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Compounding effects of white pine blister rust, mountain pine beetle, and fire threaten four white pine species

Joan C. Dudney,[1,†] Jonathan C. B. Nesmith,[2] Matthew C. Cahill,[3] Jennifer E. Cribbs,[2] Dan M. Duriscoe,[4] Adrian J. Das,[5] Nathan L. Stephenson,[5] and John J. Battles[1]

[1]*Department of Environmental Science Policy and Management, University of California at Berkeley, Berkeley, California 94720 USA*
[2]*Sierra Nevada Network Inventory & Monitoring Program, National Park Service, Three Rivers, California 93271 USA*
[3]*The Nature Conservancy, 999 SW Disk Dr. # 104, Bend, Oregon 97702 USA*
[4]*National Park Service, Three Rivers, California 93271 USA*
[5]*Western Ecological Research Center, U.S. Geological Survey, Three Rivers, California 93271 USA*

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Abstract. Invasive pathogens and bark beetles have caused precipitous declines of various tree species around the globe. Here, we characterized long-term patterns of mountain pine beetle (*Dendroctonus ponderosae*; MPB) attacks and white pine blister rust, an infectious tree disease caused by the pathogen, *Cronartium ribicola*. We focused on four dominant white pine host species in Sequoia and Kings Canyon National Parks (SEKI), including sugar pine (*Pinus lambertiana*), western white pine (*P. monticola*), whitebark pine (*P. albicaulis*), and foxtail pine (*P. balfouriana*). Between 2013 and 2017, we resurveyed 152 long-term monitoring plots that were first surveyed and established between 1995 and 1999. Overall extent (plots with at least one infected tree) of white pine blister rust (blister rust) increased from 20% to 33%. However, the infection rate across all species decreased from 5.3% to 4.2%. Blister rust dynamics varied greatly by species, as infection rate decreased from 19.1% to 6.4% in sugar pine, but increased in western white pine from 3.0% to 8.7%. For the first time, blister rust was recorded in whitebark pine, but not foxtail pine plots. MPB attacks were highest in sugar pines and decreased in the higher elevation white pine species, whitebark and foxtail pine. Both blister rust and MPB were important factors associated with elevated mortality in sugar pines. We did not, however, find a relationship between previous fires and blister rust occurrence. In addition, multiple mortality agents, including blister rust, fire, and MPB, contributed to major declines in sugar pine and western white pine; recruitment rates were much lower than mortality rates for both species. Our results highlighted that sugar pine has been declining much faster in SEKI than previously documented. If blister rust and MPB trends persist, western white pine may follow similar patterns of decline in the future. Given current spread patterns, blister rust will likely continue to increase in higher elevations, threatening subalpine white pines in the southern Sierra Nevada. More frequent long-term monitoring efforts could inform ongoing restoration and policy focused on threats to these highly valuable and diverse white pines.

Key words: abiotic–biotic interactions; fire effects; forest insects and pathogens; forest management; global change; infectious disease; plant pathogens; Sierra Nevada; tree pathogens; wildfire.

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† **E-mail:** jdudney@berkeley.edu

Introduction

Biotic agents of mortality are major drivers of disturbance in forest ecosystems (Campbell and Antos 2000, Das et al. 2016). Pathogens can incite changes in forest composition (Lewis and Lindgren 2000), which can alter ecosystem structure and function (O'Halloran et al. 2012). Invasive tree pathogens—Dutch elm disease, chestnut blight, red needle cast, and kauri dieback—are increasingly threatening forest ecosystems and have caused widespread declines of tree species around the globe (Webber and Brasier 2005, Ghelardini et al. 2017, Fei et al. 2019). Long-term studies measuring the impacts of tree pathogens are rare, however, greatly limiting our ability to characterize and predict shifts in pathosystems (Rohr et al. 2011).

White pine blister rust (blister rust), caused by *Cronartium ribicola* Fisch., is an invasive, lethal disease that infects white pines (Genus *Pinus,* Subgenus *Strobus*). Since its introduction to North America in 1906 (Maloy 1997, Geils et al. 2010), blister rust has infected many white pine populations throughout the USA and Canada (Maloy 1997, Tomback and Achuff 2010). The impacts on white pine forests have been so severe that blister rust ranks as one of the worst tree disease epidemics in modern history (Campbell and Antos 2000). Early efforts to control blister rust, including *Ribes* eradication (one of the alternate hosts required by the pathogen to complete its life cycle) and topical fungicides, were ineffective (Maloy 1997, Geils et al. 2010). These efforts were some of the most expensive and widespread tree pathogen eradication campaigns to date (Rohr et al. 2011). The dramatic declines caused by blister rust and other agents have resulted in the listing of whitebark pine (*Pinus albicaulis* Engelm.) as an IUCN endangered species (Mahalovich and Stritch 2011), and as a candidate species for protection under the Endangered Species Act in the USA (U.S. Fish and Wildlife Service 2011).

Because blister rust is an introduced pathogen, frequencies of genetic resistance and associated mechanisms are low across North American hosts (Hoff et al. 1980, Zambino 2010). Due in part to high susceptibility among white pines, populations within nine of the 11 North American white pine species are known to sustain infections (Kinloch 2003, Blodgett and Sullivan 2004). The presence of both the pine hosts, as well as the alternate host species from the genera *Ribes, Castellja* and *Pedicularis* (McDonald et al. 2006, Geils et al. 2010), is required for blister rust to complete its life cycle. Aeciospores produced on pine hosts can travel hundreds of kilometers via wind currents to infect alternate hosts (Kearns and Jacobi 2007) during the spring and summer. In contrast, fragile basidiospores produced on the alternate host travel much shorter distances (several kilometers) to infect pine hosts through needle stomata during late summer (Maloy 1997, 2001).

Other mortality agents in white pine systems may interact with blister rust spread, which can dampen or increase host infections. For example, native mountain pine beetle (*Dendroctonus ponderosae* Hopkins; MPB) may preferentially select trees weakened by blister rust infections (Shanahan et al. 2016), often resulting in more rapid mortality than caused by blister rust alone (Keane and Arno 1993, Larson 2011, Bockino and Tinker 2012). In addition, blister rust spread could be impacted by forest fires, which have been increasing in extent and severity in the western United States (Miller et al. 2009, Stephens et al. 2013). Tomback et al. (1995) hypothesized that fire may facilitate selection for resistant individuals and ultimately reduce blister rust spread by inciting a pulse of seedling regeneration that faces higher selective pressures—individuals that survive to maturity may therefore be more resistant to blister rust. While many studies have documented interactions between MPB and blister rust (Schwandt and Kegley, 2004, Larson 2011, Bockino and Tinker 2012), few studies have investigated the impacts of fire on blister rust (though see Tomback et al. (1995)).

In response to major declines in several white pine species, various national and regional efforts are underway to help conserve and restore these species. Restoration efforts are guided by several key strategies, including protecting and maintaining genetic diversity, documenting current conditions and trends, protecting known rust-resistant seed sources, and using forest management practices to improve forest health (Millar et al. 2007, Schoettle and Sniezko 2007, Keane et al. 2012). Multiple restoration tools include the following: (1) increasing genetic resistance to blister rust by

identification, propagation, and planting of rust-resistant seedlings; (2) use of MPB anti-aggregation pheromones to deter attacks; (3) and the use of mechanical thinning, prescribed fire, and managed wildland fire to increase forest resilience to wildfire, drought, pathogen outbreaks, and warming temperatures (Keane and Schoettle 2011, Keane et al. 2017). Managers, however, often lack information on when and where these approaches and tools may best be prioritized. Long-term monitoring efforts can support prioritization of restoration strategies, which could be essential for sustaining white pine species in an era of rapid change.

Sequoia and Kings Canyon National Parks (SEKI), located in the southern Sierra Nevada of California, have a high diversity of white pines all susceptible to impacts from blister rust, MPB, and fire, making it an ideal system to investigate blister rust's complex pathosystem. Historically, the southern Sierra Nevada white pine populations experienced lower levels of blister rust infections and MPB outbreaks (Dunlap 2012, Maloney et al. 2012) compared to other regions in western North America (Gibson et al. 2008, Buotte et al. 2016). Due to the diversity of white pines in SEKI, characterizing drivers of white pine mortality can inform broader conservation and management objectives (Schoettle and Sniezko 2007, Logan et al. 2010, Schwandt et al. 2010). To measure long-term changes in the occurrence and severity of blister rust, as well as possible interactions with fire and bark beetles, we remeasured long-term monitoring plots in SEKI that were originally established between 1995 and 1999. Specifically, we quantified the following: (1) change in stand structure between surveys, (2) long-term changes in blister rust extent and infection rates, and (3) long-term mortality rates across the four white pine species. With these results, we addressed two questions: (1) Are trees with blister rust more vulnerable to MPB attack? (2) Does fire reduce the spread of blister rust in white pine populations?

Materials and Methods

Study area

The jointly administered Sequoia and Kings Canyon National Parks encompass 350,443 ha in the southern Sierra Nevada of California. The climate is Mediterranean, characterized by hot, dry summers and wet, cold winters (Stephenson 1988). Elevations range from 300 to 4200 m, supporting a large diversity of forested communities. At higher elevations, thunderstorms are common during the summer, and snowpack accumulates during the winter starting around 1500 m elevation (Margulis et al. 2016).

Forests in the southern Sierra Nevada host five white pine species, all potentially threatened by blister rust and MPB. Throughout SEKI, these white pines have distinct ranges with moderate overlap (Figure 1). Sugar pine (*Pinus lambertiana* Dougl.) is a co-dominant species in mixed conifer forests, growing between 1000 and 2300 m and often associated with ponderosa pine (*P. ponderosa* Lawson & C. Lawson), white fir (*Abies lowiana* [Gord. & Glend.]), black oak (*Quercus kelloggii* Newberry), giant sequoia (*Sequoiadendron giganteum* [Lindl.] J. Buchholz), and incense cedar (*Calocedrus decurrens* [Torr.] Florin).

