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Inventory of White Pine Blister Rust, Fire, and Bark Beetles in Sugar Pine at Yosemite National Park

Aeciospores and bole canker on a sapling near Crane Flat in Yosemite National Park.

Inventory of white pine blister rust, fire, and bark beetles in sugar pine at Yosemite National Park

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Abstract

Invasive white pine blister rust (*Cronartium ribicola*, WPBR) threatens white pine populations throughout North America. Sugar pine (*Pinus lambertiana*), for example, has been declining in Sequoia and King Canyon National Parks (SEKI) due to WPBR, as well as other mortality agents, including fire, drought, and mountain pine beetle (*Dendroctonus ponderosae*, MPB). Whether these declines reflect population trends farther north in Yosemite National Park, however, is largely unknown. To this end, we surveyed 56 plots between June and October, 2023 in Yosemite. To test whether fire impacted WPBR or sugar pine recruitment, 23 plots were established in the Rim Fire footprint. Average extent (% of plots with ≥ 1 infection) and infection rate (% of all live stems with ≥ 1 infection) was 48.2% and 3.7%, respectively, though the extent was much lower in the Rim Fire plots (26.1%) compared to the primary plots (63.6%). Our generalized linear mixed models of infection rate suggested that fire and the presence of alternate hosts were important correlates of WPBR. As fire severity increased, WPBR infections declined, suggesting that high severity fire may dampen infection rates. Additionally, MPB was typically found in larger diameter stems, and the extent was higher in primary plots (54.6%) compared to the Rim Fire plots (30.4%). Recent surveys from SEKI show that sugar pine and WPBR infection rates are declining, likely due to complex interactions with drought, MPB, and fire. Comparable infection rates in Yosemite suggest that both sugar pine and WPBR may be following a similar trajectory. Though long-term monitoring is needed to quantify trends, our results underscore that restoration will help ensure the persistence of this ecologically important species.

Acknowledgments

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Introduction

White pine blister rust (WPBR), caused by the invasive fungal pathogen*, Cronartium ribicola*, threatens white pines throughout North America. Following its accidental introduction in the early 20th century, the disease spread rapidly across the continent. Sugar pine (*Pinus lambertiana*, PILA), often referred to as the "King of Pines," has been heavily impacted, particularly in the Sierra Nevada. Earlier disease surveys reported that WPBR infections were much higher in sugar pine compared to the four higher-elevation white pine hosts (Duriscoe & Duriscoe, 2002). These infections contributed to rapid declines of sugar pine in the southern Sierra Nevada, and some regions may experience local extirpations unless restoration action is taken (Dudney et al., 2020; Foster et al., 2024). Though WPBR impacts have been well-documented in Sequoia and Kings Canyon National Parks (SEKI), the effects on Yosemite's sugar pine remain largely unknown.

The complex life cycle of *C. ribicola* includes white pines and alternate hosts (e.g., the genera *Ribes*, *Castilleja*, and *Pedicularis*). The five spore stages of this macrocyclic heteroecious rust have variable sensitivities to moisture and temperature. Basidiospores—that spread from alternate hosts to infect pine hosts through needle stomata—require high moisture and mild temperatures, ranging from 10–20°C (Van Arsdel et al., 2006; Dudney et al., 2021). In contrast, aeciospores that spread from white pines to alternate hosts are more resilient and can purportedly travel for hundreds of kilometers on wind currents (Geils et al., 2010). Given the complex life cycle and climate sensitivity, WPBR infections often occur during "wave years," approximately every 7–10 years. If the pathogen successfully infects a needle, within a few years it can spread through the branch to the bole. The fungal mycelia occlude the flow of water and nutrients (Kinloch & Dupper, 2002) which can girdle and kill the tree, particularly smaller stemmed individuals that are less resistant to infection (Kinloch et al., 2003).

WPBR often co-occurs with other agents of disturbance that can moderate its spread and infection rate (Dudney et al., 2020). For example, severe drought can directly and indirectly reduce the likelihood of infection. Spores require high moisture to survive and infect hosts (direct effects) and severe drought often increases moisture stress in pines, which leads to higher rates of stomatal closure (indirect effects) (Dudney et al., 2021). Pine host stress during drought can also incite nonlinear MPB outbreaks, which may dampen disease pressure if infected hosts die quickly following attack (Dudney et al., 2021). MPB has also been shown to select WPBR-weakened trees, though this interaction is highly context dependent and was not significant during the extreme drought between 2012–2016 in SEKI's sugar pine (Dudney et al., 2020). Previous research in SEKI, however, only considered immediate drought effects, and little is known about whether this interaction emerges in the absence of drought.

