



Whitebark Pine in Crater Lake and Lassen Volcanic National Parks

Initial Assessment of Stand Structure and Condition

Natural Resource Report NPS/KLMN/NRR—2017/1459





ON THE COVER

Photograph of whitebark pine below Lassen Peak in Lassen Volcanic National Park
Photograph courtesy of Erik S. Jules

ON THIS PAGE

Photograph of whitebark pine (foreground) along the crater rim in Crater Lake National Park
Photograph courtesy Erik S. Jules

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⁵This report is dedicated to Daniel A. Sarr (1964-2015). Daniel was the first Klamath Network Inventory and Monitoring Program Manager. He served as Manager for 13 years and one of his many contributions was initiating a robust program aimed at assessing threats to five-needle pine. ecosystems.

June 2017

U.S. Department of the Interior
National Park Service
Natural Resource Stewardship and Science
Fort Collins, Colorado

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Please cite this publication as:

Jules, E. S., J. I. Jackson, S. B. Smith, J. C. B. Nesmith, L. A. Starcevich, and D. A. Sarr. 2017. Whitebark pine in Crater Lake and Lassen Volcanic National Parks: Initial assessment of stand structure and condition. Natural Resource Report NPS/KLMN/NRR—2017/1459. National Park Service, Fort Collins, Colorado.

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Abstract

Whitebark pine (*Pinus albicaulis*) is vulnerable to a number of threats including an introduced pathogen (*Cronartium ribicola*), epidemic levels of native mountain pine beetle (*Dendroctonus ponderosae*), fire suppression, and climate change. To describe the structure of whitebark pine populations in two parks in the southern Cascades (Crater Lake [CRLA] and Lassen [LAVO] National Parks), we surveyed trees in 30 50×50 m plots in both parks. We used these plots to describe the extent of white pine blister rust (the disease caused by *Cronartium ribicola*), mountain pine beetle occurrence, and mistletoe infestation, and to elucidate factors influencing the presence of pests and pathogens, cone production, and canopy kill. In each plot, we recorded both tree-level and stand-level data related to tree health, including symptoms of blister rust and mountain pine beetle, and reproductive vigor (cone production). In both parks, encroachment from other species, particularly mountain hemlock (*Tsuga mertensiana*), was negatively associated with cone production. In CRLA, water stress was a good predictor of blister rust infection and cone production. The presence of mountain pine beetle and blister rust was associated with higher canopy kill for whitebark pine in both parks. Lastly, we found evidence for a pest-pathogen interaction; mountain pine beetle attack was greater for trees that showed symptoms of blister rust infection in CRLA. Our results indicate that whitebark pine populations in the southern Cascade range are experiencing moderate levels of blister rust infection compared with other sites across the species range, and that competition from shade-tolerant species may be presenting an additional threat in both parks.

Acknowledgments

We are grateful to the following people for help with fieldwork: Alex Borst, Emily DeStigter, Kelsey Guest, Kasey Graue, David McLean, Rachel Patton, and April Sahara. Sean Mohren provided critical support with the database we used to archive data. Jen Beck and Elena Thomas in Crater Lake National Park, and Mike Magnuson in Lassen Volcanic National Park, helped us understand the whitebark pine system and provided us with logistical support throughout the study. Alice Chung-MacCoubrey and Devin Stucki provided useful feedback on earlier versions of this report. Funding for this work was provided by the National Park Service (Task Agreement No. P12AC10931, Contract for Services Order # P15PX04316).

Introduction

Background

Five-needle white pines (Family Pinaceae, Genus *Pinus*, Subgenus *Strobus*), and in particular whitebark pine (*Pinus albicaulis*), limber pine (*P. flexilis*), and foxtail pine (*P. balfouriana*), are foundational species (Tomback and Achuff 2010) in upper subalpine and treeline forests of several National Park Service (NPS) Pacific West Region parks. At these higher elevations, five-needle pines are often dominant species and are thought to serve key ecosystem functions, including modulating springtime snowmelt (thereby increasing summer water availability), moderating local environments allowing for establishment of shade-tolerant species, and producing large seed crops critical to wildlife, such as Clark's nutcrackers (*Nucifraga columbiana*; Tomback 1982, Keane et al. 2011). However, these same taxa are currently facing unprecedented challenges from climate change, upsurges of pests and pathogens, and fire exclusion (Keane et al. 2011).

High-elevation forests in Crater Lake National Park (CRLA) and Lassen Volcanic National Park (LAVO) are known for their whitebark pine, which often exhibit a stunted, twisted appearance near treeline, and are an important part of the visitor experience at both parks. A particularly pernicious threat to whitebark pine is the exotic fungal pathogen *Cronartium ribicola* (Division Basidiomycota, Order Pucciniales), which was accidentally introduced into North America in 1910 and causes white pine blister rust (herein referred to as 'blister rust') in all five-needle white pines (McDonald and Hoff 2001). The fungus exhibits a complex life cycle that includes five different spore types alternating between five-needle white pines and plants of the genera *Ribes*, *Pedicularis*, and *Castilleja* (McDonald et al. 2006). Blister rust damages and can ultimately kill five-needle white pines by girdling branches and boles. Whitebark pine is also impacted by increasing populations of the native mountain pine beetle (*Dendroctonus ponderosae*), competition with encroaching vegetation (such as mountain hemlock, *Tsuga mertensiana*) due to fire exclusion, and changing climate (Keane et al. 2011, Millar et al. 2012). These factors, acting singly or in combination, are likely to change the structure, function, and composition of high elevation forests.

In 2012, scientists from the Klamath Inventory and Monitoring Network (KLMN) began collaborating with scientists at Humboldt State University (Arcata, CA) to establish 30 long-term Inventory and Monitoring plots ("plots" from here on) in both CRLA and LAVO using the Pacific West Region Inventory & Monitoring Program Five Needle Pine Protocol ("NPS PWR Five-Needle Pine Protocol" from here on; McKinney et al. 2012). The purpose of the work was to determine the extent of mortality and the distribution of causal agents such as blister rust and to evaluate the patterns of disease and pest incidence to inform management of whitebark pine populations. In addition, the plots were established with the intention of resampling each plot every three years to provide robust estimates of survivorship, growth, and recruitment of whitebark pine. Previous work at CRLA was conducted by Murray (2010), who noted that mortality rates approached 1% per year in established reference stands. These results were echoed in a pilot study conducted by the KLMN in 2009 reported in Smith et al. (2011). Whitebark pine are known to occur at LAVO, but no monitoring or research has been reported prior to this monitoring project.

Whitebark pine

Whitebark pine is a long-lived conifer that ranges in structure and size from an upright tree growing up to ~15 m in height (often found in protected sites), to a short and twisted form referred to as *krummholz* found in windy, exposed sites (Weaver 2001). Individuals are generally slow-growing and known to live more than 1,000 years (Perkins and Swetnam 1996). The species has a broad range, extending from northern British Columbia southward in the Rocky Mountains of Idaho and Wyoming, as well as southward along the Cascades and Sierra Nevada (McGaughey and Schmidt 2001). In addition, several isolated regions of Nevada and eastern Oregon contain whitebark pine. Within its range, whitebark pine is generally restricted to high elevation sites, though this varies considerably from north to south. For instance, at the northern edge of its range, whitebark pine is found as low as 900 m (McGaughey and Schmidt 2001), but in the southern Cascades of California it is not encountered below 2500 m (Jackson et al. 2014).

Whitebark pine can occur in some habitats as the only tree taxon, for instance on cold, dry sites near treeline, but is found in mixed stands on other sites (Arno 2001). In the southern Cascades where our study was conducted, the most important tree associated with whitebark pine is mountain hemlock, which is shade-tolerant and increasing in abundance in many whitebark pine stands, presumably because of fire exclusion (Beck and Holm 2014). Lodgepole pine (*Pinus contorta* ssp. *murrayana*) is often found along with whitebark pine and in dense stands at adjacent, lower-elevation sites. This arrangement may be important because lodgepole pine is a common host of mountain pine beetle (Beck and Holm 2014).

Whitebark pine is often described as a keystone or foundation species because of the multiple, critical roles that it plays in subalpine ecosystems (e.g., Ellison et al. 2005, Keane et al. 2012). These roles include the initiation of succession on harsh sites after disturbances such as fire, the reduction in snowmelt rates during the warm season, and the supply of food for wildlife through seed production (Tomback et al. 2001). Seeds of whitebark pine are notable for being large and nutrient-rich relative to most pines and are therefore attractive for many animals. Across the range of whitebark pine,



Mature female, seed-bearing cones of whitebark pine remain closed (left) unless opened by an animal (right). Seeds have been removed from the cone on the right, either by a Clark's nutcracker or a Douglas squirrel. Photographs by Erik S. Jules.

seeds are utilized by several bird and mammal species, including red squirrels (*Tamiasciurus hudsonicus*), Douglas squirrels (*Tamiasciurus douglasii*), grizzly bears (*Ursus arctos horribilis*), and Clark's nutcrackers (Tomback et al. 2001, Mattson et al. 2001). The Clark's nutcracker has developed a mutualistic relationship with the whitebark pine. This boisterous, robin-sized bird with flashy black-and-white wings and tail has a specialized pouch under its tongue for storing seeds, which it caches widely in the soil. Seeds that are not eaten by the nutcracker serve as the primary dispersal mechanism and maintain populations of the whitebark pine. McKinney et al. (2009) found that nutcracker visitation decreases in whitebark stands as tree mortality increases.

Numerous studies have assessed the prevalence and impacts of blister rust on populations of whitebark pine, and some of these studies have simultaneously tried to understand the role of mountain pine beetle (e.g., Campbell and Antos 2000, Zeglan 2002, Hatala 2010, Smith 2013). The results of this work show that the role of the disease varies considerably across the range of the pine and that the factors controlling its spread probably vary geographically as well. For example, in western Montana, Keane and Arno (1993) resurveyed plots 20 years after they were established in 1971 and found an average of 42% mortality over that time with the highest mortality found in the northwest region of the study area. In their study, blister rust was observed to be the primary cause of death, with mountain pine beetle attacking only trees that had blister rust. Larson (2011) found significant differences in blister rust between six mountain ranges from southwest Montana to western Oregon. In his study, average infection rates of trees varied from 5-66% among ranges, and were positively related to several site characteristics, including colder winter temperature and less dense stand structure. Interestingly, Larson (2011) attributed mountain pine beetle as the primary agent of mortality for 83% of the dead trees he observed, while blister rust is not attributed as the cause of any whitebark pine mortality. In California, blister rust incidence varied by region, from 0.0% in the Great Basin to 24.2% in the Northern Sierra Nevada (Maloney 2011), although this study does not report on the impacts of mountain pine beetle.