Western white pine (*P. monticola* Douglas ex D. Don) occurs between 2100 and 3200 m and often grows on well-drained exposed sites with thin soils (Graham 1990). Associated species include foxtail pine (P. *balfourniana* Grev. and Balf.), whitebark pine, red fir (*Abies magnifica* A. Murray), and lodgepole pine (*P. contorta* Douglas; Graham 1990, Miller and Urban 2000). Foxtail pine is endemic to California and dominates more arid regions of the southern Sierra Nevada, typically above 2800 m (Mastrogiuseppe and Mastrogiuseppe 1980). Whitebark pine often grows in denser stands on the western slopes of the Sierra Nevada and overlaps with foxtail pine and western white pine between 2800 and 3000 m throughout SEKI (Tomback and Achuff 2010, Nesmith et al. 2019). Whitebark pine is associated with mountain hemlock (*Tsuga mertensiana* [Bong.] Carr), and lodgepole pine (Fites-Kaufman et al. 2007, Tomback and Achuff 2010). Because limber pine (*P. flexilis* Engelm.) occurs in very low abundances in SEKI; this study focused on the four dominant white pines: sugar pine, western white pine, whitebark pine, and foxtail pine.

Sampling design

A total of 154 plots were originally established in 1995–1999 using a stratified random sampling design based on the range of white pine species within SEKI (Duriscoe and Duriscoe 2002). The

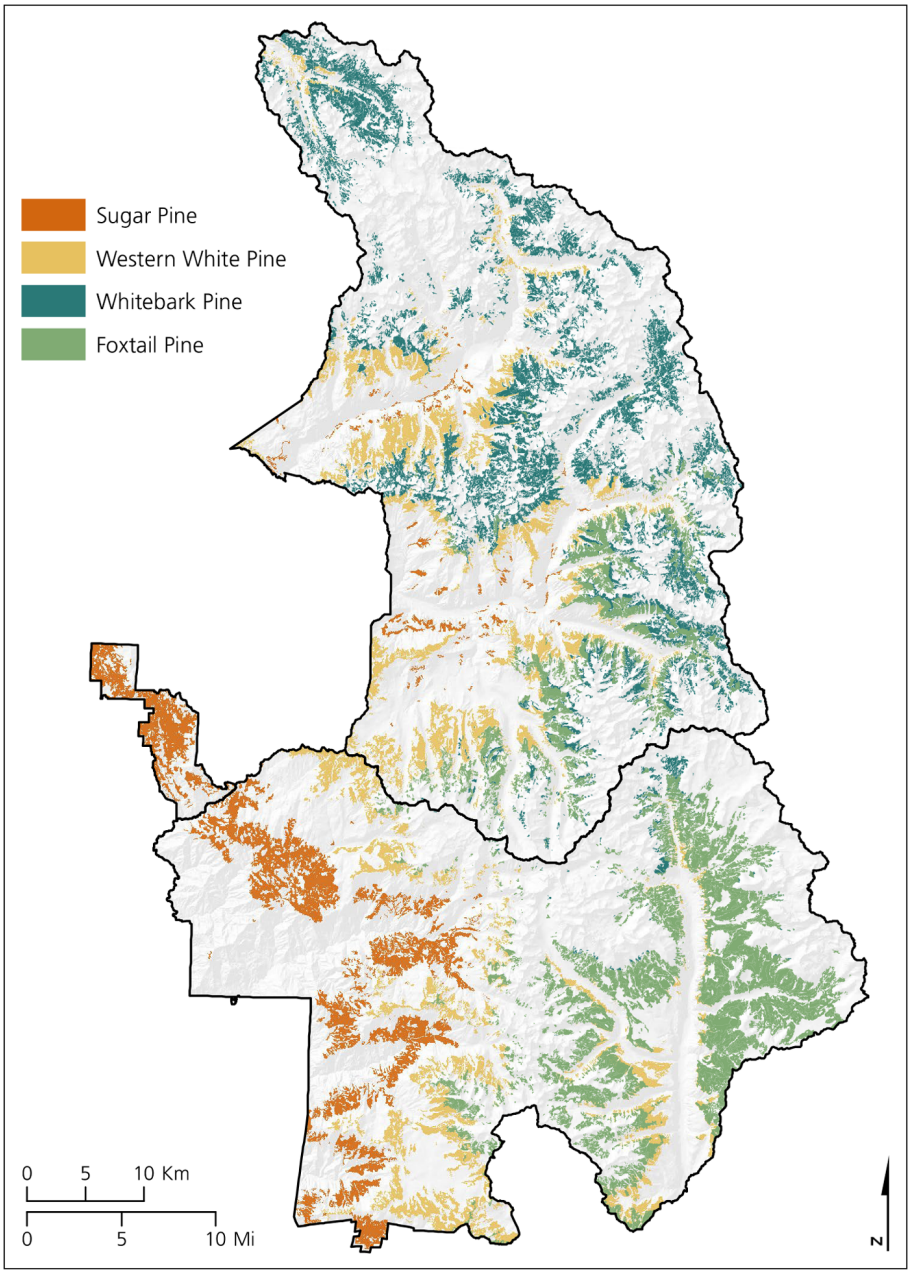

Fig. 1. Distribution of four white pine species within Sequoia and Kings Canyon National Parks. Limber pine is not shown due to its infrequent occurrence. Permission to use this figure granted by NPS, Alex Eddy (map author).

original sampling method subdivided all major watersheds based on physiographic features for a total of 50 subunits. Plot locations were randomly generated within each subunit to fall within the predicted range of a white pine species; plot size averaged 30 × 50 m, though plot length was adjusted to capture a minimum of 30 white pine stems. Plot sizes ranged from 0.1 to 3.4 ha.

Plot establishment and first survey, 1995–1999

Crews navigated to the randomly selected points and established a plot if more than 30

white pine stems greater than or equal to one meter tall were within 500 m of the random point (Duriscoe and Duriscoe 2002). The plot starting points were marked with brass tags. The location (NAD27), slope (%), aspect (°), elevation (m) at the plot tag, and presence/absence of *Ribes* in the plot were recorded. Using the plot tag as the origin, a centerline was located along the contour to define the long axis of the rectangular plot. The location of each live white pine tree within 15 m (though occasionally wider up to 40 m) of the centerline was mapped (x = distance from plot tag, y = distance from centerline). For each mapped tree, Duriscoe and Duriscoe (2002) determined the species, measured diameter at breast height (DBH; breast height = 1.37 m), height (m), and documented any symptoms of blister rust following methods adapted from the Whitebark Pine Ecosystem Foundation (Tomback et al. 2005). Tall host trees were searched using binoculars for symptoms of blister rust (described below). In four plots dominated by whitebark pine growing as *krummholz* (a multi-stemmed, shrub-like growth form), individual stem measurements were not recorded. Instead, the trees within the transect area were searched for signs of blister rust and the size and location of clumps were recorded.

Second survey, 2013–2017

Each white pine stem from the original survey was relocated based on mapped distances to the brass plot marker. Two of the original 154 plots were impossible to remeasure due to dramatically altered conditions from fire and inadequate or erroneous tree location data, reducing our sample size to 152 plots. New trees ≥1 m tall within the transect area were mapped, and the same information was recorded. For analyses, new trees were considered regeneration if their DBH was <10 cm; otherwise, they were treated as a tree that had been missed during the original survey. In addition, the following observations were added to the re-survey: status (dead or alive), presence or absence of MPB, and presence or absence of fire damage. If the total number of live white pines within the original transect area was less than 30, the transect was extended up to 200 m to meet the same minimum number of live trees that was used in the original survey. In some cases, the 200-m transect length limit was reached prior to recording 30 live trees, due to high mortality or fewer than 30 trees being measured during the original survey. This occurred in 23 sugar pine plots, four western white pine plots, and two whitebark pine plots.

Remeasuring whitebark pine proved difficult because the species typically grows with multiple stems on the same tree. It was not always possible to determine which stem was measured in the original survey. In the four plots where no diameter was recorded for whitebark pine in the original survey, a new centerline that followed the contour was located from plot origin following the original plot establishment guidelines. A transect was then established to allow for the collection of individual tree data during the re-survey. These plots were not included in the analysis when individual tree data were needed (e.g., to calculate mortality rates). The primary purpose of installing a new transect to record individual tree data was to maintain consistency in sampling across all plots and enable these trees to be revisited in the future.

The remeasurements occurred during 2013–2017, a period of extreme drought in California (Griffin and Anchukaitis 2014). It is estimated that over 147 million trees died in the Sierra Nevada from 2010 to 2018, primarily due to the 2012–2016 drought (USDA 2019). Much of this mortality was concentrated in lower elevation mixed conifer forest and significantly impacted sugar pine (Fettig et al. 2019). Because of the timing of this survey, some plots were sampled in the early stages of the drought in 2013 or 2015, when drought-induced mortality was relatively low, while others were sampled in 2016 and 2017, when the cumulative impacts of drought were much more severe (Stephenson et al. 2019).

Blister rust and bark beetle identification

Sampling methods for the presence or absence of blister rust were adapted from Duriscoe and Duriscoe (2002), with an emphasis on consistency, so that results would be comparable across sample periods. Crews scanned all branches and the main stem of each tree from all sides searching for signs of blister rust, using binoculars on tall trees (Smith et al. 2008, Dudney 2019), and counted branch and bole cankers. Branch cankers were recorded if sporulating aecia or old aecial sacs were observed, or if all of the following

symptoms were present: pitching, swelling or sunken bark, and discoloration of the bark on a specific section of the branch (Appendix S1: Fig. S1). Rodent chewing and aeciospores were included in the diagnosis when present (Hoff 1992). Bole cankers were verified by the following symptoms: heavy pitching from a specific area, swelling, or sunken bark and an entry point (i.e., a branch canker that clearly led to bole canker). While these symptoms of blister rust are not necessarily definitive, blister rust is the most probable causal agent. This identification system is also consistent with other monitoring programs in the western USA (GYWPMWG 2011, McKinney et al. 2012). Because it is significantly more challenging to diagnose blister rust in trees that have been dead for some time, data on blister rust infections were only analyzed from live trees.

Starting in 2015, crews searched each plot tree for signs and symptoms of MPB. Many of the plots measured in 2013 were dominated by western white pine, so data on beetle activity and fire damage are limited for this species to the 19 plots that were sampled from 2015 to 2017. Attacks of MPB were identified based on the presence of beetle galleries, pitch tubes, frass, or exit holes (Stephenson et al. 2019). We are likely underestimating MPB attacks for three reasons: (1) We did not remove bark to look for galleries on live trees; (2) pitch tubes likely decomposed on old standing dead trees; and (3) pitch tubes are not always produced on drought-stressed trees.