Additionally, increases in fire frequency, extent, and severity in the Sierra Nevada may also interact with WPBR, though the effects are likely context dependent. Fire may initially reduce WPBR by eliminating pine hosts and alternate hosts for a few years—until they recruit back (Maloney et al., 2008). High severity fire patches often lead to hotter, drier microenvironments that can limit pine seedling recruitment and pathogen reproduction, which could suppress disease pressure. Previous research, however, has found little evidence that fire impacts WPBR in the Sierra Nevada (van Mantgem et al., 2011; Dudney et al., 2020), which may reflect study limitations or the spatio-temporal dynamics of fire impacts that exert little influence on the disease. Recent increases in fire occurrence in Yosemite provide an ideal opportunity to test whether fire influences WPBR spread, an effect that would have important management implications.

To assess the extent and severity of WPBR in Yosemite's sugar pine populations, as well as potential interactions with MPB and fire, we conducted a field study between June and October 2023. Our project had three main goals: 1) quantify the current extent, severity, and infection rate of WPBR in Yosemite's sugar pine to establish a baseline for future management, 2) identify sugar pine stands with high WPBR infection rates to select uninfected trees that may be rust-resistant for restoration efforts and 3) determine the important correlates of WPBR infection rates to develop disease risk maps.

Methods

Study area

Yosemite National Park (YOSE) is located in the southern Sierra Nevada of California (37.8651° N; 119.5383° W). The park's ecosystems span a large elevational gradient, from 600–4,000 meters, and a diversity of forest types, including mixed conifer, montane, and subalpine forests. The lower elevation mixed conifer forests comprise the highest diversity of conifer species, including ponderosa pine (*Pinus ponderosa*), incense cedar (*Calocedrus decuryearens*), white fir (*Abies concolor*), giant sequoia (*Sequoiadendron giganteum*), and the study species, sugar pine. Yosemite's Mediterranean climate is characterized by hot, dry summers and cool, wet winters. Mixed conifer forests are frequently exposed to biotic and abiotic disturbances, including bark beetles, pathogens, fire, and drought. Fire suppression over the past century has led to rapid densification of lower elevation forests, which has increased vulnerability to high severity fire.

Sampling design

To assess WPBR infection rates in YOSE sugar pine, we used a stratified random sampling design across known sugar pine habitat (Figure 1). Using spatial packages in R, we overlaid the YOSE sugar pine occurrence maps with PRISM climate data (800 m; (Daly et al., 2008)). We then created five climate strata across the sugar pine range map that included the known climate optimum in SEKI (Dudney et al., 2021). Using the sgsR package (Goodbody et al., 2023), we randomly selected eight plots in each stratum (avoiding steep slopes (<30%) and areas < 50 m from roads). These plots are referred to as "primary plots." To accurately assess the effects of fire on WBPR, we established an additional stratified random sampling design that selected five plots across the same climate strata overlayed on moderate and high severity patches, using data provided by Monitoring Trends in Burn Severity (MTBS) and later ground truthed with our observational data, within the Rim Fire perimeter (Figure 1). These plots are referred to as "Rim Fire plots." This approach enabled us to up-sample high severity burn areas that would otherwise be missed in our larger stratified random sampling design.