In 1998, Goheen et al. (2002) surveyed whitebark pine stands in an area just north of, and adjacent to, CRLA (i.e., Umpqua National Forest). They found 46% of living trees were infected with blister rust and 10% of trees were dead. Of the dead trees, 67% were killed by blister rust, 13% by mountain pine beetle alone, and 18% were killed by mountain pine beetle and exhibited sign of blister rust. Within CRLA, Murray and Rasmussen (2003) surveyed 1,200 whitebark pine trees in 24 transects to determine the level of blister rust in the park. They found that transects showed an average of 8% infection (range 0.0%-20%). In a separate study conducted from 2003-2009, Murray (2010) surveyed whitebark pine in permanent plots across CRLA and found an average annual loss of 1% of trees across all size classes. Blister rust was found in 31% of trees in his study. However, most mortality appeared to be due to mountain pine beetle, and his study reversed what some believed to be the primary cause of mortality of whitebark pine in CRLA. In 2009, Smith et al. (2011) surveyed whitebark pine in CRLA and found that 21% of tree deaths were attributed to mountain pine beetle, 20% to blister rust, and 54% were of unknown causes. To the best of our knowledge, no work has been done on the condition of whitebark pine stands in LAVO, although numerous biologists have noted through casual observation that prior to our work, blister rust was not common in the park.

Study Objectives

This report summarizes findings that were developed from the collaborative work outlined above, and utilizes the completion of the initial establishment of 30 long-term demographic plots in both CRLA and LAVO. In particular, the specific objectives of our work in CRLA and LAVO on which we report here are to:

- 1) describe the size and structure of whitebark pine stands including, for example, descriptions of size distributions of both living and dead trees and of recruitment in our plots;
- 2) report the extent of blister rust distribution, mountain pine beetle occurrence, and mistletoe infestation in whitebark pine stands;
- 3) determine the relationship of the above causal agents with environmental and demographic characteristics of whitebark pine stands; and
- 4) highlight patterns or relationships that might be important for managers in each park.

Methods

Study Area and Plot Establishment

Our study was conducted in CRLA and LAVO during the summers of 2012-2014. In CRLA, whitebark pine is found across ~2,000 ha (2.1% of the total park), and in LAVO whitebark pine covers 257 ha (0.6% of the total park; Figures 1 and 2). Over the three years, 30 long-term whitebark pine plots were established in each of the two parks (10 plots per year per park). Plot design and sampling followed the NPS PWR Five-Needle Pine Protocol (McKinney et al. 2012). We delineated the sampling frames for Crater Lake and Lassen using a combination of known whitebark pine locations and aerial photos. Sampling frames excluded slopes greater than 30 degrees, and locations <100 m or >1 km from a road or trail. The sampling points for all three field seasons were generated using the Generalized Random Tessellation Stratified (GRTS) algorithm in GIS (Stevens and Olsen 2004) prior to plot establishment in the first year. An oversample of points was also drawn using the GRTS algorithm to support any eventual site rejections.. As defined, the sampling frame captures approximately 75% of the whitebark pine habitat in the park. Sites were rejected if (1) no whitebark pine were present, or (2) they would result in unsafe working conditions (e.g., terrain that was too steep to work on). The points generated in the GIS were used as the southwest corner of the 50 x 50 m plots if one or more whitebark pine ≥ 1.37 m in height were found within the plot boundary. If there were no whitebark pine individuals in a plot, an offset procedure was employed. We selected a direction at random by rotating an upside down compass according to the number of seconds on our watch and walked at that azimuth for a distance of 50 m from the original coordinates. This location was considered the new southwest corner. If the second plot did not contain whitebark pine, then a new random direction was determined, and we walked 50 m from the last offset coordinates. If the offset procedure did not generate a usable plot, a new point was used from the oversample described above. Additional details on plot locations, oversample plots used, and the GRTS algorithm can be found in McKinney et al. (2012) and Jackson et al. (2014). Each 50 x 50 m plot consisted of five 10 x 50 m subplots and nine regeneration plots where we recorded heights and diameter (cm) at breast height (dbh) of all species and tagged all whitebark pine seedlings <1.37 m in height (Figure 3; details of site locations and characteristics are in Appendices A and B and in Jackson et al. [2014]).

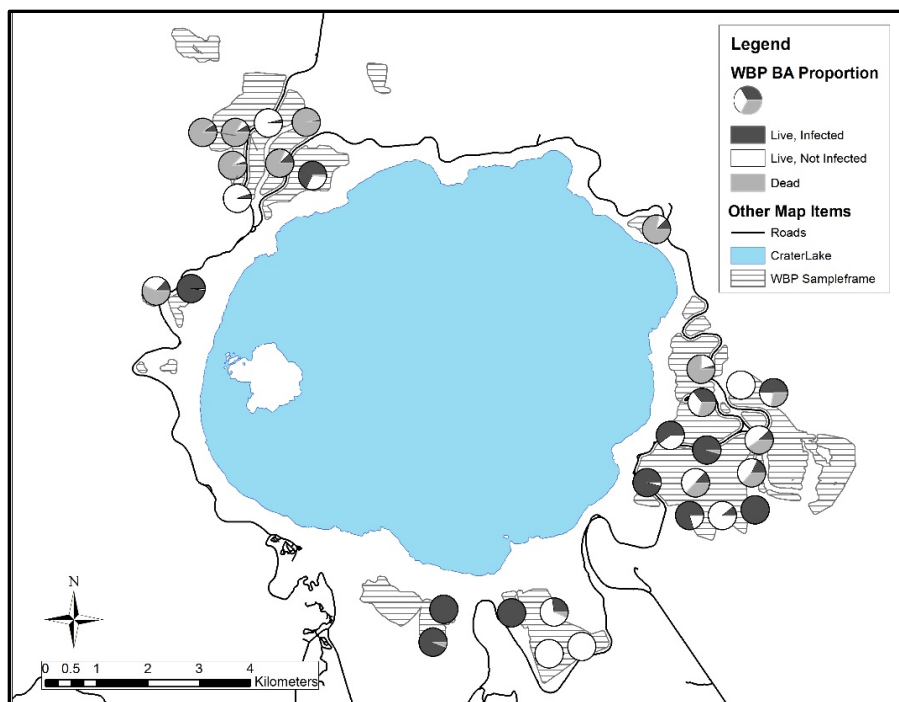


Figure 1. The whitebark pine sampling frame from Crater Lake National Park. Circular symbols show the 30 plots installed between 2012 and 2014, and each symbol is divided into the basal area of whitebark pine that is live, infected with blister rust (black), live, not infected with blister rust (white), and dead.

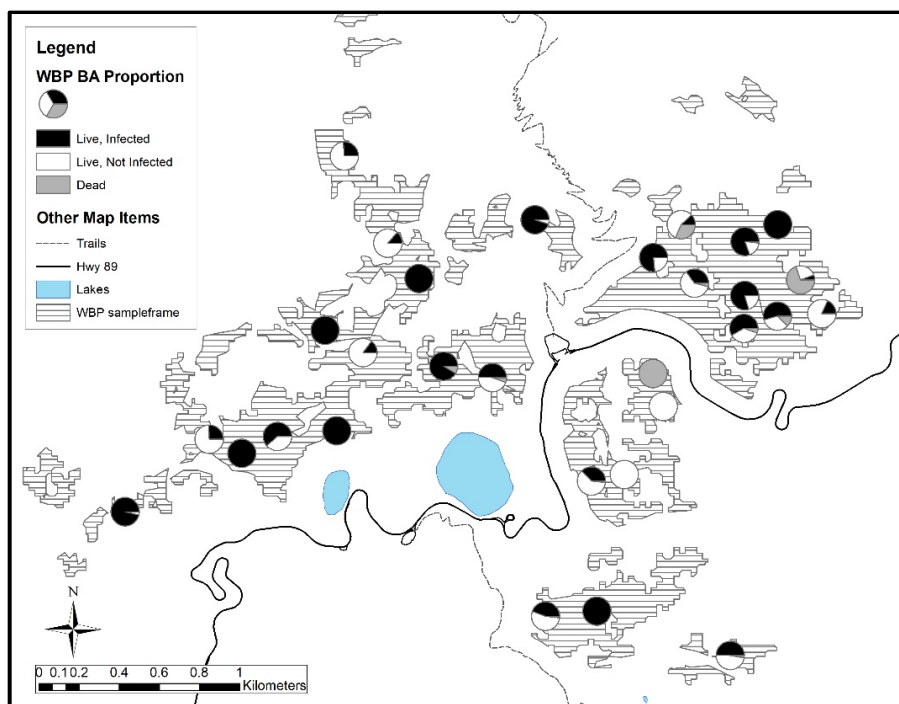


Figure 2. The whitebark pine sampling frame from Lassen Volcanic National Park. Circular symbols show the 30 plots installed between 2012 and 2014, and each symbol is divided into the basal area of whitebark pine that is live, infected with blister rust (black), live, not infected with blister rust (white), and dead.