Fire history

Fire history data were obtained from SEKI (data are also available through the Wildland Fire Management Information database). Using ArcGIS Desktop 10.5.1, we extracted fire histories for every plot. We validated this documentary evidence with field observations of recent fires. Three plots were recently burned (characterized by the presence of charred standing dead trees, scattered biochar, and multiple pitching white pine tree scars) but were just outside the mapped fire boundary, so they were included as burned plots. We categorized a plot as burned if one or more fires occurred in the plot between surveys. Fire sizes in the areas where the plots occurred during the time period between surveys averaged approximately 3520 ha and ranged between 0.1 ha and 61,108 ha. Seventy percent of the fires were human caused, including controlled burns. While 45 percent ($n = 19$) of the sugar pine plots burned over the past 20 yr, only seven percent ($n = 4$) of western white pine plots burned; no fires burned in whitebark pine or foxtail pine plots. On average, plots had burned eight years prior to the second survey.

Calibrating surveys

To ensure consistency across crews and maintain accurate field measurements throughout the season, field technicians were trained by the same forest pathologist and entomologist at the beginning of each summer in the identification of blister rust and bark beetles. In addition, a crew member from the first survey in the late 1990s trained all new crews during the second survey. Because the re-survey occurred over multiple years with different crews, approximately eight percent of the plots in the second survey were measured a second time to determine among-crew variation. On average, the difference between original and calibration surveys was a $\pm$ 0.5 canker count. This difference likely did not significantly affect our results (Appendix S1: Table S1).

Statistical analyses

Statistical analyses were conducted with R software (R Core Team, 2013). Generalized linear mixed models (GLMMs; Zuur et al. 2009) were estimated using R package lme4 (Bates et al. 2020). Continuous independent variables were centered and standardized prior to analysis for all GLMMs, and model results were evaluated for multicollinearity and variance inflation.

Demographic rates

We calculated annual tree mortality and recruitment (Sheil et al. 1995, Kohyama et al. 2018) as discrete rate variables (Table 1). For mortality, we summarized species-specific cohort data by plot. Uncertainty was estimated using maximum likelihood. Specifically, we obtained confidence intervals of mortality using profile likelihood as outlined by Eitzel et al. (2015). We estimated per-capita recruitment based on the final density (Table 1). Given the rarity of recruitment in many plots, we were unable to evaluate plot-level heterogeneity and therefore calculated

Table 1. Equations used in calculating extent (E), infection rate (IR), spread rate (SR), mortality (M), and recruitment (R).

Variable	Equation	Description
Extent	$E = (N_i/N) \times 100$	Overall measure of disease presence (%). N_i = number of plots with ≥1 infection; N = total number of plots surveyed. For plots with varying sample sizes, extent is a mean of resampled estimates
Infection rate	$\left(\sum_{j=1}^{N} \frac{T_{ij}}{T_j}\right)/N$	Plot-level measure of infection at a specific sampling time. T_{ij} = number of infected trees in plot j; T_j = total number of trees in plot j. Plots with varying sample sizes are a mean of resampled T_{ij}. N = number of plots
Spread rate	$SR = \left(\sum_{j=1}^{N} \left(\frac{IR_{jt1} - IR_{jt0}}{\Delta t}\right) \times 20\right)/N$	Plot-level measure of change in infection rate. t_0 = 1995–1999; t_1 = 2013–2017. IR_{jt1} = infection rate of plot j at t_1; IR_{jt0} = infection rate for plot j at t_0; Δt = time interval between t_1 and t_0. N = number of plots; SR is normalized to 20 yr
Mortality	$M = 1 - \left(\frac{T_S}{T_0}\right)^{\frac{1}{\Delta t}}$	Discrete measure of per-capita annual tree mortality (Kohyama et al. 2018); a species-specific measure. T_s = number of live stems from first survey (1995–1999) that survived to the second survey (2013–2017); T_0 = number of live stems at first survey; Δt = time interval
Recruitment	$R = 1 - \left(\frac{T_S}{T_0}\right)^{\frac{1}{\Delta t}}$	Final density-based measure of per-capita annual tree recruitment (Kohyama et al. 2018); a species-specific measure. T_s = number of live stems from first survey that survived to the second survey; T_1 = number of live stems at second survey (i.e., T_s + recruits); Δt = time interval

Note: Extent, infection rate, and spread rate are calculated for each species (4 times) and across all species (1 time).

annual recruitment by species. To estimate uncertainty, we resampled counts of recruits and survivors using Poisson distributions with the rate parameter defined by the observed number of recruits and survivors (sensu Crowley 1992). Results were based on 1000 iterations and reported as means ± 95% confidence intervals.

Blister rust extent, infection rate, and spread rate

We estimated the extent, infection rate, and spread rate of blister rust for each species (see Table 1 for detailed equations and descriptions of these terms). We defined extent (E_y) simply as the proportion of plots dominated by species y with at least one white pine tree infected by blister rust. Infection rate (IR_y) is a plot-level measure of blister rust infection at a specific sampling time for species y and across all species. Spread rate (SR) calculates the change in infection rate over time.

Given that extent, infection rate, and spread rate are based on plot-level assessments (Table 1), we took care in our analysis to account for biases related to sample size. First, we only included plots that had at least 20 individuals of the target species in both surveys. This minimum was set to ensure a reasonable probability of detecting blister rust if it was present. This reduced the number of plots used to model blister rust dynamics to 138. Assuming an infection rate of 3.5% (lowest of infection rated observed), the probability of observing at least one infected tree in a plot with a sample size of 20 is greater than 50%. Filtering using other sample minima—sample size between 15 and 25 trees—made no difference to the overall trends reported here.

Second, because the probability of detecting blister rust within a plot is partially a function of the number of trees within that plot, we needed to correct for differences in sample size among plots. To do this, we equalized plot-level sample size differences between surveys using a resampling method. Specifically, we identified the minimum sample size for each plot as the target number (for plots with $n \geq 20$). For the survey period that had more stems, we sampled without replacement to get the target number of stems. To account for resampling error in the simulations of tree infection (i.e., the uncertainty around the estimated number of infections in every random draw), we included a plot-level binomial uncertainty in each iteration. Only the plot-level simulations of infection rate included the binomial uncertainty, however, since there was no sampling uncertainty when all trees were included. We then calculated extent, infection rate, and spread rate for each simulation (Table 1). The reported value for spread rate was normalized to a 20-year time interval. Final results were based on 1000 iterations with mean

values representing the central tendency and the 95% confidence intervals representing the uncertainty.

Modeling blister rust infections and mountain pine beetle activity

To identify factors associated with blister rust infections, we developed four logistic regression GLMMs to explain: (1) first survey infections of blister rust in sugar pine, (2) first survey infections in western white pine, (3) infections that were detected during the second survey for sugar pine, and (4) infections that were detected during the second survey for western white pine. Models were not developed for whitebark pine and foxtail pines because there were too few blister rust infections to build a reliable model (Case and Ambrosius 2007).

All four blister rust models estimated tree-level infections (presence/absence) using the lme4 package glmer function with the binomial family link (Bates et al. 2020). We included plot as a random effect. DBH (cm) was the only independent tree-level variable. The remaining plot-level variables included distance to nearest stream (m), occurrence of fire, slope, aspect (south, southeast and southwest facing = 1, north, northeast and northwest facing = 0), presence/absence of *Ribes* spp., and elevation. We verified that independent variables were not highly correlated ($r > 0.5$; Appendix S1: Fig. S2). An additional check for variance inflation using R package (car; Fox et al. 2019) found that the covariances of the independent variable estimates were not highly inflated (inflation factor >2).

To identify factors associated with MPB attack, we developed species-specific logistic regression GLMMs. Plot was included as a random effect. Tree-level explanatory variables included DBH and blister rust infection status. Plot-level variables included occurrence of fire, slope, aspect, and elevation. We checked for variance inflation following the same methods outlined above.

Influence of blister rust on probability of mortality

To assess the effect of blister rust on probability of mortality, we evaluated health status (live or dead) of sugar pine and western white pine from plots where blister rust had been observed in the original study ($n = 42$ plots). Using DBH and blister rust observations from the original survey, we constructed a logistic regression GLMM (using R package lme4 with binomial family link). Current health status was the binomial-dependent variable. Independent variables included the following: tree size (DBH), blister rust infection status from the first survey, and an interaction term between blister rust infection and DBH to account for the impact of blister rust on the probability of mortality relative to tree size. Plot was treated as a random effect. Model discrimination was evaluated using the area under the receiver operating characteristic curve (AUC; Hosmer et al. 2013). Model calibration was estimated with Brier's quadratic probability score using the val.prob function in the rms package (Harrell et al. 2019). The Brier score ranges between 0 and 1 with a score of 0 indicating exact agreement between predicted probabilities and realized probabilities and a score of 1 indicating no agreement (Wilks 2010).

Results

Changes in stand structure

Over the course of the two survey periods, there were noticeable changes in stand structure among species, especially in sugar pine (Table 2). In the initial survey, plot size averaged 3998 m^2 to capture a minimum of 30 trees. As is typical in old-growth forests, stands exhibited a reverse-j shaped size distribution with many more small trees than large ones (Appendix S1: Figure S3). In the re-survey, plot size increased to an average of 4310 m^2 to capture a minimum of 30 trees. The necessary extension of the plots was particularly frequent in sugar pine-dominated areas, as plot size increased from an average of 5819 to 6796 m^2 (an increase of 17%). Even with plot extensions, however, the average number of live sugar pine sampled decreased from an average of 46.6 to 32.8 live trees, resulting in a decrease in sugar pine density from 137.8 to 73.6 trees/ha (Table 2). In contrast, white pine basal area increased slightly between surveys from an average of 20.5 to 21.8 m^2/ha.

White pine demographic rates

The mortality rate of trees from the original survey was strongly linked to species (Figure 2). Sugar pine had the highest mortality: 52% of the trees measured in the first survey died

Table 2. Changes in plot size and composition of white pine (density and basal area) for study areas in Sequoia–-Kings Canyon National Parks.

	1995–1999			2013–2017		
Species	Plot area (m^2)	Density (stems/ha)	Basal area (m^2/ha)	Plot area (m^2)	Density (stems/ha)	Basal area (m^2/ha)
Sugar pine	5819 (104)	138 (2)	13.7 (0.2)	6796 (100)	74 (1)	14.1 (0.2)
Western white	3576 (50)	194 (3)	22.8 (0.3)	3763 (59)	182 (3)	25.5 (0.3)
Whitebark pine	2616 (27)	219 (2)	10.3 (0.2)	2622 (26)	224 (2)	11.3 (0.2)
Foxtail pine	3233 (39)	196 (2)	34.1 (0.4)	3252 (40)	202 (2)	36.2 (0.4)
All	3998 (38)	182 (1)	20.5 (0.2)	4310 (40)	163 (1)	21.8 (0.2)

Note: Means (with SEs in parentheses) summarized for the two survey periods.