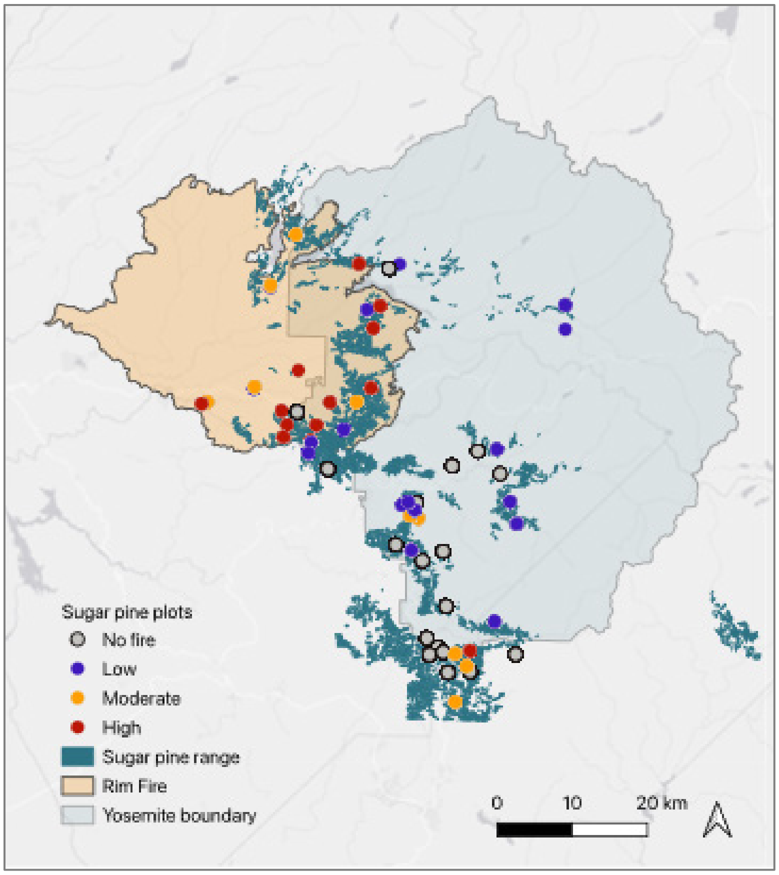

Figure 1. Map of the WPBR survey plots in Yosemite. Green polygons show the distribution of sugar pine, yellow polygon shows the perimeter of the Rim Fire, and colored dots show the plot's fire severity classification. NPS

Plot establishment

Plot establishment followed protocols outlined by Duriscoe & Duriscoe (2002) and Dudney et al. (2020). From original plot points, crew identified the nearest stand of sugar pine and randomly selected a starting point and direction (azimuth) to begin a transect perpendicular to the slope. Sugar pine (PILA) stems were surveyed sequentially along the transect until a minimum of 20 PILA were observed; this resulted in various plot sizes. To assess fire impacts and ensure that we captured moderate to high severity fire effects (i.e., can kill 50–100% of live stems), crew initiated the transect at the original plot point in Rim Fire plots. Primary plots outside of the Rim Fire were rejected if: 1) there were fewer than 20 live PILA stems within 500 m of the random waypoint or 2) the area was unsafe due to natural hazards, including very recent fire or steep rock outcrops. Rim Fire plots were rejected if they did not include at least one live PILA stem, which helped control for initial plot conditions that would otherwise confound the effect of fire on WPBR.

Field observations

Plot-level measurements

At each plot, crew recorded the location (NAD83), slope (%), aspect (°), elevation (m), associated tree species, and presence/absence of alternate host species, including *Ribes* spp., *Castelleja* spp., and

Pedicularis spp. Crew also documented the presence/absence of sugar pine seedlings ≥ 1 meter. To account for variability in fire effects within each plot, we visually classified each plot's fire severity along the transect. Every 50 meters, crew documented average fire severity based on the following classes: low: 0–25% mortality; moderate: 26–79% mortality; and high: ≥80% mortality of overstory trees. This classification approach provided detailed estimates of each plot's severity rating, which improved the accuracy of our estimates of fire impacts on WPBR.

Tree-level measurements

For each PILA stem ≥ 1 m, crew measured height (m) and percent live crown; crew only measured diameter at breast height (DBH) for stems ≥ 1.37 m. Crew surveyed for symptoms of WPBR, including branch cankers, bole cankers, flags, and dead tops (following protocols outlined by Dudney et al. 2020). MPB symptoms were also documented, including pitch tubes and exit holes, and fire effects were documented, including fire scars and/or char. Tall sugar pine stems are particularly challenging to assess for WPBR. As a result, crew observed tall trees from multiple angles using binoculars, and possible symptoms high in the canopy that were not easily observed through binoculars were classified as "suspected cankers" (Dudney et al., 2020).

Identification of potentially rust-resistant individuals

Healthy, uninfected sugar pine stems growing in stands with high WPBR infection rates are more likely to express genetic resistance (*Cr1*, major gene resistance) due to higher selection pressures. To identify potentially rust-resistant individuals for future genetic testing and restoration, crew conducted health assessments of PILA located in high incidence areas. Crew identified the healthiest sugar pine stems in the area to map (using GPS units) and measure (i.e., DBH and height). Trees with any signs of blister rust, including dead tops, suspected cankers, or old dead branches above the base of the canopy—where dieback due to suppression is less common—were excluded. Finally, crew supported the Ancient Forest Society (AFS) during cone collections. Specifically, crew identified 20 of the candidate sugar pines in Mariposa Grove, Crane Flat, and Tuolumne Grove during the summer of 2024, which were later climbed and sampled by AFS when the cones were ready for harvesting. These cones will undergo genetic testing at USFS Placerville nursery for WPBR gene resistance.