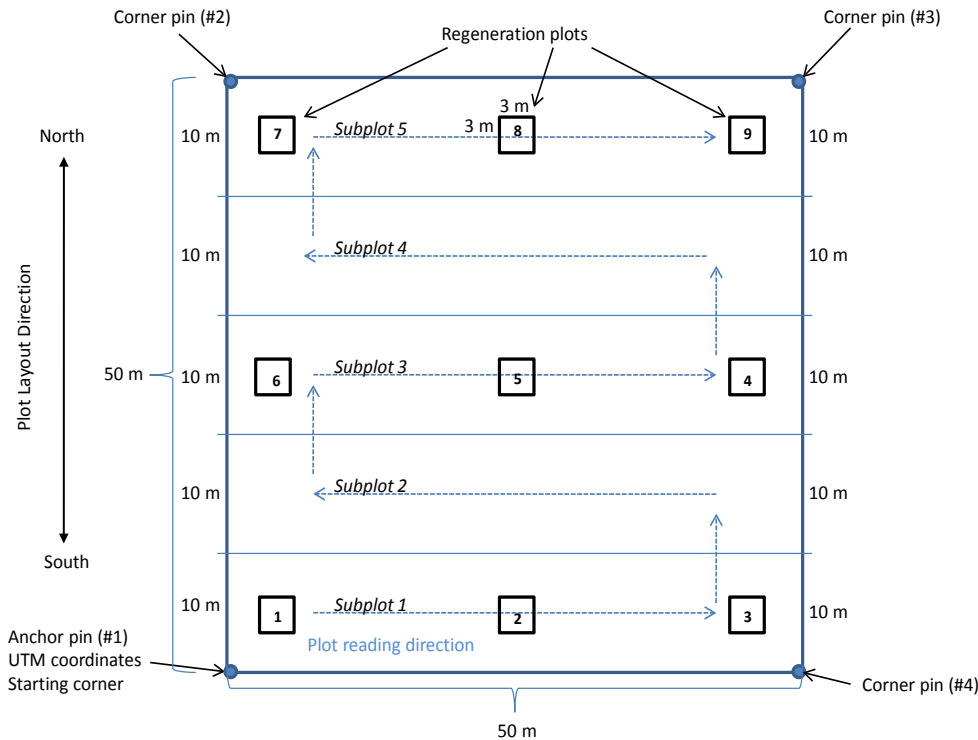


Figure 3. Whitebark pine 50 x 50 m plot design as described in the NPS PWR Five-Needle Pine Protocol (McKinney et al. 2012).

Tree Measurements

Within the 50 x 50 m plot, all trees ≥ 1.37 m in height were identified to species and tagged with a unique identification number. The dbh and height of each tree was recorded. In addition, each whitebark pine was assessed for symptoms of blister rust. The upper, middle, and bottom thirds of each tree were assessed separately and assigned to one of three conditions: (1) absent – no sign of rust infection, (2) active cankers (aeciospores present), or (3) inactive cankers, defined by the presence of at least three of the following six indicators of infection: rodent chewing, flagging, swelling, roughened bark, oozing sap, and old aecia. For all whitebark pine individuals, mountain pine beetle activity was recorded if pitch tubes, frass, and/or J-shaped galleries were found. Dead trees ≥ 1.37 m in height were also tagged with unique identification numbers and their dbh measured. Seedlings (trees < 1.37 m in height) were counted by species and height class in the nine regeneration plots. In 2013 and 2014, all whitebark pine seedlings in the regeneration plots were tagged with an identification number.

Climate Water Deficit

To estimate climate water deficit, a measure of water stress, we used a Thornthwaite-type water balance model to make estimates for all plots in both parks (Thornthwaite 1948, Thornthwaite and Mather 1955, Hamon 1963, Willmott et al. 1985, Dingman 2002). Thornthwaite-type methods are most appropriate for the development of water-balance models when inputs are limited to precipitation and temperature (Vorosmarty et al. 1998). In the Thornthwaite-type model, water is considered either to be stored in snowpack, transpired by vegetation, evaporated from the soil, or as

surplus in the form of runoff which reflects potential evapotranspiration (PET) (Lutz 2009). These calculations assume that the terrain is flat; however, other researches have combined measure of PET and heat load to generate more accurate estimates of climate water deficit (Lutz 2009). Therefore, we used a dimensionless heat-load (HL) index developed by McCune and Keon (2002) where equations for direct radiation are based on latitude, slope, and aspect. Direct radiation is a metric that reflects the greater temperatures and evaporative demands that occur in the afternoon (Lutz 2009). Using HL values to scale PET values, we were able to account for the variability in terrain for calculations of climate water deficit. Model outputs included estimates of monthly climate water deficit (mm), which we chose to average for the entire year.

Climate data (precipitation and temperature normals spanning 1981-2014) were sampled for each plot location at a spatial resolution of 800 m (~30 arc seconds) from the Parameter-elevation Regression on Independent Slopes Model developed by the PRISM Group at Oregon State University (Daly et al. 1994, 2000, 2002; PRISM Climate Group). We sampled soil water availability for both parks from the Soil Survey Geographic Database (SSURGO) at the 2 km grid resolution from the Natural Resources Conservation Service (Soil Survey Staff 2016).

Data Analysis

We first used our data to provide general summaries of the size and structure of whitebark pine stands in our plots. This included describing size distributions of trees (both alive and dead), the proportion of dead trees, cone production, and the amount of new recruitment present. We calculated the proportion of average canopy kill by averaging all values of percent canopy kill recorded for the lower, middle, and upper portions of each tree. In addition, we summarized the current prevalence of blister rust and mountain pine beetle across the plots.

Next, to assess potential drivers of pathogen and pest occurrence, reproductive output, and proportion of average canopy killed, we used a series of generalized linear mixed effects models (GLMM). For models where the dependent variable takes the response 0 or 1 (this includes predictions of blister rust infection, mountain pine beetle infestation, and the presence of cones), we used the binomial family and logit link function. To model the proportion of average canopy killed, we employed beta regression. Beta regression is a favorable approach to modeling proportions that fall between 0 and 1 but not values of exactly 0 or 1. In both parks, the proportion average canopy killed included proportions of 0 and 1, and therefore, we used a common transformation of the dependent variable that constrains the distribution to values that occur within the interval (0, 1) (Smithson and Verkuilen 2006).

Our models did not account for the design weights associated with the GRTS sample design to adjust the model based estimators. Because equiprobable samples were drawn within each park with a probabilistic method unrelated to the outcome of interest, the design can be ignored in a model-based approach (Schreuder et al. 2001). However, nonresponse error due to inaccessible sites may impact inference if the mean of the outcome of interest for accessible sites is significantly different from the mean at inaccessible sites. In CRLA, two of 32 sites were not successfully surveyed. One site was deemed to be outside of the target population because no whitebark pine were present, and this is considered frame error. One site was inaccessible, which is considered nonresponse error because the

site is assumed to be within the target population to which inference is made. This small proportion of nonresponse at CRLA is unlikely to impact inference and does not provide a large enough sample of missing sites for standard nonresponse adjustment procedures. At LAVO, three of 53 sites were classified as outside the target population. However, the rate of nonresponse was much higher at LAVO where 20 of the target 50 sites were not surveyed due to inaccessibility. If the blister rust prevalence rate is substantially different at the inaccessible sites, then inference based on only the accessible sites may be biased. We therefore conducted an analysis to examine how the nonresponse rate might have influenced the results by examining three different approaches to calculating estimates of blister rust prevalence (Appendix C). We found no evidence of biased blister rust inference from treating the missingness as completely random and applying the GLMM to the observed data.

For all analyses we chose to include the following predictor variables as stand-level metrics: average yearly climate water deficit, basal area of other tree species (includes both live and dead trees), and basal area of whitebark pine (both live and dead; Table 1). We chose to include dead trees here for several reasons. The basal area of dead non-whitebark pine was a relatively small fraction of the total non-whitebark pine basal area. For CRLA, we observed ~12% dead basal area (median among plots = 6%), and in LAVO we observed ~3% dead basal area (median = 0.2%). While this is a small amount, we assume that dead trees can reduce aboveground resources for living trees (i.e., space, light). Second, removing dead trees has the potential to omit the increased competition these trees created when they were alive (both above- and below-ground), which may have been recently enough to influence long-lived trees such as whitebark pine. Tree-level covariates included dbh (Dbh), blister rust presence (Wpbr, both active and inactive infections combined), and mountain pine beetle presence (Mpb, includes all symptoms; Table 1). We calculated basal area for all species at the plot level, and chose to combine basal area estimates of all non-whitebark pine individuals into a single covariate (BaOther; Table 1), the majority of which is mountain hemlock. We also summed basal area estimates of whitebark pine into a single covariate (BaWBP).

Table 1. Stand- and tree-level variables included in generalized linear mixed effects models (GLMMs) and zero-inflated Poisson (ZIP) regression models conducted for all dependent variables in two parks Crater Lake and Lassen Volcanic National Parks. The acronyms WBP, stands for whitebark pine and CWD, climate water deficit (mm).

Code	Description
Stand-level variables	
BaOther	Summed basal area of all non-WBP individuals in a plot (m ² /ha)
BaWBP	Summed basal area of all WBP individuals in a plot (m ² /ha).
Cwd*	Average climate water deficit (potential evapotranspiration-actual evapotranspiration; mm)
Tree-level variables	
Dbh	Diameter at breast height (cm)
Wpbr	Blister rust infection (Active and inactive cankers) (y/n)
Mpb	Mountain pine beetle infestation (y/n)
Cones	Female cones (y/n)

*Thorntwaite-type model; see Methods

All stand- and tree-level variables we included in the analysis represent measures of the major threats facing whitebark pine populations, namely, climate induced water stress, intraspecific (BaWBP) and interspecific (BaOther) competition, mountain pine beetle, and blister rust. Our models also incorporate tree-level covariates (Dbh, Wpbr, and Mpb), allowing all inferences for stand-level variables to be evaluated after accounting for individual differences.

For all models, we began by rescaling continuous covariates so that each was standardized around a mean of 0.0 and a standard deviation equal to that of the unscaled variable. Standardizing variables aids in the interpretation of coefficients, especially if they are on very different scales (Gelman 2008). Standard errors, *P*-values, and 95% confidence intervals were generated for each model. To determine the sensitivity of candidate models (the number of correctly classified trees) we used the area under the receiver operating characteristic (ROC) curve (Saveland and Neuenschwander 1990). The ROC curve (AUC [Area under curve]) >0.80 suggests excellent model discrimination (i.e., the ability of the model to correctly classify those with and without the disease; Hosmer and Lemeshow 2000). To assess model fit, we computed both marginal and conditional R^2 for models employing the binomial distribution ($R^2_{GLMM_m}$ and $R^2_{GLMM_c}$, Nakagawa and Schielzeth 2013) and pseudo R^2 values for models employing the beta distribution (Ferrari and Cribari-Neto 2004). We assessed all models (except for those utilizing beta regression) for overdispersion, a common problem associated with modeling count data, where the variance of the response variable is greater than the mean (Hilbe 2011).