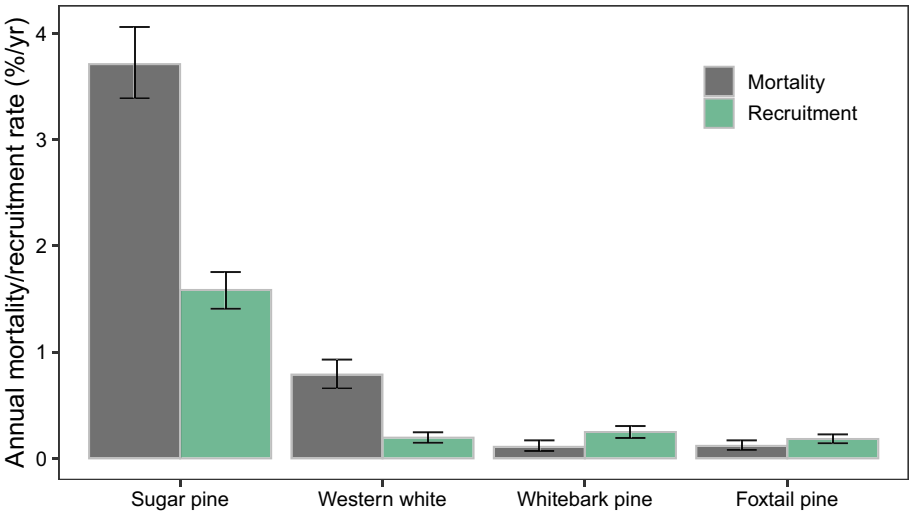

Fig. 2. Annual mortality (gray bars) and recruitment rates (green bars) by white pine species. Error bars represent 95% confidence intervals.

(specifically, 910 of 1760 surveyed trees died). The annualized sugar pine mortality rate was 3.7% (95% confidence interval [CI] = 3.4–4.1%). Western white pine experienced the next highest mortality: 13%, or 243 of 1826 trees from the original survey died, which results in an annualized mortality rate of 0.8% (CI = 0.7–0.9%). The other higher elevation white pines fared better, as the cumulative mortality for whitebark pine and foxtail pine was only 2% (29 of 1368 trees and 41 of 1875 trees, respectively). This translated to an annualized rate of 0.1% (CI = 0.1–0.2%) for both species.

Both foxtail and whitebark pine recruitment rates (approximately 0.2%/year for both species) were slightly higher than mortality rates, while sugar pine and western white pine recruitment rates (1.6%/year and 0.15%/year, respectively) were much lower than mortality rates (Figure 2). Recruitment in sugar pine, though highest among all white pine species, did not offset the high mortality rate. Consequently, the average number of trees per hectare declined from 137.8 to 73.6 between surveys. Most of these losses occurred in the smallest size classes (Appendix S1: Fig. S3). Trees per hectare also declined in western white pine but increased in whitebark pine and foxtail pine (Table 2).

Changes in blister rust extent and infection rate and patterns of mountain pine beetle attacks

The extent (i.e., proportion of plots with at least 1 infection) of blister rust increased from 20.3% to 32.6% across the landscape between surveys (Table 3). By 2017, almost one-third of the plots had at least one tree infected by blister rust

Table 3. Summary statistics of blister rust extent, infection rate and spread rate in Sequoia–Kings Canyon National Parks.

Dominant species	No. plots	No. trees	Extent (%)		Infection rate (%)		Spread rate (Δ/20 yr)
			1995–1999	2013–2017	1995–1999	2013–2017	
Sugar pine	32	1090	65.6 (59.4, 71.9)	53.1 (43.7, 62.5)	19.1 (16.8, 21.7)	6.4 (4.8, 8.1)	-13.2 (−16.5, −10.3)
Western white pine	40	1578	17.5 (12.5, 22.5)	55.0 (45.0, 62.5)	3.0 (2.1, 4.0)	8.7 (7.4, 10.1)	6.3 (4.6, 8.1)
Whitebark pine	29	1242	0	13.8 (6.9, 20.7)	0	1.1 (0.5, 1.8)	1.1 (0.5, 1.8)
Foxtail pine	41	1770	0	0	0	0	0
All species	138	5931	20.3 (18.1, 22.5)	32.6 (29.0, 35.5)	5.3 (4.7, 5.9)	4.2 (3.7, 4.8)	-1.0 (−1.9, −0.1)

Notes: Results calculated for each white pine species in plots with ≥20 individuals sampled. No. plots is the number of qualified plots; no. trees is the number of trees used in the simulations based on the minimum number of live trees between survey periods. Year range indicates the survey period. Means reported from 1000 simulations with 95% confidence intervals in parentheses.

(Figure 3). Infection rate across all species, however, declined from 5.3% to 4.2%, though this varied greatly by species. The infection rate decreased from 19.1% to 6.4% in sugar pine (Table 3); the decline of infections was observed across all size classes below 60 cm DBH. In contrast, infection rates increased from 3.0% to 8.7% in western white pines; they also experienced the highest increase in extent over the past twenty years from 17.5% to 55.0% (Table 3). Only 1.1% of whitebark pines were infected, and no infections were found on foxtail pines. Some trees also changed in infection status. Specifically, 15% ($n = 70$ sugar pines and $n = 4$ western white pines) of infected trees during the first survey were still alive but showed either no signs of blister rust infections or no suspected infections in the second survey (Appendix S1: Fig. S1).

At the landscape scale, there was a strong association among blister rust infection, MPB, and elevation, as blister rust and MPB were more common at lower elevations (Figure 4). Mean observed signs of MPB attacks declined in the higher elevation white pines (Figure 4). MPB was more frequent than blister rust in sugar pines and foxtail pines, while blister rust infections were more abundant in western white pines and whitebark pines (Appendix S1: Fig. S4). Interestingly, the relationship between blister rust and elevation appears to have shifted between survey periods. In models that included all white pine species, the maximum probability of infection shifted upslope into higher elevations (Figure 4).

At the species level, correlates of blister rust differed between sugar pine and western white pine (Figure 5). For sugar pine, in the first survey, tree size was negatively associated with blister rust (estimate = −0.36, $P < 0.01$) and the presence of *Ribes* spp. (estimate = 1.80, $P = 0.02$) was positively associated with blister rust, while tree size (estimate = 0.26, $P < 0.01$) was positively associated with blister rust in the second survey. For western white pine, elevation was negatively associated with blister rust infection in both surveys (estimate = −4.61, $P < 0.01$ in first survey, estimate = −2.76, $P < 0.01$ in second survey), while tree size (estimate = 0.25, $P = 0.02$) and the presence of *Ribes* (estimate = 1.56, $P = 0.02$) were positively associated with blister rust in the second survey.

Factors associated with MPB attack also varied by species and included increasing tree size (estimate = 0.49, $P < 0.01$) and the occurrence of blister rust infections (estimate = 1.01, $P = 0.009$) for sugar pine, higher basal area for western white pine (estimate = 1.20, $P = 0.03$), and lower elevation for western white pine (estimate = −7.33, $P = 0.007$) and foxtail pine (estimate = −11.68, $P = 0.006$; Figure 6). None of the other variables tested had a significant association with the presence of MPB. Overall, less than 3% of surveyed sugar pines and less than 1% of western white, foxtail, and whitebark pines showed signs and symptoms of MPB attacks (Appendix S1: Fig. S4).

Relationship of mountain pine beetle, fire, and blister rust on mortality

White pine mortality was driven by multiple factors, and their occurrences differed among species. For sugar pine, western white pine, and whitebark pine, MPB was an important factor associated with mortality (Figure 7a).

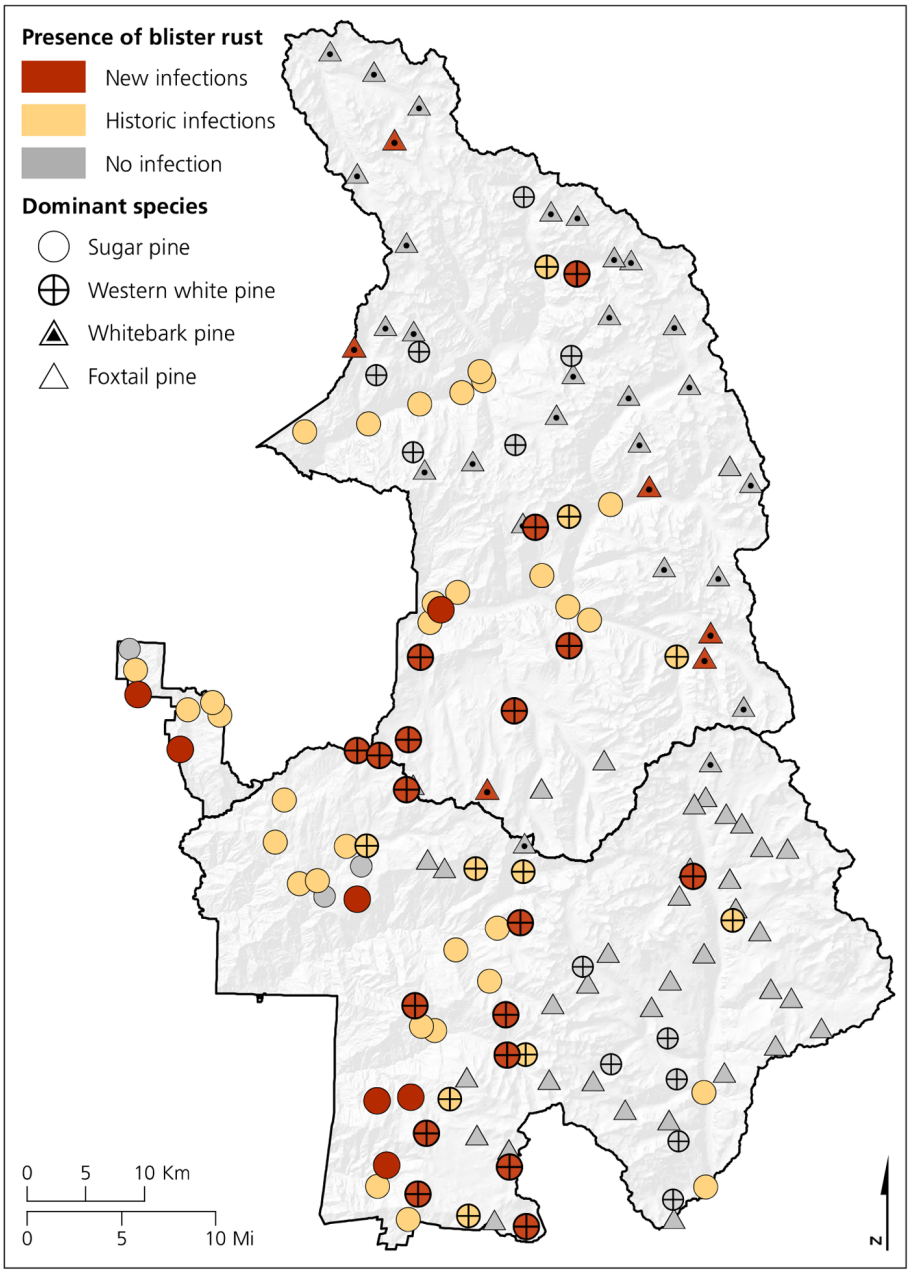

Fig. 3. Historic and current blister rust infections across all long-term monitoring plots in Sequoia and Kings Canyon National Parks. Red denotes new infections (spread), yellow denotes historic (first survey) infections, and shapes indicate the dominant white pine species in each plot Permission to use this figure granted by NPS, Alex Eddy (map author).