Analysis

Extent, severity, and infection rate

We calculated disease extent, severity, and infection rate for primary plots and Rim Fire plots of WPBR in sugar pine. Disease extent was estimated using the following formula:

$$Extent = \frac{N_i}{N}$$

where N_i is the number of plots with at least one infected individual and N is the total number of plots surveyed.

Initial calculations for severity were based on the count of cankers and size of infected pines (Duriscoe & Duriscoe, 2002):

$$Severity = \frac{cs + (50 - DBH\ in)}{5}$$

where *cs* is the canker severity rating and DBH is the diameter at breast height for the individual stem measured in inches. The canker severity (cs) ranking system assigned each tree a numerical ranking from 0 to 5: 0 = no branch or bole cankers, 1 = one branch canker, 2 = two branch cankers, 3 = three to four branch cankers, 4 = five or more branch cankers, and 5 = one or more bole canker(s). To avoid negative values and control for the fact that larger trees > 50 DBH were likely to experience similar effects of infections, all stems above 50 inches were assigned the same DBH of 50 inches.

Infection rate was calculated as follows:

$$Infection\ rate = \frac{W_j}{S_j}$$

where W_j is the number of sugar pine trees in plot *j* with signs of WPBR and S_j is the number of sugar pine trees in plot *j*. Infection rate was also calculated across plots (*W/S*), diameter class, and fire severity classifications.

Mortality and recruitment were coarsely estimated given that we only have one time period. Plot-level mortality was calculated as follows:

$$Mortality = \frac{M_j}{T_j}$$

where M_j is the number of standing dead sugar pine trees in plot *j* and T_j is the total number of sugar pine trees measured in plot *j*. Finally, sugar pine recruitment was estimated for each plot by summing the total number of live stems between 0 and 3 cm DBH for each plot.

Statistical analysis

We used a hypothesis-based approach to develop our statistical models. Previous research indicated that important variables associated with WPBR infections include alternate host species, pine host species, tree size, temperature, and moisture (Dudney et al., 2020; Dudney et al., 2021). To test whether these variables were also correlated with WPBR infections in Yosemite, we estimated a generalized linear mixed model (GLMM) with a logit link function. We estimated the likelihood of a tree infection (0 = no infection; 1 = infected) as a function of alternate host species presence, MPB presence, DBH, live PILA density, fire severity, and maximum vapor pressure deficit (VPDmax), with plot as a random effect. VPDmax values were obtained from PRISM historical climate data (PRISM Climate Group), which estimates the difference between the saturation vapor pressure and the actual vapor pressure. All analyses were conducted with R software, and statistical models were estimated using the R package lme4. Prior to estimating the GLMM, continuous independent variables were centered and standardized, and model results were evaluated for multicollinearity and variance inflation. To determine which factors were associated with tree-level MPB attacks, we estimated a second binomial GLMM with presence/absence of MPB as the outcome variable and VPDmax, live PILA density, slope, DBH, and fire severity classes as predictor variables.

Results

Extent, severity, and infection rate

In total, 56 plots were surveyed, including 33 primary plots and 23 Rim Fire plots (Table 1). Average WPBR plot-level extent was 48.2% and varied by plot type: WPBR extent was 63.6% in primary plots and 26.1% in Rim Fire plots. In total, 1,473 live sugar pine stems were assessed across all plots and 54 of these stems were infected with WPBR, which resulted in a 3.7% infection rate (Table 1). Additionally, the infection rate was 54% lower in the Rim Fire plots compared to the primary plots (2.0% and 4.3%, respectively). Infection rate also varied across the plots, peaking at 16.7% (Figure 2). Finally, infection rate varied by diameter class, peaking in saplings from 3.8–10.2 cm DBH (Figure 2C).

Table 1. Summary statistics of WPBR and MPB. (Top) Summary statistics for WPBR in Rim Fire and primary plots. (Bottom) Summary statistics for MPB across Rim Fire and primary plots.