We assessed the relationship between predictor variables and each measured effect (i.e., cone production, Mpb, etc.) by referring to both the associated *P*-values and confidence intervals generated by each model. Here, *P*-values represent the significance of the Z statistic (Wald test). Separately, confidence intervals represent the level of uncertainty around the measure of effect, which in the case of binomial models, is expressed as an odds ratio. However, some factors have confidence intervals that barely overlap zero and have marginally significant *P*-values (<0.1). By convention, these cases are included as useful and predictive factors.

We performed all statistical analysis in R version 3.2.3 (R Development Team 2015). For beta regression we utilized the function `glmmADMB` in the R library `glmmABMB` (Fournier et al. 2012), for models utilizing the binomial distribution we used the `glmer` function in the R library “lme4” (Bates et al. 2015), and for zero-inflated Poisson regression we used the `zeroinfl` function in the R package “pscl” (Zeileis et al. 2008).

Results

Crater Lake National Park

A total of 3637 live trees ≥ 1.37 m in height were found across the 30 CRLA plots, of which 952 (26%) were whitebark pine, 2344 (64%) were mountain hemlock, 259 (7%) were lodgepole pine, 73 (2%) were red fir (*Abies magnifica*), three (0.08%) were Englemann spruce (*Picea engelmannii*), four (0.10%) were subalpine fir (*Abies lasiocarpa*), and two (0.05%) were western white pine (*Pinus monticola*); Table 2, Figure 4). Living whitebark pine represented 11% of the total basal area in the 30 plots, while most basal area was from other species (Tables 2 and 3, Figure 5). Mountain hemlock represented 82%, lodgepole pine 6%, and red fir represented 1% of the basal area of living trees. We failed to record dbh values for a few trees or we recorded erroneously large values (~ 16 trees; 1.7% of whitebark pine), and these were left out of analyses that included dbh. On average, 16% of whitebark pine individuals ≥ 1.37 m in height were dead, and 26% of the total whitebark pine basal area was dead (Table 2, Figure 5). Most living whitebark pine were small, with only 3% of trees being >40 cm dbh (Figure 4), which represented 33% of the total basal area of living whitebark pine. A total of 34 seedlings were found in the 30 CRLA plots (Figure 6). Seedlings are only assessed in regeneration plots, which cover 81 m² in each plot (Figure 6). Mean values of whitebark pines with female cones per plot are shown in Figure 7.

Table 2. Summary statistics of living and dead trees sampled in 30 plots in each of two parks Crater Lake (CRLA) and Lassen Volcanic (LAVO) National Parks. Mean values among plots ($n = 30$) in each park and 1.0 standard deviations (SD) are shown.

Parameter	CRLA		LAVO	
	Mean	SD	Mean	SD
Live Trees (# individuals/ha)				
mountain hemlock	312.53	444.57	525.87	505.55
whitebark pine	126.93	218.24	87.60	86.30
lodgepole pine	34.53	55.67	0.13	0.73
red fir	9.73	45.90	5.73	10.85
western white pine	0.27	1.46	0.13	0.73
Live Trees (basal area; m ² /ha)				
mountain hemlock	20.01	25.69	14.47	14.52
whitebark pine	2.60	3.73	2.79	3.73
lodgepole pine	1.33	2.46	0.00005	0
red fir	0.26	1.37	0.16	0.43
western white pine	0.004	0.01	0.00002	0
Dead whitebark pine (# individuals/ha)	7.08	9.01	10	18.66
Dead whitebark pine (basal area; m ² /ha)	1.85	3.49	0.40	1.06
Proportion blister rust infected trees (basal area; m ² /ha)	0.51	0.32	0.54	0.35
Proportion mountain pine beetle infested trees (basal area; m ² /ha)	0.02	0.07	0.01	0.03

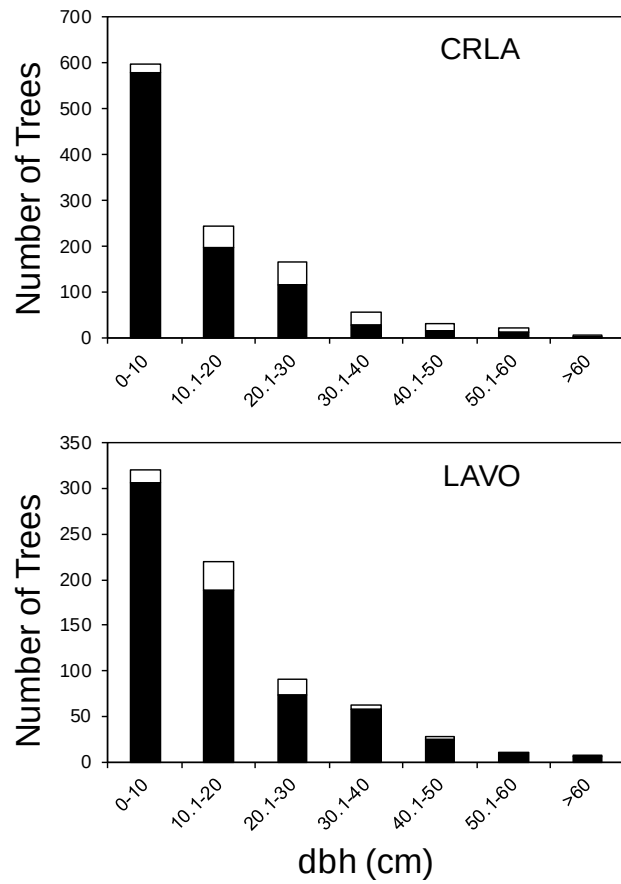


Figure 4. The total number of whitebark pine found in 30 plots established in both Crater Lake (CRLA) and Lassen Volcanic (LAVO) National Parks sorted by size class. Black bars represent living trees and white bars represent dead trees.

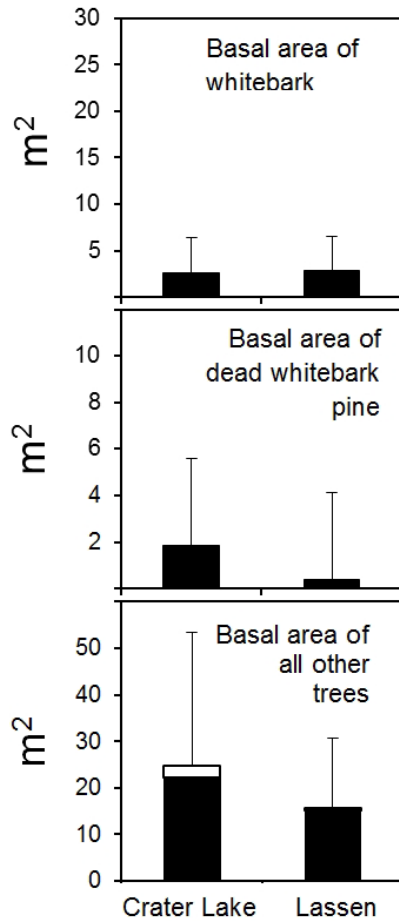


Figure 5 Basal area statistics from 30 whitebark pine plots in Crater Lake and Lassen Volcanic National Parks. Means with ± 1.0 SD are shown.

Table 3. Summary statistics of unstandardized covariates included in each of the five generalized linear mixed effects models in both Crater Lake (CRLA) and Lassen Volcanic (LAVO) National Parks. The values below represent averages and standard deviations for each covariate across all plots ($n = 30$) in each park.

Covariate	CRLA	LAVO
BaWBP (m2/ha)	4.45 (5.55)	3.19 (3.99)
BaOther (m2/ha)	29.76 (28.76)	16.99 (15.2)
Cwd (mm)	8.04 (2.32)	8.81 (1.74)
Dbh (cm)	14.11 (7.04)	15.32 (13.33)

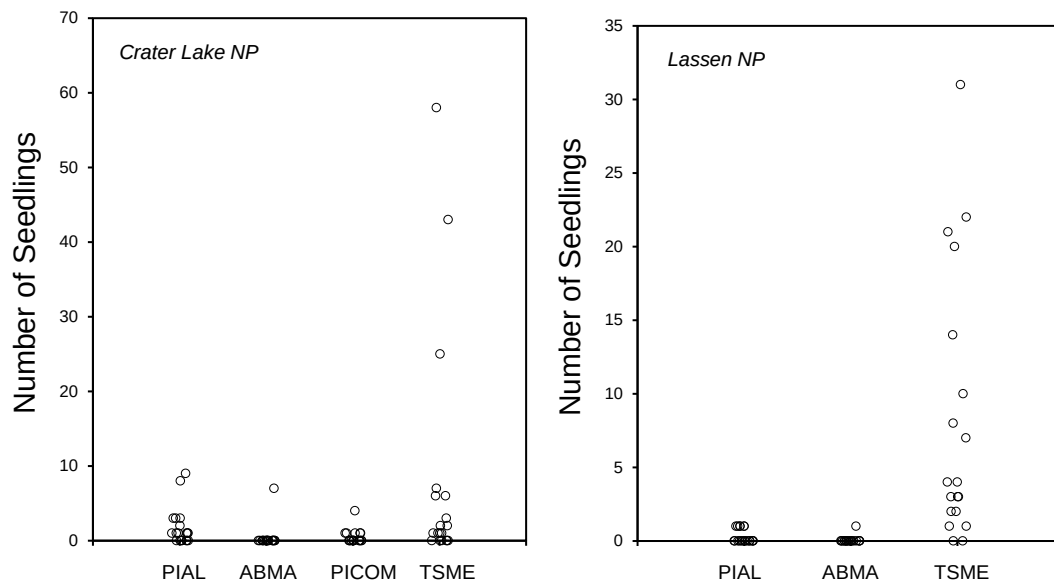


Figure 6. Number of seedlings in 30 whitebark pine plots in Crater Lake and Lassen Volcanic National Parks. Points are jittered to allow easier viewing.