Signs of attack were observed in 29%, 49%, and 33% of dead trees for these three species, respectively, compared to only <1%, 10%, and 7% in live trees. MPB attacks were rare in foxtail pine and were observed in <10% of both dead and live trees.

Fire was also an important factor in mortality for both sugar pine and western white pine. The

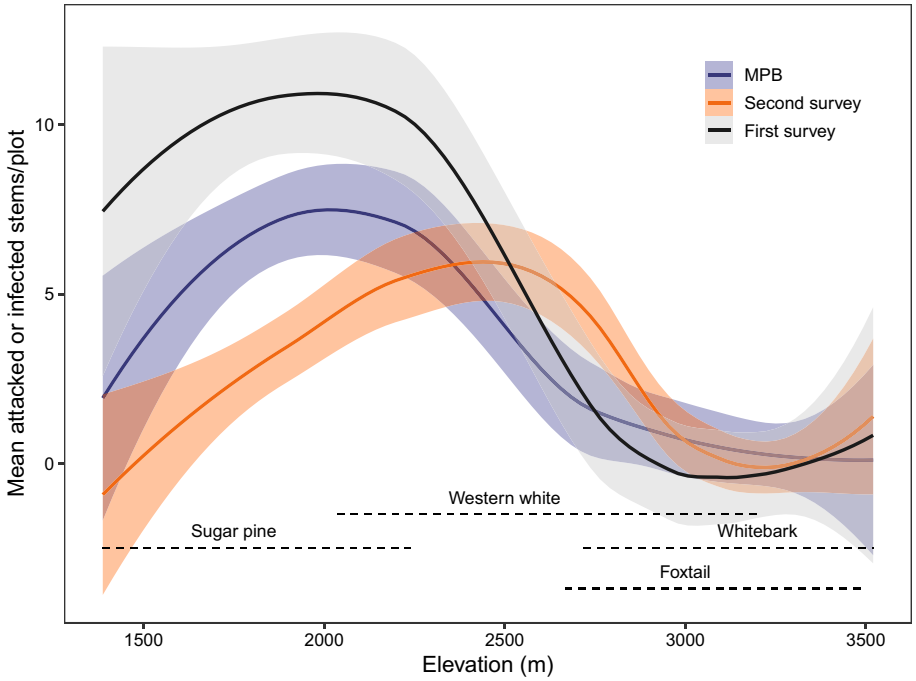

Fig. 4. Association among infection rate, mountain pine beetle (MPB) attack, and elevation for white pine species at Sequoia and Kings Canyon National Parks. For blister rust, infection rate is presented for the first (gray line) and second survey (orange line). For MPB attack, results are only available for the second survey (blue line); includes dead and live trees with MPB attacks. Shaded areas represent 95% confidence intervals around local non-parametric regression (loess) estimates.

percent of trees that died in burned plots was 61% for sugar pine and 50% for western white pine, while the percent of trees that died in unburned plots was only 29% for sugar pine and 6% for western white pine (Figure 7b). Fire was extremely rare in plots dominated by whitebark pine or foxtail pine and likely did not influence mortality for these species.

To assess the effect of blister rust infection on mortality, we examined trees within plots where blister rust was observed in the original survey. These data included 1756 trees (1319 sugar pine and 437 western white pine) from 42 plots. A small number of whitebark pine (eight trees) and foxtail pine (19 trees), that occurred within two of the western white pine-dominated plots, were excluded from this analysis due to the low sample sizes. Separate models were created for sugar pine and western white pine. The sugar pine model had moderately high predictive power, correctly classifying 76% of the trees as alive or dead with an AUC value of 0.83. Model calibration was good (Briar score = 0.17), though it tended to under-predict the probability of mortality at low probability values and overpredict at high probability. DBH, blister rust infection status, and the interaction between DBH and blister rust were all significant predictors of mortality for both sugar pine and western white pine (Figure 8). The western white pine model had moderately high predictive power, correctly classifying 84% of the trees with an AUC value of 0.87. Model calibration was also good (Briar score = 0.12). Overall, 74% (270 of 364) of sugar pine infected with blister rust in the original study died compared to 46% (439 of 955) of uninfected sugar pine. Mortality rates were lower for western white pine, but blister rust infection was still a strong predictor of mortality, as 61% (51 of 84) of infected western white pine died compared to only 16% (57 of 353) of uninfected western white pine. Larger trees were also less likely to have died between surveys compared to smaller trees (Figure 8).

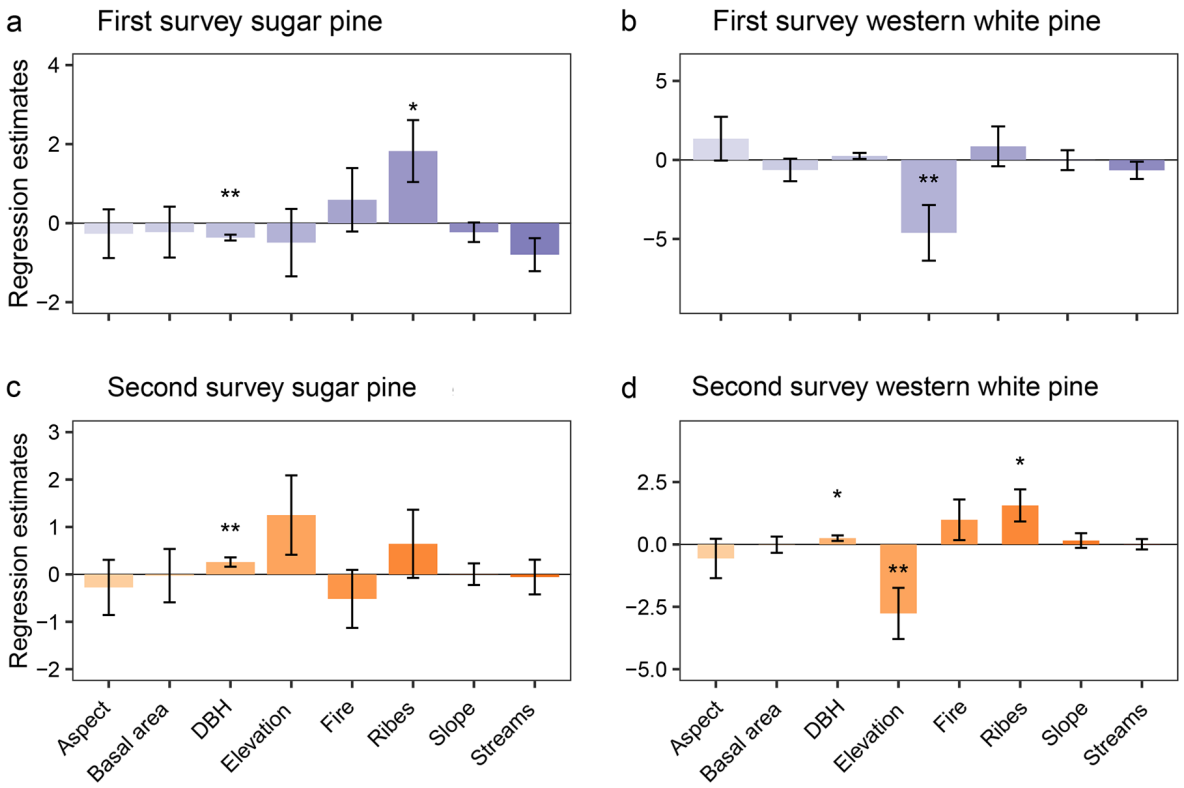

Fig. 5. Factors associated with blister rust infection from the first survey (a, b) and the second survey (c,d) for sugar pine and western white pine. Bars show coefficient estimates and standard errors from logistic regression outputs. Streams = distance to nearest stream. Significance codes: $^{**}P < 0.01$, $^{*}P < 0.05$.

Discussion

During the first survey, blister rust infection rates in SEKI were highest in sugar pine populations, followed by much lower infection rates in western white pine, and no detected infections in whitebark or foxtail pine plots. Twenty years later, sugar pine populations experienced high mortality rates and a major decline of blister rust infections, as infected trees were more likely to have died than uninfected trees. While mortality was lower in western white pines, blister rust extent and infection rate increased and spread further into subalpine white pines—the first infections were detected in whitebark pine plots. Historically, the southern Sierra Nevada has had lower blister rust and MPB outbreaks compared to other regions (Smith and Hoffman 2000). Our results show that these trends are changing and negatively impacting white pines in the southern Sierra Nevada. Understanding the drivers of these changes, particularly factors affecting white pine susceptibility, is critical for assessing the future vulnerability of these white pine populations.