Outcome Variable	Summary Statistic	Rim Fire Plots	Primary Plots
White pine blister rust (WPBR)	Infected plots	6	21
	Total plots	23	33
	WPBR extent (%)	26.1%	63.6%
	Infected live stems (#)	9	45
	Total live stems (#)	457	1016
	WPBR infection rate (%)	2.0%	4.4%
Mountain pine beetle (MPB)	Plots with MPB (#)	7	18
	MPB extent (%)	30.4%	54.5%
	Total live stems with MPB (#)	26	68
	Total live PILA stems (#)	457	1016
	MPB occurrence (%)	5.7%	6.7%

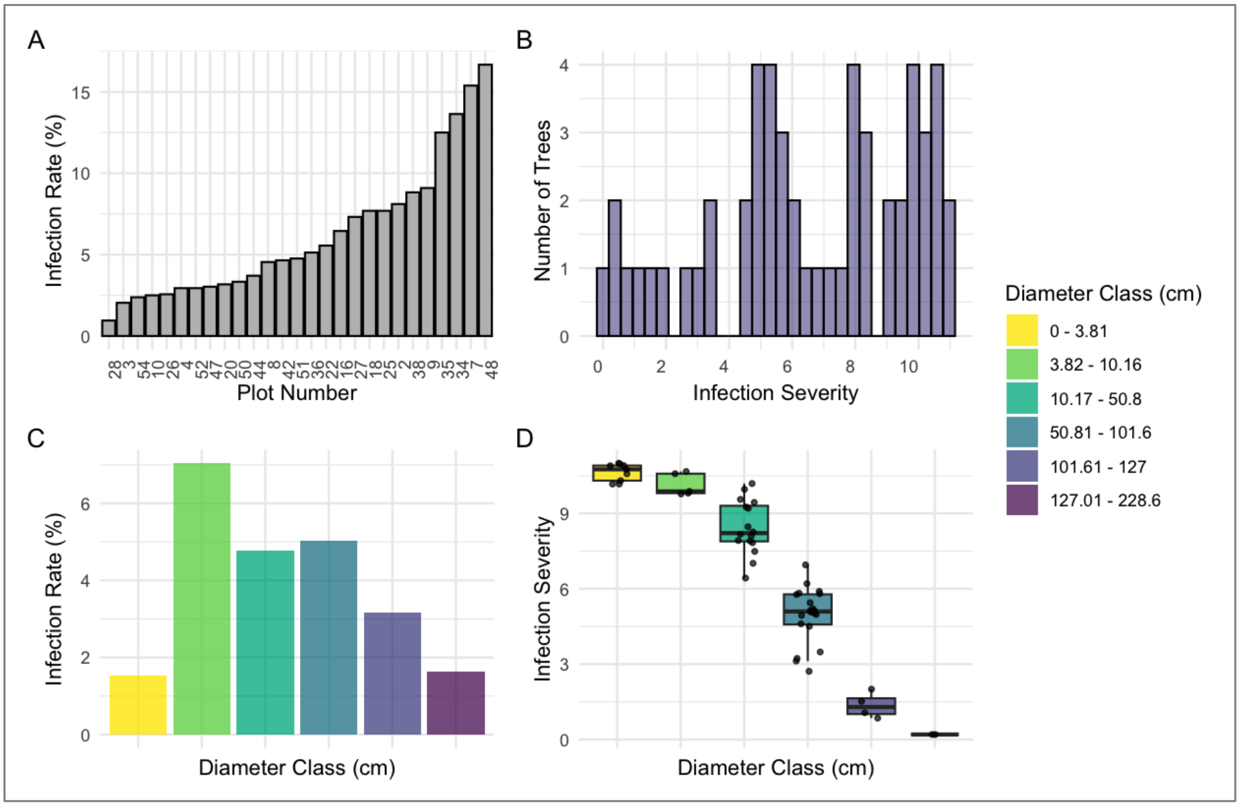

Figure 2. Variation in WPBR infection rates and severity. A) Plot-level infection rate (% of infected trees/total live trees) varied across all plots with ≥ 1 WPBR infection. B) Count of trees across WBPR severity for all trees with ≥ 1 infection. C) Infection rate across diameter class. D) Variation in WPBR severity across diameter classes. Boxplots show the 25–75% quantile range and the 50% quantile center line. Whiskers depict data points within 1.5 times the interquartile range; includes jittered data points in black. NPS

Infection severity was also highly variable across plots, diameter class (Figure 2B, D), and fire severity (Figure 3). Infection severity decreased precipitously with increasing diameter class and was highest in small stemmed sugar pine (seedlings and saplings) (Figure 2B, D). Infection severity was also highest in unburned plots compared to burn plots, while there was not a strong trend among fire severity classes (Figure 3B). Though WPBR severity ratings do not perfectly correlate with the probability of mortality, these trends suggest that smaller stemmed sugar pine are more likely to die from infection.