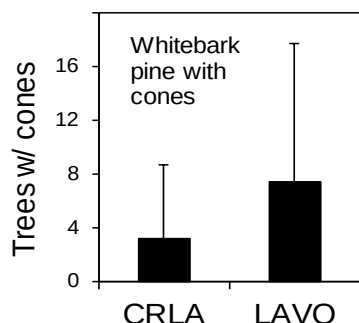


Figure 7. Number of whitebark pine trees with cones from 30 whitebark pine plots in Crater Lake (CRLA) and Lassen Volcanic (LAVO) National Parks. Means with +1.0 SD are shown.

The incidence of infection of whitebark pine by blister rust in CRLA ranged from 0.0% to 100% of trees per plot, and the average rate of infection among plots was 51% (Figure 8; Appendix D). Of the 952 live trees assessed, 443 showed signs of infection. Of the 177 dead trees that could be identified as whitebark pine in CRLA, 40 (23%) showed evidence of mountain pine beetle, 28 (16%) had signs of blister rust cankers, and we observed witches brooms in branches of two (1%) trees, which is indicative of mistletoe. Forty (22%) trees also showed evidence of bark beetles other than mountain pine beetle, and one (1%) appeared to have died from a broken stem. We did not observe symptoms of any specific mortality agent in the remaining 67 (38%) dead whitebark pine.

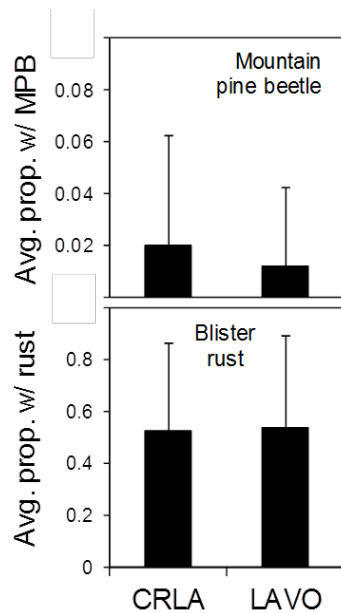


Figure 8. Incidence of mountain pine beetle and white pine blister rust from 30 whitebark pine plots in Crater Lake (CRLA) and Lassen Volcanic (LAVO) National Parks. Means with ± 1.0 SD are shown. Here, “rust” is blister rust and “MPB” is mountain pine beetle.

GLMMs revealed that the probability of blister rust occurrence on individual trees in CRLA increased with both tree size (dbh; cm) ($\beta = 0.372$, 95% CI = 0.203 to 0.540; Table 4) and average yearly climate water deficit ($\beta = 0.596$, 95% CI = 0.101 to 1.091; Table 4). The model predicting the incidence of blister rust provided moderate discrimination and correctly classified 68% of all observed cases of blister rust (AUC = 0.756, error rate = 0.318). The $R^2_{\text{GLMM}_m}$ and $R^2_{\text{GLMM}_c}$ for this model were 0.131 and 0.394, respectively. The probability of observing mountain pine beetle infestation increased with previous infection by blister rust ($\beta = 2.359$, 95% CI = 0.881 to 3.387; Table 4). The model correctly classified 97.5% of all observed cases of mountain pine beetle and provided moderate discrimination (AUC = 0.797, error rate = 0.0242). The $R^2_{\text{GLMM}_m}$ and $R^2_{\text{GLMM}_c}$ for this model were 0.372 and 0.372, respectively. The probability of observing cones decreased with increases in the basal area of other species ($\beta = -1.24$, 95% CI = -2.123 to 0.362; Table 4) and increased with tree size (dbh; cm) ($\beta = 1.425$, 95% CI = 1.128 to 1.721; Table 4) and average yearly climate water deficit ($\beta = 0.717$, 95% CI = -0.086 to 1.521; Table 4). The final model provided excellent model discrimination and correctly classified 90.8% of all observed cases (AUC = 0.906; error rate = 0.091). The $R^2_{\text{GLMM}_m}$ and $R^2_{\text{GLMM}_c}$ for this model were 0.423 and 0.605, respectively. The proportion of average canopy killed increased with tree size ($\beta = 0.243$, 95% CI = 0.182 to 0.304; Table 4), the basal area of other species ($\beta = 0.185$, 95% CI = 0.061 to 0.310; Table 4), and the basal area of whitebark pine ($\beta = 0.303$, 95% CI = 0.092 to 0.515; Table 4). Average canopy kill was also higher on trees with current or past blister rust infection ($\beta = 0.228$, 95% CI = 0.104 to 0.351; Table 4) and on trees with mountain pine beetle infestation ($\beta = 0.433$, 95% CI = 0.083 to 0.782; Table 4). The beta dispersion parameter for this model was found to be 4.6123 (standard error = 0.20376) and pseudo R^2 was 0.16.

Table 4. Estimated effects of site characteristics from the best supported Generalized Linear Mixed Model (GLMM) of the probability of producing cones (no=0, yes=1), probability of white pine blister rust infection (uninfected=0, infected=1), the probability of mountain pine beetle infestation (uninfested=0, infested=1), and the proportion of average canopy kill in Crater Lake National Park. *P*-values indicate significance of the Wald Z-test statistic. The acronym CWD, stands for climate water deficit (mm).

Characteristic	Model	Est	Std. Error	<i>P</i>	95 % CI
Incidence of white pine blister rust	Dbh	0.372	0.086	<0.001	(0.203 – 0.540)
	Cwd	0.596	0.252	<0.05	(0.101 – 1.091)
	BaWBP	-0.365	0.321	0.255	(-0.994 – 0.263)
	BaOther	-0.069	0.185	0.707	(-0.434 – 0.294)
Incidence of mpb	Wpbr	2.359	0.754	<0.01	(0.881 – 3.387)
	Cwd	0.384	0.263	0.144	(-0.131 – 0.900)
	dbh	-0.273	0.268	0.308	(-0.798 – 0.252)
	BaOther	0.160	0.231	0.488	(-0.293 – 0.614)
	BaWBP	-0.127	0.263	0.628	(-0.644 – 0.389)
Production of cones	Dbh	1.425	0.151	<0.001	(1.128 – 1.721)
	BaOther	-1.24	0.449	<0.01	(-2.123 – -0.362)
	Cwd	0.717	0.410	0.080	(-0.086 – 1.521)
	Wpbr	0.157	0.279	0.572	(-0.389 – 0.704)
	Mpb	0.645	0.749	0.389	(-0.823 – 2.114)
	BaWPB	-0.077	0.374	0.836	(-0.811 – 0.657)
Proportion of average canopy killed	Dbh	0.243	0.031	<0.001	(0.182 – 0.304)
	Wpbr	0.228	0.063	<0.001	(0.104 – 0.351)
	BaOther	0.185	0.063	<0.01	(0.061 – 0.310)
	BaWBP	0.303	0.107	<0.01	(0.092 – 0.515)
	Mpb	0.433	0.178	<0.05	(0.083 – 0.782)
	Cwd	-0.028	0.085	0.739	(-0.194 – 0.138)

Lassen Volcanic National Park

In LAVO, a total of 4647 live trees ≥ 1.37 m in height were found across the 30 plots, of which 657 (14%) were whitebark pine, 3944 (85%) were mountain hemlock, 43 (0.9%) were red fir, and one (0.02%) was lodgepole pine (Table 2, Figure 4). Western white pine is another host of blister rust, and a single western white pine (0.02%) was found on a LAVO plot. Living whitebark pine represented 16% of the total basal area in the LAVO plots, while most basal area in the plots was from other species (Tables 2 and 3, Figure 5). Mountain hemlock represented 83%, and red fir represented 1% of living basal area. As with the CRLA data, dbh for a few trees (20; 3% of whitebark pine) were removed due to suspect values or our inability to identify the species and were not included in the basal area estimates. On average, 10% of whitebark pine individuals ≥ 1.37 m in height were dead, and $<1\%$ of the total whitebark pine basal area was dead (Table 2, Figure 5). Most living whitebark pine were small, with only 7.5% of trees being >40 cm dbh (Figure 4). A total of six seedlings were found in the 30 LAVO plots (i.e., 25 seedlings/ha; Figure 6). Mean values of whitebark pines per site with female cones are shown in figure 7.

In LAVO, the incidence of infection of whitebark pine by blister rust ranged from 0.0% to 100% of whitebark pine per plot, and the average rate of infection among plots was 54% (Figure 8; Appendix E). Of the 657 live trees assessed, 316 showed signs of infection. Of the 75 dead trees that could be identified as whitebark pine in LAVO, three (4%) appeared to have died from mountain pine beetle, eight (11%) from blister rust, 14 (19%) from other bark beetles, and 50 (67%) died from unknown causes.

For trees in LAVO, our model indicated that none of the covariates significantly influenced the probability of observing blister rust on live trees. The model correctly classified 78.9% of observed cases and provided excellent model discrimination (AUC = 0.854, error rate = 0.210). The $R^2\text{GLMM}_m$ and $R^2\text{GLMM}_c$ for this model were 0.063 and 0.504, respectively. The probability of observing cones increased with tree size (dbh; cm) ($\beta = 1.087$, 95% CI = 0.849 to 1.325; Table 5) and decreased with increases in the basal area of other species ($\beta = -0.325$, 95% CI = -0.672 to 0.022; Table 5). The final model provided excellent model discrimination and correctly classified 76% of all observed cases of cone production (AUC = 0.826; error rate = 0.233). The $R^2\text{GLMM}_m$ and $R^2\text{GLMM}_c$ for this model were 0.267 and 0.349, respectively. The proportion of average canopy killed decreased with increases in average yearly climate water deficit ($\beta = -0.232$, 95% CI = -0.441 to -0.023; Table 5).

Table 5. Estimated effects of site characteristics from the best supported Generalized Linear Mixed Model (GLMM) of the probability of producing cones (no=0, yes=1), probability of blister rust infection (uninfected=0, infected=1), the probability of mountain pine beetle infestation (uninfested=0, infested=1), and the proportion of average canopy in Lassen Volcanic National Park. *P*-values indicate significance of the Wald Z-test statistic. The acronym CWD stands for climate water deficit (mm).