While previous studies suggested that sugar pine populations were declining slowly over the past few decades in the southern Sierra Nevada (van Mantgem et al. 2004, Das et al. 2016), our study found that the rates of decline are much greater than previously documented and driven by multiple factors, including blister rust, fire, and MPB. We reported an annual mortality rate more than double the annual recruitment rate (Figure 2). As a result, the sugar pine population was reduced by more than half over the last 20 yr in our study. Sugar pine mortality was best explained by fire, MPB, blister rust, and size class (smaller size classes had higher probabilities of mortality), which is consistent with previous studies (van Mantgem et al. 2004, Nesmith et al. 2011, Das et al. 2016). In addition, a large

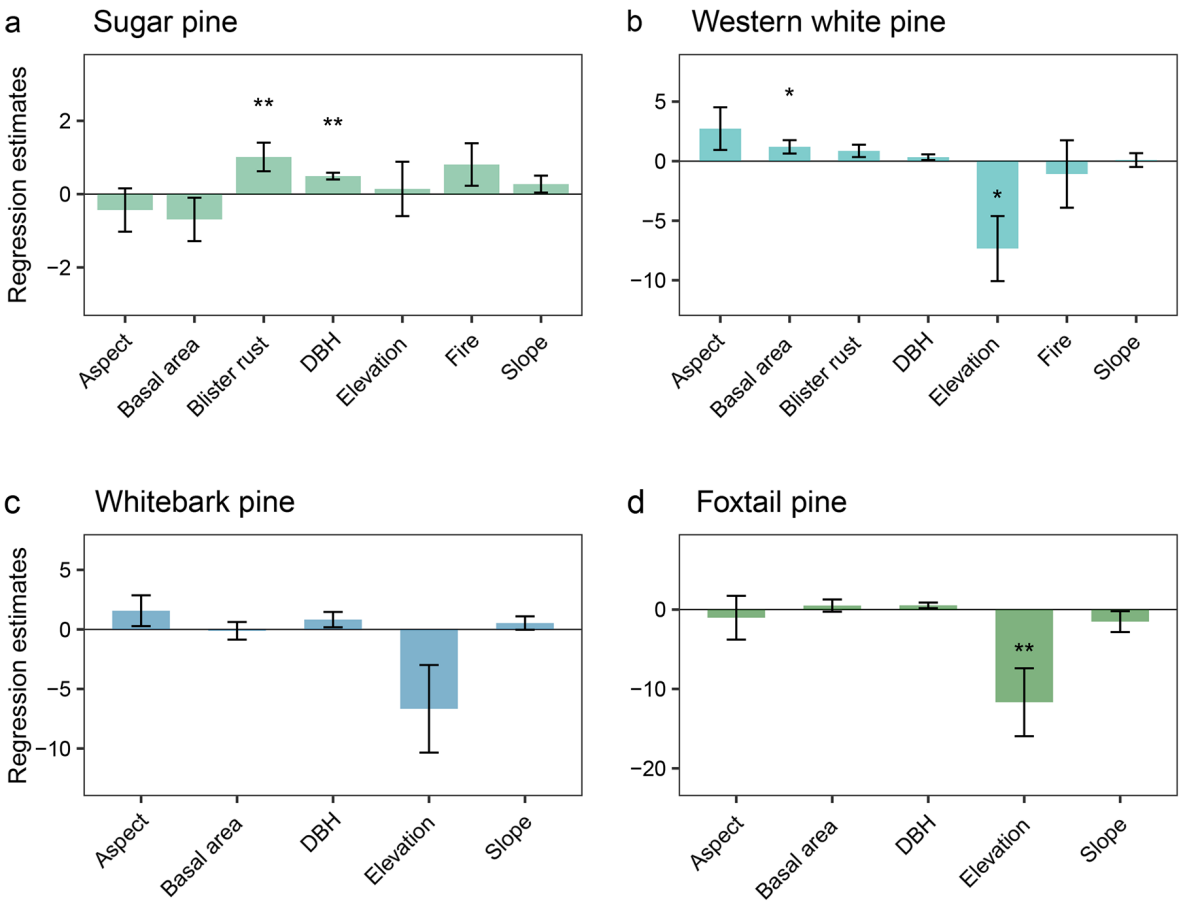

Fig. 6. Factors associated with MPB attack in the second survey. Bars show coefficient estimates and standard errors from logistic regression outputs; significance codes: $^{**}P < 0.01$, $^{*}P < 0.05$.

proportion of the sugar pine plots were surveyed in 2015 before the full effect of the recent 2012–2016 drought had been realized. Other surveys in 2017 showed mortality in sugar pine was as high as 80% (Nesmith, *unpublished data*), indicating that our results may underestimate current sugar pine mortality rates. Though western white pines experienced much lower annual mortality compared to sugar pines, mortality rates were still four times greater than recruitment rates (Figure 2), leading to a 13% decline in western white pines over the last 20 yr.

Blister rust threatens white pines in SEKI

Because the prevalence of blister rust in southern Sierra Nevada subalpine forest communities has been lower in the past two decades compared to northern California (e.g., 35% in Tahoe Basin whitebark pine and 12% in northern foxtail pines; Dunlap 2011), as well as the northern Rocky Mountains and Canadian Rockies (Zeglen 2002, Smith et al. 2012), some have hypothesized that the southern Sierra Nevada may be a potential refuge against blister rust. If rising temperatures create more suitable conditions for blister rust spread in the subalpine zone, however, this refuge will be threatened. Additionally, the increase in blister rust at higher elevations is particularly concerning for western white pine. While infection rates remain lower compared to regions of the Intermountain West (e.g., 50–80%; Kim et al. 2003, Tomback and Achuff 2010), blister rust was the most abundant biotic agent of mortality in western white pine (Appendix S1: Fig. S4). Given western white pine's low resistance to blister rust in the Sierra Nevada (Kinloch et al. 2003), western white pine populations could follow demographic trends found in sugar

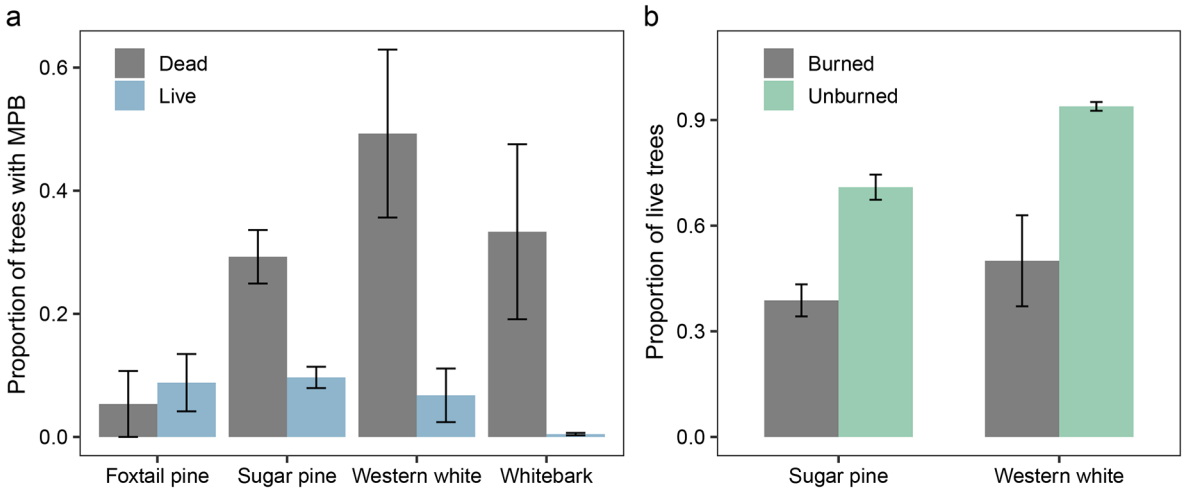

Fig. 7. (a) Proportion of live and dead trees with signs of beetle activity for sugar pine, western white pine, whitebark pine, and foxtail pine (includes all trees within plots where beetle activity was recorded from the second survey). (b) Proportion of live trees in burned and unburned plots for sugar pine and western white pine. Both figures displaying standard error bars.

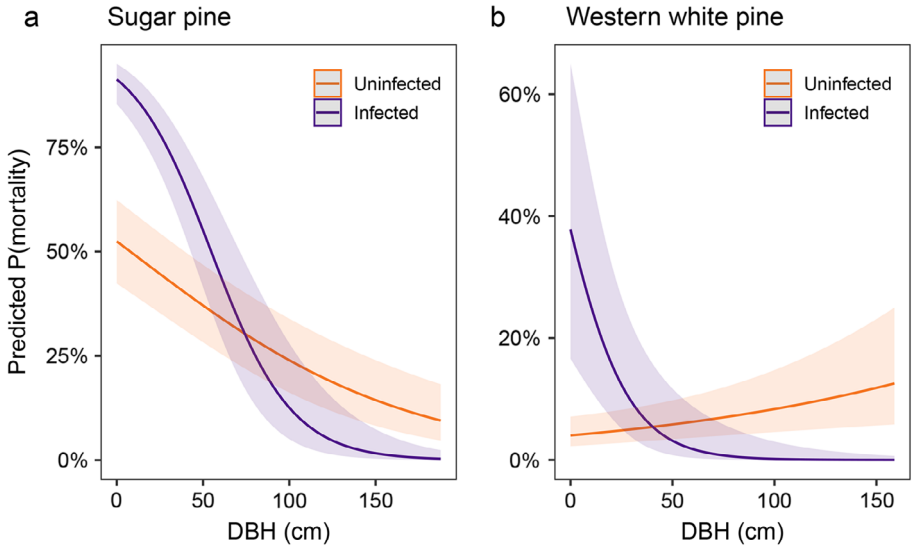

Fig. 8. Modeled effects of tree size and blister rust infection from the first survey on the probability of mortality for (a) sugar pine and (b) western white pine. Showing 95% confidence intervals.

pine today. Despite the relatively low infection rates, there is evidence that blister rust has already increased mortality rates in western white pine in SEKI (Figure 8a).

The large decline in infection rates among sugar pine was unexpected. The species has experienced very high levels of mortality since the first survey, with disproportionately high mortality among previously infected trees. The current infection rate suggests that blister rust has not spread into the remaining (and newly recruited) population at previously observed levels. There are several, non-mutually exclusive, mechanisms that might explain this pattern.

Disease spread at lower elevations may have slowed due to changes in climatic suitability for the disease (i.e., warming temperatures) and increased rarity of sugar pine hosts due to population declines. Additionally, blister rust tends to spread sporadically, with large increases in infection during wave years (Kinloch 2003). The frequency of wave years may have declined since the first survey due to warming temperatures and the recent drought event in California.

