0.02% of sampled area) and nine times lower than field plot-based estimates from our study, suggesting that ADSs are largely ineffective at detecting white pine blister rust in whitebark pine. Similarly, we observed eight times greater fire activity in California's whitebark pine stands based on plot data than statewide fire history data, likely because statewide fire history databases rarely capture small (<4 ha) fires (Safford and Van de Water 2014) that were historically common in many high elevation forest ecosystems of California (Meyer and North 2019; Coppoletta et al. 2021). Interestingly, ADSs documented substantially higher occurrences of mountain pine beetle activity in whitebark pine stands than plot-level surveys in our study and Nesmith et al. (2019), suggesting that ADSs are effective at capturing landscape-scale and regional patterns of mountain pine beetle activity as discussed by Coleman et al. (2018). Ideally, a combination of geospatial (i.e., remote-sensing) and local (i.e., field plot) data are most informative for understanding patterns of bark beetle activity and tree mortality in California's whitebark pine stands (e.g., Millar et al. 2012; Meyer et al. 2016).

Management recommendations

Our study has several implications for the management of whitebark pine forest ecosystems on national forests in California. First, our results suggest that whitebark pine stands in the northern part of the state (i.e., Warner Mountains and 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 (e.g., prescribed burning and mechanical thinning) in northern California and elsewhere in the state where whitebark pine regeneration is inadequately represented (i.e., where whitebark pine regeneration is < 247 stems/ha and this regeneration contributes to < 50% of conifer regeneration in the stand). 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), although retaining shade-tolerant subalpine species in decline (e.g., mountain hemlock and red fir) is warranted in some refugial high elevation forests of California (Meyer and North 2019; Coppoletta et al. 2021). Second, many whitebark pine forests in California's national forests, particularly in the southern Sierra Nevada, currently exhibit high ecosystem integrity. Management actions in the Sierra Nevada may ideally target seral whitebark pine sites (where they exist), select mixed stands containing whitebark pine (e.g., where restoration actions can promote whitebark pine recruitment), and areas of high human impact (e.g., ski areas, stands burned at high severity) (Keane et al. 2012, 2022; USDI and USDA 2020). Third, in whitebark pine stands experiencing elevated mortality rates and containing few young seedlings or cones of whitebark pine (e.g., Warner Mountains, Central Sierra), planting white pine blister rust-resistant whitebark pine may be warranted to prevent the loss of this foundation species, especially within higher elevation stands with low climate exposure (Keane et al. 2022). Lastly, regional and statewide inventory and monitoring efforts are essential in tracking the future health and status of California's whitebark pine stands, especially in areas with mountain pine beetle outbreaks and recent wildfire activity. 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*a*) and Nesmith et al. (2019), will prove critical in assessing whitebark pine condition and trend within and 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.

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Data availability

Field plot data generated or analyzed during this study are available from the corresponding author upon reasonable request. Geospatial data analyzed in this study are provided in full within the published article.

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Competing interests

The authors declare there are no competing interests relevant to this study.

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Supplementary material

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