Characteristic	Model	Est	Std. Error	P	95 % CI
Incidence of white pine blister rust	Dbh	-0.049	0.106	0.644	(-0.257 – 0.159)
	Cwd	0.312	0.357	0.383	(-0.375 – 1.005)
	BaWBP	-0.604	0.451	0.180	(-1.475 – 0.261)
	BaOther	-0.161	0.347	0.642	(-0.830 – 0.508)
Production of cones	Dbh	1.087	0.121	<0.001	(0.849 – 1.325)
	BaOther	-0.325	0.177	0.067	(-0.672 – 0.022)
	Cwd	0.079	0.176	0.651	(-0.264 – 0.424)
	Wpbr	-0.102	0.236	0.664	(-0.566 – 0.361)
	BaWPB	0.199	0.206	0.333	(-0.202 – 0.603)
	Mpb	-0.712	0.871	0.413	(-2.41 – 1.00)
Proportion of average canopy killed	Wpbr	0.464	0.074	<0.001	(0.293 – 0.635)
	Cwd	-0.232	0.106	0.030	(-0.441 – -0.023)
	Mpb	0.509	0.265	0.055	(-0.011 – 1.030)
	Dbh	-0.031	0.038	0.421	(-0.107 – 0.044)
	BaOther	0.074	0.102	0.471	(-0.127 – 0.275)
	Ba_WBP	0.064	0.131	0.623	(-0.322 – 0.193)

The proportion of average canopy killed increased for trees with current or past blister rust infection ($\beta = 0.464$, 95% CI = 0.293 to 0.635; Table 5) and for trees with mountain pine beetle infestation ($\beta = 0.509$, 95% CI = -0.011 to 1.030; Table 5). The beta dispersion parameter for this model was calculated at 4.832 (standard error= 0.26145) and pseudo R^2 was 0.15.

We chose not to model the incidence of mountain pine beetle in LAVO because of low sample sizes (total # of infested trees = 11). However, of the 11 infested individuals, eight showed signs of blister rust infection. Thus, eight of 316 blister rust-infected trees (2.5%) had mountain pine beetle, while three of 338 uninfected trees (0.89 %) had mountain pine beetle. A chi-square test demonstrated that the difference in the proportion of blister rust-infected trees with mountain pine beetle was marginally significant ($X^2 = 2.579$, $df = 1.0$, $P = 0.1082$).

Discussion

Rates of blister rust infection in LAVO and CRLA were similar between parks with nearly half of all whitebark pine surveyed showing signs of active or inactive infections (Figure 8; Appendices D and E). We also found that the proportion of dead trees in CRLA (~16%) was slightly greater than in LAVO (~11%). In addition, mountain hemlock is the dominant species in our plots in CRLA and LAVO and appears to pose a threat to whitebark pine through increased competition.

We also found strong evidence that blister rust infection, mountain pine beetle infestation, and whitebark pine survivorship and fecundity are influenced by several site and demographic factors. These may help managers focus their efforts on higher risk sites and individual trees. Our results from CRLA match many other studies of the factors controlling blister rust, but this was not true in LAVO. In the two sections below, we discuss the patterns we found in each park separately. We then discuss the overall implications of our study for understanding the current status of whitebark pine in KLMN parks and implications for management.

CRLA National Park

Blister rust incidence in CRLA was highest in sites with greater values of average yearly climate water deficit (Table 4) which adds to a number of studies that have demonstrated that water stressed trees are more vulnerable to attack by mountain pine beetle and blister rust (Six and Adams 2007, Larson 2011). Climate induced stressors directly and indirectly impact forest dieback by influencing blister rust and bark beetle dynamics and reducing tree fitness through chronic or acute stress, which may predispose trees to insect and pathogen attack (Logan and Powell 2001). For trees in CRLA, it is plausible that the effect of climate (and ultimately blister rust infection) will be more pronounced on the east side of the park. Conditions on the west side of the park are cooler and wetter while the east side conditions are generally warmer and drier (Beck and Holm 2012), and we found that many plots exhibit the same trend with respect to climate water deficit. A *t*-test demonstrated that trees in plots on the east side of the park experienced greater levels of climate water deficit over those located on the west side of the park ($t = 3.37$, d.f. = 28, $P = 0.002$), although this is not necessarily the case with all plots (i.e., CRWB11; Appendix D). Our study found that east side plots are drier and have higher blister rust, but a direct link between these measures has not been established.

In addition, blister rust was more commonly found on larger whitebark pine in CRLA (Table 4). These patterns match those found in several other studies where larger trees show higher blister rust incidence (Campbell and Antos 2000, Smith and Hoffman 2001, Kearns et al. 2014) but contrasts other studies where infection was equally likely to be found in all size classes (Goheen et al. 2002, Zeglan 2002, Smith et al. 2008). We note that most studies of whitebark pine and blister rust do not assess the relationship of tree size and infection risk, and those that do are hindered by the significant, previous mortality that may obscure the proportion of large trees that are infected. Other studies have assessed the role of alternate blister rust hosts, such as *Ribes* spp., and results of those studies vary (see Smith and Hoffman 2001, Goheen et al. 2002, Maloney 2011, Smith et al. 2011). Significant positive correlations between *Ribes* and blister rust infection were found by Smith et al. (2011) in CRLA on drier east-side sites, but not on west-side sites. Our study cannot be used to

assess the role of alternate hosts at this point because we do not have complete vegetation data associated with our plots.

Mountain pine beetle infestation was important in CRLA, and it was more likely to be found in trees with previous blister rust infection, where infection is defined as either active or inactive (Table 4). The preferential selection of blister rust-infected trees is intriguing and has been noted in other studies (Six and Adams 2006, Bockino 2008, Bockino and Tinker 2012) and suggests that beetles preferentially select trees weakened by stress. Note that we found some, albeit weak, evidence of this same pattern in LAVO (see *Results*).

Pests and pathogens are important factors influencing tree health. In CRLA, trees with mountain pine beetle infestation and blister rust infection demonstrated significantly higher levels of canopy kill over uninfested or uninfected trees (Tables 4 and 5), and a comparison of plot level averages of canopy kill indicate that trees are responding similarly to stressors in both parks (CRLA mean = 0.28 [± 0.14 1.0 SD], LAVO mean = 0.27 [± 0.16 1.0 SD]). In addition, we found that the proportion of average canopy kill was greater for trees in CRLA in stands with higher basal area of both whitebark pine and other tree species (Table 4). This may indicate that trees in plots with higher basal area are experiencing higher levels of intraspecific and interspecific competition, which is affecting crown health. Increases in canopy kill can reduce the reproductive potential of trees by killing cone bearing branches (Smith et al. 2008), which limits seed dispersal (McKinney et al. 2007). Although trees are likely to survive, reductions in canopy can limit the reproductive potential of a tree throughout its life resulting in fewer successful cone crops and limited opportunities for dispersal (Smith et al. 2008).

Whitebark pine plots were dominated by mountain hemlock in CRLA. Including both living and dead trees, hemlock represented 61% of the trees and 77% of the basal area, while whitebark pine represented 29% of the trees and 16% of the basal area. Including only living trees, mountain hemlock represented 64% of the trees and 82% of the basal area, while whitebark pine represented 26% of the trees and 11% of the basal area. Beck (2014) suggests that competition between whitebark pine and mountain hemlock is intense, especially along the west side of the caldera. Our study demonstrates the importance of increased encroachment by mountain hemlock. First, the proportion of cone producing whitebark pine was reduced in plots that had higher levels of basal area of other species, which is primarily mountain hemlock. Second, mountain hemlock vigor in these sites may also be seen at the seedling level; seedlings were considerably more abundant than for any other species within our plots, including whitebark pine (Figure 6). The role of competition, and its relationship with fire exclusion, is a key consideration for whitebark pine management (Keane et al. 2012).

LAVO National Park

Blister rust incidence was surprisingly high, with an average rate of infection among plots of 54% (Figure 8, Appendix E). Although we are not aware of any studies of blister rust in LAVO, several biologists had told us that little blister rust had been discovered in the park. Our study shows clearly that blister rust is well-established in LAVO, though it is unclear how long it has been there. In contrast, the record of blister rust in CRLA is quite robust, and we are certain it was in CRLA since at least 1936 (reviewed in Beck 2014). Interestingly, a study conducted in 2013 by Kauffmann et al.

(2014) indicated that among five areas surveyed in the surrounding LAVO National Forest blister rust incidence was quite variable. Three of the five sites in that study were infected (70%, 14%, and 13%), while the other two showed no infection.

In LAVO, strong relationships relating environmental variables to whitebark stand structure or condition were not found using our GLMM (Table 5). For example, we were unable to find any significant relationships driving blister rust infections on live trees. Unlike CRLA, we suspect that the simple view of east-side slopes being drier may be more complicated in LAVO. The whitebark pine sampling area was much smaller in LAVO as compared with CRLA (Figures 1 and 2). In CRLA, the large caldera separates stands of whitebark pine on all sides of the lake, while in LAVO stands are restricted to a small area that may not have an easily detected east-west gradient.

Although we were unable to run similar models predicting mountain pine beetle incidence in LAVO because of low sample sizes, we found that of the 11 trees infested with mountain pine beetle, eight were infected with blister rust. We believe that differences in infestation rates between LAVO and CRLA are influenced by differences in proximity to alternate beetle hosts and differences in the mosaic of whitebark pine stands across the landscape. Whitebark pine is represented in fewer numbers and is found in sparse stands in LAVO, compared to the dense, homogenous stands present on the rim and east side of CRLA. Furthermore, we found greater numbers of alternate host trees in CRLA than were present in LAVO (see *Results*). Perhaps whitebark pine in LAVO have, so far, been buffered from mountain pine beetle attacks because tree densities do not support mountain pine beetle outbreaks, or mountain pine beetle have not yet moved out of lower elevation lodgepole pine forests (found on the east side of Lassen Peak) to whitebark pines found at higher elevations. However, with continued warming trends, we expect that mountain pine beetles will continue to move upward in elevation and more whitebark pine will fall prey to mountain pine beetle infestation (Millar et al. 2012, Weed et al. 2015). Furthermore, given the rate of blister rust incidence in LAVO is comparable to that of CRLA (where we found associations between mountain pine beetle and blister rust), whitebark pine in LAVO may be increasingly susceptible to mountain pine beetle infestation and mortality in the future.