Mountain pine beetle and fire interactions with blister rust spread

For sugar pine, the presence of MPB was associated with blister rust infections. The link between MPB and blister rust is a common pattern found in montane regions (Campbell and Antos 2000, Schwandt and Kegley, 2004, Larson 2011, Bockino and Tinker 2012). Blister rust infections can predispose white pines to beetle attack by weakening their defense mechanisms, though this trend was found to decline in larger diameter trees (Bockino and Tinker, 2012). Successful MPB attacks can kill a tree within one year, while blister rust often kills trees much more slowly and sometimes not at all (e.g., a few small diameter stems with bole cankers in our plots were still alive 20 yr later). MPB attacks can therefore reduce blister rust propagules by killing pine hosts more quickly, an effect that may be particularly important where climatic conditions are marginal for pathogen reproduction. We did not, however, find evidence for this relationship in western white pine, suggesting that the importance of these biotic–biotic interactions may vary by species and across strong environmental gradients (altitude).

While we expected the presence of fire to be associated with blister rust infection, we did not find strong evidence of this relationship in our study. Fires may affect the blister rust pathosystem through four mechanisms: (1) increasing selection for rust resistance in recruiting individuals (Tomback et al. 1995), (2) reducing spore propagules by burning both the white pine and alternate hosts, (3) preferentially removing small trees, resulting in lower exposure time for the recruiting population, and (4) increasing surface temperatures and reducing humidity that may lead to unsuitable climate conditions for blister rust reproduction. For example, *Ribes* spp. resprout following fire (Quick 1962, Zambino 2010) and nearby infected regions could disperse spores into burned areas. Fire impacts are therefore likely temporally, spatially, and species specific. While fires contributed to high mortality in sugar pine, the effect on blister rust infection rate was undetectable. We may have missed the most immediate effects of fire (i.e., reduced numbers of infected hosts) because a significant amount of time had passed following the majority of fires (~8 yr) by the time we remeasured the trees.

Future directions

Increasing the frequency of long-term monitoring programs will be critical to further disentangle the drivers of blister rust spread from various confounding factors, particularly fire, climate warming, and beetles. This information may guide management decisions and help identify the most appropriate and effective strategies for restoration through a better understanding of the main drivers of change in these ecosystems. For example, protecting large cone-bearing sugar pine from beetle attack using anti-aggregation pheromones during, or immediately following, drought could be an effective strategy to ensure continued recruitment. Given the increasing extent of wildfires (Stephens et al. 2013), and likely future increases in prescribed fires, due to recent management imperatives (Brown 2018), investigation into the impacts of fire severity and fire-by-environmental conditions would also help elucidate the potentially complex blister rust-fire relationship. Additionally, studies investigating gene-by-environment effects, particularly for foxtail pines, will be important to better understand the susceptibility of white pines in the Sierra Nevada. While recent trials demonstrated that foxtail pine is one of the most susceptible species (R. Sniezko, *personal communication*), our in situ results indicated that foxtails are the least susceptible. We did, however, find evidence of blister rust infections in foxtail pine (see Appendix S1: Fig. S5) outside of the monitoring plots. These findings suggest unknown environmental constraints may be acting on blister rust in SEKI foxtail pines.

Conclusion

Blister rust dynamics in SEKI have changed significantly over the last 20 yr in three of the four white pine species we studied. Both species-

level and landscape-level factors have contributed to significant shifts in blister rust extent and infection rates, resulting in an overall increase in extent, despite a decrease in infection rate. Although infection rates were very low in whitebark, and none were found in foxtail pine plots, current trends suggest that blister rust may increasingly threaten subalpine white pines. This was evident in western white pine, where blister rust has become much more common over the last 20 yr. More frequent long-term monitoring efforts and targeted conservation and restoration actions could help manage the ongoing threats to these highly valuable and diverse Sierra Nevada white pines.

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Literature Cited

Bates, D., et al. 2020. lme4: linear Mixed-Effects Models using "Eigen" and S4. https://github.com/lme4/lme4/

Blodgett, J. T., and K. F. Sullivan. 2004. First report of white pine blister rust on Rocky Mountain bristlecone pine. Plant Disease 88:311.

Bockino, N. K., and D. B. Tinker. 2012. Interactions of white pine blister rust and mountain pine beetle in whitebark pine ecosystems in the southern Greater Yellowstone Area. Natural Areas Journal 32:31–40.

Brown, E. G. 2018. Executive Order B-62-18. Governor Edmund G. Brown Jr. https://www.ca.gov/archive/gov39/2019/01/04/executive-order-b-62-18/index.html

Buotte, P. C., J. A. Hicke, H. K. Preisler, J. T. Abatzoglou, K. F. Raffa, and J. A. Logan. 2016. Climate influences on whitebark pine mortality from mountain pine beetle in the Greater Yellowstone Ecosystem. Ecological Applications 26:2507–2524.

Campbell, E. M., and J. A. Antos. 2000. Distribution and severity of white pine blister rust and mountain pine beetle on whitebark pine in British Columbia. Canadian Journal of Forest Research 30:1051–1059.

Case, L. D., and W. T. Ambrosius. 2007. Power and sample size. Pages 377–408 *in* W. T. Ambrosius, editor. Topics in biostatistics. Humana Press, Totowa, New Jersey, USA.

Crowley, P. H. 1992. Resampling methods for computation-intensive data analysis in ecology and evolution. Annual Review of Ecology and Systematics 23:405–447.

Das, A. J., N. L. Stephenson, and K. P. Davis. 2016. Why do trees die? Characterizing the drivers of background tree mortality. Ecology 97:2616–2627.

Dudney, J. 2019. Characterizing and managing drivers of change in Mediterranean forest and grassland communities. Dissertation. UC Berkeley, Berkeley, California, USA.

Dunlap, J. 2011. Status of white pine blister rust and seed collections in california's high-elevation white pine species. In R. E. Keane, D. F. Tomback, M. P. Murray, and C. M. Smith, editors. The Future of High-Elevation, Five-Needle WHITE PINES in Western North America: Proceedings of the High Five Symposium. 28–30 June 2010; Missoula, MT. Proceedings RMRS-P-63. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado, USA.

Dunlap, J. M. 2012. Variability in and environmental correlates to white pine blister rust Incidence in five California white pine species. Northwest Science 86:248–263.

Duriscoe, D. M., and C. S. Duriscoe. 2002. Survey and monitoring of white pine blister rust in Sequoia and Kings Canyon National Parks—Final report of 1995-1999 survey and monitoring plot network. Science and Natural Resources Management Division, Sequoia and Kings Canyon National Parks, Three Rivers, California, USA.

Eitzel, M. V., J. Battles, R. York, and P. de Valpine. 2015. Can't see the trees for the forest: Complex factors influence tree survival in a temperate second growth forest. Ecosphere 6:809–821.

Fei, S., R. S. Morin, C. M. Oswalt, and A. M. Liebhold. 2019. Biomass losses resulting from insect and disease invasions in US forests. Proceedings of the National Academy of Sciences of the United States of America 116:17371–17376.

Fettig, C. J., L. A. Mortenson, B. M. Bulaon, and P. B. Foulk. 2019. Tree mortality following drought in the central and southern Sierra Nevada, California, US. Forest Ecology and Management 432:164–178.

Fites-Kaufman, J. A., P. Rundel, N. Stephenson, and D. A. Weixelman. 2007. Montane and subalpine vegetation of the Sierra Nevada and Cascade ranges. Terrestrial vegetation of California. https://doi.org/10.1525/california/9780520249554.001.0001

Fox, J., et al. 2019. car: companion to applied regression. https://CRAN.R-project.org/package=car

Geils, B. W., K. E. Hummer, and R. S. Hunt. 2010. White pines, Ribes, and blister rust: a review and synthesis. Forest Pathology 40:147–185.

Ghelardini, L., N. Luchi, F. Pecori, A. L. Pepori, R. Danti, G. Della Rocca, P. Capretti, P. Tsopelas, and A. Santini. 2017. Ecology of invasive forest pathogens. Biological Invasions 19:3183–3200.

Gibson, K., K. Skov, S. Kegley, C. Jorgensen, S. Smith, and J. Witcosky. 2008. Mountain pine beetle impacts in high-elevation five-needle pines: current trends and challenges. USDA Forest Service Forest Health Protection. https://www.fs.usda.gov/Internet/FSE_DOCUMENTS/stelprdb5162989.pdf

Graham, R. T. 1990. *Pinus monticola* Dougl. ex D. Don. Western white pine. Silvics of North America 1:385–394.

Griffin, D., and K. J. Anchukaitis. 2014. How unusual is the 2012–2014 California drought? Geophysical Research Letters 41:9017–9023.

GYWPMWG. 2011. Greater Yellowstone Whitebark Pine Monitoring Working Group. Interagency Whitebark pine monitoring protocol for the Greater Yellowstone Ecosystem. Version Interagency Whitebark Pine Monitoring Protocol for the Greater Yellowstone Ecosystem, Version 1.1. https://irma.nps.gov/DataStore/Reference/Profile/660369

Harrell, F. E. Jr, M. F. E. Jr Harrell, and D. Hmisc. 2019. Package 'rms.' Vanderbilt University. https://cran.r-project.org/web/packages/rms/index.html

Hoff, R. J. 1992. How to recognize blister rust infection on whitebark pine. US Department of Agriculture, Forest Service, Intermountain Research Station. https://www.fs.fed.us/rm/pubs_int/int_rn406.pdf

Hoff, R., R. T. Bingham, and G. I. McDonald. 1980. Relative blister rust resistance of white pines. European Journal of Forest Pathology 10:307–316.

Hosmer, D. W. Jr, S. Lemeshow, and R. X. Sturdivant. 2013. Applied logistic regression. John Wiley & Sons, Hoboken, New Jersey, USA.

Keane, R. E., and S. F. Arno. 1993. Rapid decline of whitebark pine in western Montana: evidence from 20-year remeasurements. Western Journal of Applied Forestry 8:44–47.

Keane, R. E., L. M. Holsinger, M. F. Mahalovich, and D. F. Tomback. 2017. Restoring whitebark pine ecosystems in the face of climate change. https://www.fs.fed.us/rm/pubs_series/rmrs/gtr/rmrs_gtr361.pdf

Keane, R. E., and A. W. Schoettle. 2011. Strategies, tools, and challenges for sustaining and restoring high elevation five-needle white pine forests in western North America. In R. E. Keane, D. F. Tomback, M. P. Murray, and C. M. Smith, editors. The future of high-Elevation, Five-Needle White Pines in Western North America: Proceedings of the High Five Symposium. 28–30 June 2010; Missoula, MT. Proceedings RMRS-P-63. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado, USA.

Keane, R. E., D. F. Tomback, C. A. Aubry, A. D. Bower, E. M. Campbell, C. L. Cripps, M. B. Jenkins, M. F. Mahalovich, M. Manning, and S. T. McKinney. 2012. A range-wide restoration strategy for whitebark pine (*Pinus albicaulis*). General Technical Reports RMRS-GTR-279. US Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado, USA.

Kearns, H. S. J., and W. R. Jacobi. 2007. The distribution and incidence of white pine blister rust in central and southeastern Wyoming and northern Colorado. Canadian Journal of Forest Research 37:462–472.

Kim, M.-S., S. J. Brunsfeld, G. I. McDonald, and N. B. Klopfenstein. 2003. Effect of white pine blister rust (*Cronartium ribicola*) and rust-resistance breeding on genetic variation in western white pine (*Pinus monticola*). Theoretical and Applied Genetics 106:1004–1010.

Kinloch, B. B. 2003. White pine blister rust in North America: past and prognosis. Phytopathology 93:1044–1047.

Kinloch, B. B., R. A. Sniezko, and G. E. Dupper. 2003. Origin and Distribution of Cr2, a Gene for Resistance to White Pine Blister Rust in Natural Populations of Western White Pine. Phytopathology 93:691–694.

Kohyama, T. S., T. I. Kohyama, and D. Sheil. 2018. Definition and estimation of vital rates from repeated censuses: choices, comparisons and bias corrections focusing on trees. Methods in Ecology and Evolution 9:809–821.

Larson, E. R. 2011. Influences of the biophysical environment on blister rust and mountain pine beetle, and their interactions, in whitebark pine forests. Journal of Biogeography 38:453–470.

Lewis, K. J., and B. S. Lindgren. 2000. A conceptual model of biotic disturbance ecology in the central interior of BC: How forest management can turn Dr. Jekyll into Mr. Hyde. Forestry Chronicle 76:433–443.

Logan, J. A., W. W. Macfarlane, and L. Willcox. 2010. Whitebark pine vulnerability to climate-driven mountain pine beetle disturbance in the Greater Yellowstone Ecosystem. Ecological Applications 20:895–902.

Mahalovich, M., and L. Stritch. 2011. U. F. S., and U. F. S.-W. IUCN Red List of Threatened Species: whitebark Pine. https://www.iucnredlist.org/en

Maloney, P. E., D. R. Vogler, C. E. Jensen, and A. Delfino Mix. 2012. Ecology of whitebark pine populations in relation to white pine blister rust infection in subalpine forests of the Lake Tahoe Basin, USA: implications for restoration. Forest Ecology and Management 280:166–175.

Maloy, O. C. 1997. White pine blister rust control in North America: a case history. Annual Review of Phytopathology 35:87–109.

Maloy, O. C. 2001. White pine blister rust. Plant Health Progress 2:10.

Margulis, S. A., G. Cortés, M. Girotto, and M. Durand. 2016. A landsat-era sierra Nevada snow reanalysis (1985–2015). Journal of Hydrometeorology 17: 1203–1221.

Mastrogiuseppe, R. J., and J. D. Mastrogiuseppe. 1980. A Study of *Pinus balfouriana* Grev. & Balf. (Pinaceae). Systematic Botany 5:86–104.

McDonald, G. I., B. A. Richardson, P. J. Zambino, N. B. Klopfenstein, and M.-S. Kim. 2006. Pedicularis and Castilleja are natural hosts of *Cronartium ribicola* in North America: a first report. Forest Pathology 36:73–82.

McKinney, S. T., T. Rodhouse, L. Chow, A. Chung-MacCoubrey, G. Dicus, L. Garrett, K. Irvine, S. Mohren, D. Odion, and D. Sarr. 2012. Monitoring white pine (*Pinus albicaulis*, *P. balfouriana*, *P. flexilis*) community dynamics in the Pacific west region-Klamath, Sierra Nevada, and upper Columbia Basin networks: narrative version 1.0. Natural resource report NPS/PWR/NRR—2012/532. National Park Service, Fort Collins, Colorado, USA.

Millar, C. I., N. L. Stephenson, and S. L. Stephens. 2007. Climate change and forests of the future: managing in the face of uncertainty. Ecological Applications 17:2145–2151.

Miller, C., and D. L. Urban. 2000. Modeling the effects of fire management alternatives on Sierra Nevada Mixed-Conifer Forests. Ecological Applications 10:85–94.

Miller, J. D., H. D. Safford, M. Crimmins, and A. E. Thode. 2009. Quantitative evidence for increasing forest fire severity in the Sierra Nevada and southern Cascade Mountains, California and Nevada, USA. Ecosystems 12:16–32.

Nesmith, J. C. B., A. C. Caprio, A. H. Pfaff, T. W. McGinnis, and J. E. Keeley. 2011. A comparison of effects from prescribed fires and wildfires managed for resource objectives in Sequoia and Kings Canyon National Parks. Forest Ecology and Management 261:1275–1282.

Nesmith, J. C. B., M. Wright, E. S. Jules, and S. T. McKinney. 2019. Whitebark and foxtail pine in Yosemite, Sequoia, and Kings Canyon National Parks: initial assessment of stand structure and condition. Forests 10:35.

O'Halloran, T. L., B. E. Law, M. L. Goulden, Z. Wang, J. G. Barr, C. Schaaf, M. Brown, J. D. Fuentes, M. Göckede, A. Black, and V. Engel. 2012. Radiative forcing of natural forest disturbances. Global Change Biology 18:555–565.

Quick, C. R. 1962. Resurgence of a gooseberry population after fire in mature timber. Journal of Forestry 60:100–103.

R Core Team. 2013. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rohr, J. R., A. P. Dobson, P. T. J. Johnson, A. M. Kilpatrick, S. H. Paull, T. R. Raffel, D. Ruiz-Moreno, and M. B. Thomas. 2011. Frontiers in climate change–disease research. Trends in Ecology & Evolution 26:270–277.

Schoettle, A. W., and R. A. Sniezko. 2007. Proactive intervention to sustain high-elevation pine ecosystems threatened by white pine blister rust. Journal of Forest Research 12:327–336.

Schwandt, J. W., and S. Kegley. 2004. Mountain pine beetle, blister rust, and their interaction on whitebark pine at Trout Lake and Fisher Peak in northern Idaho from 2001-2003. R-1 FHP Rep. 04-9. U.S. Department of Agriculture, Forest Service, Northern Region, Missoula, Montana, USA.

Schwandt, J. W., I. B. Lockman, J. T. Kliejunas, and J. A. Muir. 2010. Current health issues and management strategies for white pines in the western United States and Canada. Forest Pathology 40:226–250.

Shanahan, E., K. M. Irvine, D. Thoma, S. Wilmoth, A. Ray, K. Legg, and H. Shovic. 2016. Whitebark pine mortality related to white pine blister rust, mountain pine beetle outbreak, and water availability. Ecosphere 7:e01610.

Sheil, D., D. F. R. P. Burslem, and D. Alder. 1995. The interpretation and misinterpretation of mortality rate measures. Journal of Ecology 83:331–333.

Smith, C. M., B. Shepherd, C. Gillies, and J. Stuart-Smith. 2012. Changes in blister rust infection and mortality in whitebark pine over time. Canadian Journal of Forest Research 43:90–96.

Smith, C. M., B. Wilson, S. Rasheed, R. C. Walker, T. Carolin, and B. Shepherd. 2008. Whitebark pine and white pine blister rust in the Rocky Mountains of Canada and northern Montana. Canadian Journal of Forest Research 38:982–995.

Smith, J. P., and J. T. Hoffman. 2000. Status of white pine blister rust in the Intermountain West. Western North American Naturalist 60:165–179.

Stephens, S. L., J. K. Agee, P. Z. Fulé, M. P. North, W. H. Romme, T. W. Swetnam, and M. G. Turner. 2013. Managing forests and fire in changing climates. Science 342:41–42.

Stephenson, N. L. 1988. Classification and description of the montane and subalpine forest and woodland communities of Sequoia National Park. Final contract report to the Sequoia Natural History Association. https://pubs.er.usgs.gov/publication/96527

Stephenson, N. L., A. J. Das, N. J. Ampersee, B. M. Bulaon, and J. L. Yee. 2019. Which trees die during drought? The key role of insect host-tree selection. Journal of Ecology 107:2383–2401.

Tomback, D. F., and P. Achuff. 2010. Blister rust and western forest biodiversity: ecology, values and outlook for white pines. Forest Pathology 40:186–225.

Tomback, D. F., J. K. Clary, J. Koehler, R. J. Hoff, and S. F. Arno. 1995. The effects of blister rust on post-fire regeneration of whitebark pine: the Sundance Burn of Northern Idaho (U.S.A.). Conservation Biology 9:654–664.

Tomback, D. F., R. E. Keane, W. W. McCaughey, and C. Smith. 2005. Methods for surveying and monitoring whitebark pine for blister rust infection and damage. Whitebark Pine Ecosystem Foundation, Missoula, Montana, USA.

U.S. Fish and Wildlife Service. 2011. Endangered and threatened wildlife and plants; 12-month finding on a petition to list *Pinus albicaulis* as endangered or threatened with critical habitat. Federal Register 76:42631–42654.

USDA, F. S. 2019. Survey finds 18 million trees died in California in 2018. https://www.fire.ca.gov/media/5120/2018-catreemortalitynumbersjointrelease_020519.pdf

van Mantgem, P. J., N. L. Stephenson, M. Keifer, and J. Keeley. 2004. Effects of an introduced pathogen and fire exclusion on the demography of sugar pine. Ecological Applications 14:1590–1602.

Webber, J. F., and C. M. Brasier. 2005. Global pathways for tree pathogens: the challenges of *Phytophthora* species as invasive threats. Pages 741–748 *in* Proceedings of the BCPC International Congress–Crop Science and Technology 2005. https://www.researchgate.net/publication/276274566_8A-3_Global_pathways_for_tree_pathogens_the_challenges_of_Phytophthora_species_as_invasive_threats

Wilks, D. S. 2010. Sampling distributions of the Brier score and Brier skill score under serial dependence. Quarterly Journal of the Royal Meteorological Society 136:2109–2118.

Zambino, P. J. 2010. Biology and pathology of Ribes and their implications for management of white pine blister rust. Forest Pathology 40:264–291.

Zeglen, S. 2002. Whitebark pine and white pine blister rust in British Columbia, Canada. Canadian Journal of Forest Research 32:1265.

Zuur, A. F., E. N. Ieno, N. Walker, A. A. Saveliev, and G. M. Smith. 2009. Mixed effects models and extensions in ecology with R. Springer, New York, New York, USA.

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