Similar to our findings for trees in CRLA, our model indicated that the proportion of average canopy kill was greater for trees experiencing mountain pine beetle infestation or blister rust infection. Before our study, blister rust was believed to be largely absent in LAVO, and it is unclear how long blister rust has been present in LAVO.

One unexpected result was that the proportion of canopy kill in LAVO was greater for trees in areas experiencing higher levels of climate water deficit (Table 5). We believe this may be explained through factors related to climate, such as snowpack and frost damage. Increases in climate water deficit may be more closely tied to increases in temperature, even when annual precipitation is not unusually low (Millar et al. 2012), and heavy snowpack and ice particles in the wind can cause significant foliar damage to young whitebark pine (Bartos and Gibson 1990). Other research has demonstrated that under current climate conditions, the loss of soil water equivalents (SWE) is less pronounced at elevations >2800 m and that high elevation regions in LAVO will continue to maintain deep (>800 mm SWE) April 1st snowpack (Curtis et al. 2014). This model accurately

predicted canopy kill for trees in LAVO and suggests that canopy kill is influenced by high snowpack levels.

We also found that the probability of producing cones demonstrated a negative, marginally significant relationship with the basal area of other species, similar to trees in CRLA (Table 5). McCaughey and Tomback (2001) found that unsuppressed trees produce large, full crowns with cones, and we suspect that competition for light with mountain hemlock may be the factor by which cone production is limited. We also observed more cone bearing trees in LAVO (33% (221 of 657) than in CRLA (10% (96 of 952)), yet despite these differences, we observed less whitebark pine regeneration in LAVO (Figure 5). It is unclear why so little regeneration was recorded in LAVO, and we expect that these results are more closely tied to factors regarding seedling survival over cone and seed production. Unfortunately, given so few seedlings, we were unable to associate whitebark pine regeneration to topographical and climate related variables.

Regional Patterns

In general, we found that incidence of blister rust infection was nearly equal between CRLA and LAVO. It is of interest then to consider the larger regional context of both parks. The initial introduction of blister rust into North America in 1910 in Vancouver, British Columbia, and spread of the disease along the Cascades occurred quite rapidly (McDonald and Hoff 2001). The moist conditions and ample hosts has led to variable but high infection rates in the Cascades of Oregon and Washington (e.g., Campbell and Antos 2000, Goheen et al. 2002, Larson 2011). Less is known about blister rust in the southern portion of the Cascades and in the rest of California. In an analysis of blister rust infection rates on five-needle pines in high-elevation sites of California, Maloney (2011) found a significant positive relationship of latitude with infection; many sites in southern California remain free of blister rust. Although this pattern was obscured by many local environmental influences, it suggests that the lower infection rates we found in LAVO could be a result of either (1) less favorable conditions for blister rust, or (2) simply that it had taken the pathogen longer to reach this site at the southern end of the Cascades.

Mountain pine beetle was more important in CRLA than in LAVO, and it is also worth considering why we might have observed this difference. Mountain pine beetle activity has increased markedly near and in CRLA since ~2010, presumably because of extended dry seasons and warmer temperatures (Preisler et al. 2012, Meigs et al. 2015). The same high levels of mountain pine beetle activity have been observed in a small number of whitebark pine stands of eastern California where pronounced mortality was observed from 2007-2010 (Millar et al. 2012). Interestingly, these eastern California sites have no blister rust infections. Very little is known about mountain pine beetle activity in LAVO, but they are observed within the park on lodgepole pine (Ganz et al. 2003). In our study, mountain pine beetle occurrence was nearly as high in LAVO as CRLA (Figure 8).

Conclusions

Our study provides a baseline assessment of whitebark pine populations in CRLA and LAVO and may also provide some insight into the future of whitebark pine demographics in the southern Cascades. Roughly 55% of the basal area of whitebark pine was infected with blister rust in both parks. That LAVO had similar infection rates to CRLA was somewhat of a surprise given the rarity of previous observations in LAVO. In contrast, we observed far more standing dead trees and basal area of dead trees in CRLA than in LAVO (Table 2), and this may be in part due to higher mountain pine beetle activity in CRLA since 2007. Both parks have large components of mountain hemlock within the subalpine. In areas where disturbances such as fire are removed or limited, mountain hemlock encroachment can reduce whitebark pine growth and recruitment. We found that higher densities of mountain hemlock were associated with decreased numbers of cone producing whitebark pine. In CRLA, water stress was a good predictor of blister rust infection, and in both parks the presence of mountain pine beetle and blister rust was associated with increased canopy kill for whitebark pine. The relationship between water stress and blister rust infection may not be a direct one and warrants further attention.

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Appendix A: Location information and site characteristics for whitebark pine plots established in CRLA in 2012, 2013, and 2014. Oversample plots were used in cases where any of the original ten plot locations did not contain whitebark pine.

Plot ID	Aspect (°)	Elevation (m)	Slope (°)
CRWB01	120	2062	14
CRWB02	230	2074	4
CRWB03	200	2269	11
CRWB04	243	2166	6
CRWB05	284	2078	5
CRWB06	340	2334	9
CRWB07	115	2219	5
CRWB08	320	2253	4
CRWB10	250	2277	9
CRWB11	218	2262	12
CRWB21	302	2372	12
CRWB22	216	2410	19
CRWB23	64	2302	12
CRWB24	310	2211	14
CRWB25	333	2162	8
CRWB26	210	2205	2
CRWB27	117	2286	18
CRWB28	231	2294	8
CRWB29	313	2139	9
CRWB30	170	2265	6
CRWB41	145	2096	8
CRWB42	60	2481	9
CRWB43	10	2319	9
CRWB44	70	2481	27
CRWB45	140	2122	13
CRWB46	63	2481	24
CRWB47	167	2386	25
CRWB49	90	2234	24
CRWB50	15	2318	26
CRWB51	130	2397	51

Appendix B: Location information and site characteristics for whitebark pine plots established in LAVO in 2012, 2013, and 2014. Oversample plots were used in cases where any of the original ten plot locations did not contain whitebark pine.

Plot ID	Aspect (°)	Elevation (m)	Slope (°)
LVWB03	128	2595	14
LVWB06	180	2627	15
LVWB06	256	2629	6
LVWB07	100	2539	11
LVWB08	336	2545	16
LVWB09	115	2502	5
LVWB10	186	2597	23
LVWB11	212	2752	25
LVWB12	170	2575	9
LVWB14	184	2579	23
LVWB22	40	2657	4
LVWB23	78	2815	14
LVWB24	120	2844	6
LVWB28	20	2904	5
LVWB30	20	2977	23
LVWB31	106	2983	22
LVWB32	40	2940	16
LVWB34	140	2983	24
LVWB35	120	2983	21
LVWB39	140	2983	25
LVWB42	122	2576	19
LVWB44	16	2610	23
LVWB47	134	2628	6
LVWB48	126	2627	21
LVWB49	187	2635	18
LVWB51	155	2603	15
LVWB54	213	2605	24
LVWB56	63	2577	14
LVWB59	125	2715	23
LVWB60	110	2612	26

Appendix C. Statistical assessment of ignoring design weights in model-based analyses of whitebark pine outcomes.

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MEMO: Assessment of ignoring design weights in model-based analyses of whitebark pine outcomes

Introduction

The impact of ignoring design weights in a purely model-based analysis of whitebark pine metrics was assessed by comparing estimates of whitebark pine blister rust prevalence rates for model-based, design-based, and model-assisted estimators. Equiprobable generalized random tessellation stratified (GRTS) samples (Stevens and Olsen 2003, 2004) were selected in whitebark pine habitat independently within Crater Lake (CRLA) and Lassen Volcanic (LAVO) National Parks. Binomial Generalized Linear Mixed Models (GLMM) were used to describe prevalence rates of blister rust in living whitebark pine stands identified in sampled plots (Jules et al. in progress). GLMMs included predictors for tree-level diameter at breast height and plot-level metrics including mean coarse woody debris and total basal area of whitebark pines and other trees.

Because equiprobable samples were drawn within each park with a probabilistic method unrelated to the outcome of interest, the design can be ignored in a model-based approach (Schreuder et al. 2001). However, nonresponse error due to inaccessible sites may impact inference if the mean of the outcome of interest for accessible sites is significantly different from the mean at inaccessible sites. In CRLA, 2 of 32 sites were not successfully surveyed. One site was deemed to be outside of the target population because no whitebark pine was present, and this is considered frame error. One site was inaccessible, which is considered nonresponse error because the site is assumed to be within the target population to which inference is made. This small proportion of nonresponse at CRLA is unlikely to impact inference. At LAVO, 3 of 53 sites were classified as outside the target population. However, the rate of nonresponse was much higher at LAVO where 20 of the 50 sites were not surveyed due to inaccessibility. If the blister rust prevalence rate is substantially different at the inaccessible sites, then inference based on only the accessible sites may be biased.

Nonresponse is classified in one of three categories: missing completely at random (MCAR), missing at random (MAR), and not missing at random (NMAR) (Little and Rubin, 2002). When sampling units are MCAR, the missingness is unrelated to the design, the outcome of interest, and any covariates. The obtained sample may be treated as a random sample from the target population and standard analysis techniques may be used. MAR nonresponse is related to the outcome of interest,

but that relationship may be explained with covariates that are either known for the population or may be obtained at the time of the survey. For example, if nonresponse is related to the slope at a site, then MAR weighting adjustments that incorporate classes based on the slope may be used to obtain unbiased inference. When NMAR occurs, nonresponse is related to the outcome of interest but information from the sample is insufficient to obtain unbiased inference. In this case, a nonrespondent subsample or a model of the outcome mean assuming the NMAR missingness is needed to correct the biased inference from the sample. MCAR and MAR missingness are also called “ignorable” nonresponse because the information from the sample is sufficient to obtain unbiased inference. NMAR missingness is called “nonignorable” nonresponse because additional information is needed for unbiased inference. Two methods assuming MCAR missingness (a synthetic estimator and a design-based estimator) and one method assuming MAR missingness (a weighting-class adjustment) were used to assess the results of the GLMM.

Methods

Predictions from the GLMM were used to obtain an estimate of population-level prevalence rates using a synthetic estimator (Särndal et al. 1992) which takes the mean of model predictions at the plot level and then averages across plots to obtain a population-level estimate of prevalence. This approach directly assesses the performance of the GLMM which ignores the nonresponse in the sample. Confidence intervals were obtained from cluster bootstrapping to account for the correlation of trees within the same plot.

A design-based estimator that draws on the GRTS design was also examined. The estimate of the mean prevalence was obtained from a Horvitz-Thompson estimate of plot-level prevalence metrics, and confidence intervals were constructed from the neighborhood variance estimator (Stevens and Olsen 2003) to account for the spatial balance of the sample. This design-based approach assumes MCAR missingness when adjusting design weights to account for the missing sites. This approach provided an independent set of estimates that rely only on the sampling design and not related covariates.

A weighting-class adjustment (Oh and Scheuren 1983), a model-assisted estimator that assumes MAR missingness, was applied to assess the impact of nonresponse. The weighting-class adjustment assumes that, within levels of a classification variable related to the nonresponse, nonresponse is MCAR and standard techniques may be used within the weighting classes. This MAR approach was compared to the two MCAR approaches to determine if nonresponse should be considered in the analysis.

Three covariates were evaluated as possible weighting class variables for a nonresponse adjustment: Slope, Aspect, and Elevation. Classes were initially formed using the quantiles of each covariate, but four classes did not provide enough respondents and nonrespondents within each class for an adjustment. To ensure adequate within-class replication, the median was used as the basis for two weighting classes for each of the possible classification variables. The relationship between the covariates and the probability that a site was successfully surveyed (*i.e.* the response rate) was assessed to determine if any of the covariates would be useful for weighting class adjustment.

Pearson's correlation tests were used to assess the linear relationship between blister rust prevalence rate and covariate values for successfully sampled sites.

Results

The covariate classes were examined with a logistic regression model to identify the best predictors of the response rate. Model selection with AIC resulted in a model containing each of the main effects for Slope, Aspect, and Elevation. Slope was found to be a highly significant predictor that a site was successfully surveyed (*i.e.* the site “responded”) (regression coefficient = -3.035, SE = 0.9017, p-value = 0.0008). This result indicated that odds of successfully surveying sites below the median slope (17.70 degrees) were 20.8 (90%-CI: 4.72, 91.68) times higher than the odds of surveying sites above the median slope. Aspect was also loosely associated with the response rate (regression coefficient = -1.6756, SE = 0.8514, p-value = 0.0491), but combining the two weighting classes resulted in small sample sizes of responding and nonresponding sites within each weighting class. Therefore, the two-category Slope classification was used in a weighting class adjustment to estimate the mean of the blister rust prevalence rate at LAVO. Because only one target site was missing at CRLA, a weighting adjustment cannot be applied to data from that park.

Pearson's correlation tests were used to assess linear relationship between the proportion of live whitebark pines with blister rust for successfully sampled sites (Figure 1), but correlations were not significant for Slope (correlation = 0.1312, p-value = 0.4896), Aspect (correlation = 0.1198, p-value = 0.5283), or Elevation (correlation = 0.1559, p-value = 0.4107). This result may indicate that missingness is ignorable in the sense that the information in the sample is sufficient for unbiased estimation.

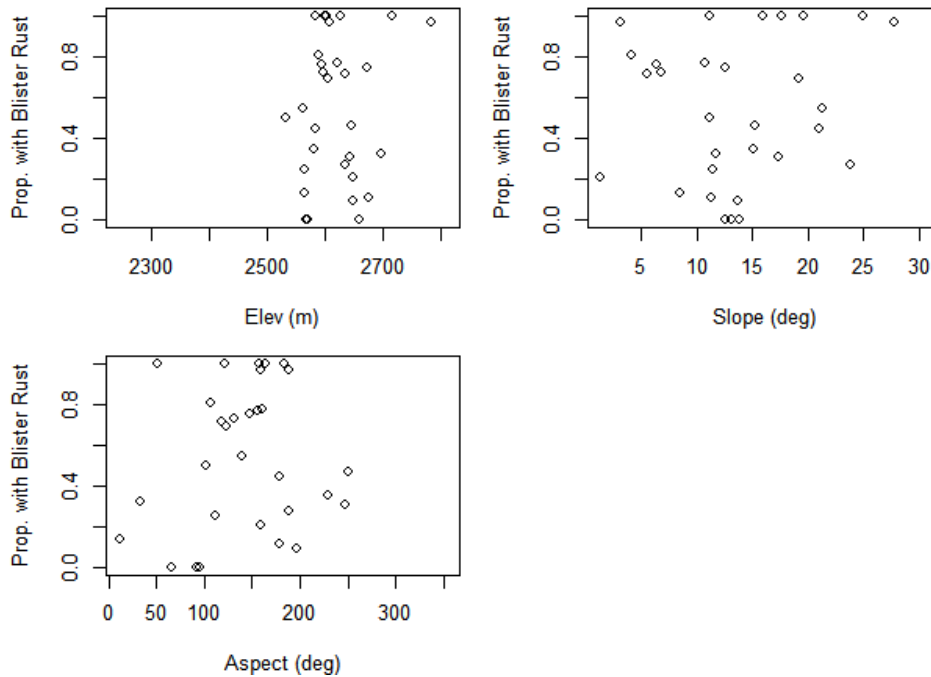


Figure C.1: Proportion of live whitebark pine trees with blister rust plotted against three possible covariates for successfully-surveyed sites

The results of the three estimation approaches indicate that the model-based approach from the GLMM (Jules et al. in progress) yields results similar to the MCAR design-based approach and the MCAR model-assisted approach (Table 1). Additional variance encumbered by the nonresponse adjustment is evident in the weighting-class adjustment confidence intervals, which are wider than the confidence intervals for both the model-based and design-based estimators.

Table C.1: Estimates of blister rust prevalence for three analysis methods and two parks.

Park	Model-based synthetic estimate based on GLMM (95% CI from bootstrapping)	Design-based Horvitz-Thompson estimate (95% CI from neighborhood variance estimator)	Model-assisted weighting-class adjustment estimate (95% CI from a Taylor's series approximation)
CRLA	0.5318 (0.4331, 0.6326)	0.5232 (0.4203, 0.6260)	-
LAVO	0.5637 (0.4509, 0.6663)	0.5479 (0.4420, 0.6538)	0.5654 (0.4010, 0.7297)

Discussion

The results indicate that similar results are obtained when missingness relative to the slope of a site is considered but cannot prove that bias is absent in the estimates. If nonresponse is nonignorable, then the blister rust prevalence rate is significantly different at unsurveyed sites and weighting class adjustment would be ineffective in addressing the bias. Subsampling of missing sites (perhaps using additional technology if available) or modeling the missingness for a range of possible prevalence rates would provide the basis of an evaluation of the ignorable nonresponse assumption.

The range of slopes for missing sites (10.4 to 30.8 degrees) is almost completely contained in the range of successfully-surveyed sites (1.4 to 27.8 degrees), so the assumption of ignorable nonresponse may be reasonable for these data. Treating the nonresponse as MCAR and applying the GLMM yield similar inference on the prevalence rate of blister rust in LAVO whitebark pine to that obtained from the MAR weighting class adjustment. Based on the available evidence, the application of the GLMM to the observed sample does not appear to substantially impact inference.

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Appendix D: Summary statistics for 30 whitebark pine plots established in CRLA in 2012, 2013, and 2014. Seedlings are specifically those of whitebark pine.

Plot ID	Live PIAL (#)	Dead PIAL (#)	Dead PIAL (%)	PIAL infected (%)	Seedlings (#)
CRWB01	16	5	24	44	1
CRWB02	30	36	55	57	0
CRWB03	67	0	0	58	0
CRWB04	57	3	5	82	1
CRWB05	17	6	26	24	1
CRWB06	11	0	0	82	0
CRWB07	23	0	0	87	0
CRWB08	78	7	8	58	3
CRWB10	10	3	23	100	0
CRWB11	1	0	0	100	0
CRWB21	43	1	2	49	0
CRWB22	28	1	3	96	0
CRWB23	8	6	38	75	3
CRWB24	1	0	0	0	0
CRWB25	14	5	26	71	0
CRWB26	2	0	0	100	0
CRWB27	2	0	0	0	0
CRWB28	53	13	20	26	1
CRWB29	9	0	0	33	0
CRWB30	5	1	17	100	0
CRWB41	9	0	0	11	0
CRWB42	2	0	0	50	0
CRWB43	3	0	0	0	0
CRWB44	68	22	4	14	0
CRWB45	11	20	65	55	8
CRWB46	6	5	45	17	2
CRWB47	66	8	11	26	1
CRWB49	11	7	39	18	9
CRWB50	9	7	44	44	1
CRWB51	292	22	7	38	3

Appendix E: Summary statistics for thirty whitebark pine plots established in LAVO in 2012, 2013 and 2014. Seedlings are specifically those of whitebark pine.

Site	Live PIAL (#)	Dead PIAL (#)	Dead PIAL (%)	PIAL Infected (%)	Seedlings (#)
LVWB03	13	2	13	69	0
LVWB05	22	1	4	27	0
LVWB06	41	1	2	46	1
LVWB07	4	0	0	0	0
LVWB08	74	3	4	16	0
LVWB09	2	0	0	50	0
LVWB10	11	0	0	55	0
LVWB11	31	1	3	97	0
LVWB12	69	6	8	72	1
LVWB14	32	0	0	97	0
LVWB22	11	0	0	9	0
LVWB23	2	12	86	0	1
LVWB24	4	11	73	25	0
LVWB28	58	3	5	22	1
LVWB30	20	1	5	35	2
LVWB31	34	0	0	32	0
LVWB32	72	21	1	11	0
LVWB34	9	1	10	44	0
LVWB35	1	0	0	0	0
LVWB39	36	0	0	31	0
LVWB42	11	2	15	100	0
LVWB44	12	0	0	100	0
LVWB47	7	0	0	71	0
LVWB48	4	0	0	75	0
LVWB49	6	0	0	100	0
LVWB51	17	1	6	82	0
LVWB54	5	0	0	100	0
LVWB56	18	6	25	78	0
LVWB59	9	0	0	100	0
LVWB60	22	3	12	77	0

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NPS 106/138720, 111/138720, June 2017

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