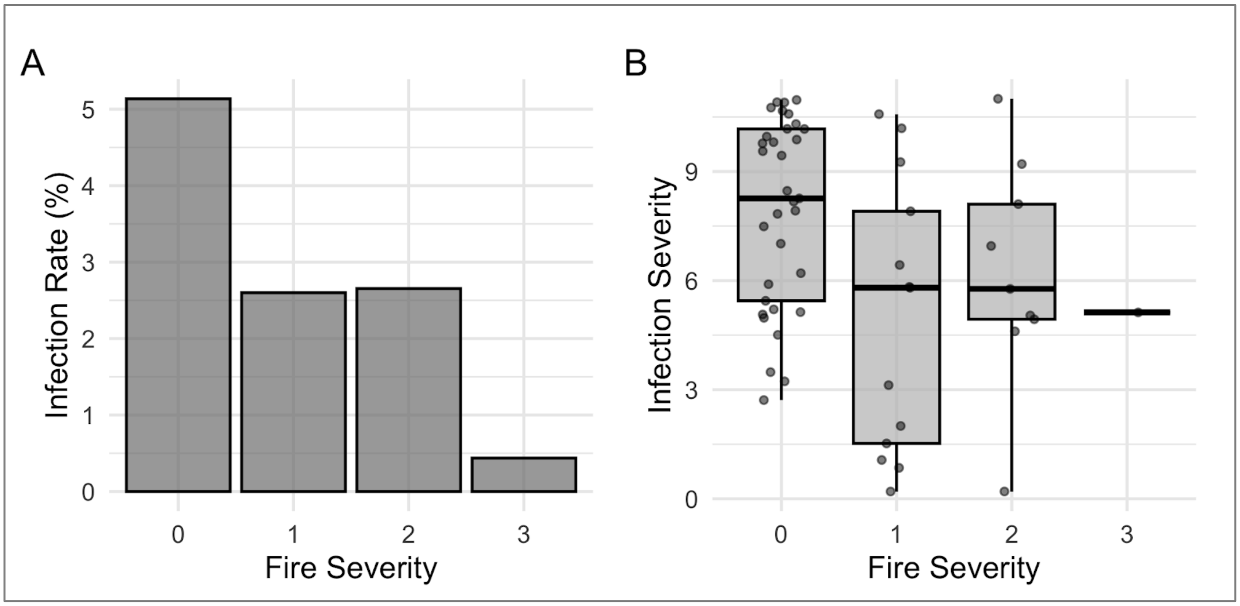

Figure 3. Average WPBR infection rate and severity across fire severity. A) Infection rate (percent; number infected stems/total stems) across fire severity (0 = no fire, 1 = low, 2 = moderate, 3 = high). B) WPBR severity across fire severity. Boxplots show the 25–75% quantile range and the 50% quantile center line. Whiskers depict data points within 1.5 times the interquartile range; includes jittered data points in dark grey. NPS

Variables associated with WPBR infections

Our GLMM results suggested that alternate hosts and fire were important determinants of WPBR infections in Yosemite's sugar pine (Appendix A; Figure 3). Specifically, the presence of alternate host species was significantly and positively associated with WPBR infections (Estimate = 0.04, P-value = 0.016) (Appendix A), and WPBR infections decreased with increasing fire severity (Estimate = −0.07, P-value = 0.005). Interestingly, higher density of live sugar pine stems was negatively correlated with WPBR infections (Estimate = −1.16, P-value = 0.019). Climate variables, including VPDmax (Estimate = 0.00, P-value = 0.858) were not strongly correlated with infections, nor was the presence of MPB (Estimate = −0.01, P-value = 0.580).

Variation in MPB attacks

MPB attacks in live sugar pine increased with stem diameter, peaking in the 101.61–127 cm category, where 10% of measured stems showed signs of MPB attack (Figure 4). No MPB attacks were found in stems < 12 cm DBH. Our GLMM estimating tree-level MPB attacks suggested that low severity fire was positively associated with MPB, but high severity fire was negatively correlated with MPB (Appendix A). VPDmax was also negatively correlated with MPB, suggesting that fewer attacks were found in hotter, drier regions (Appendix A).

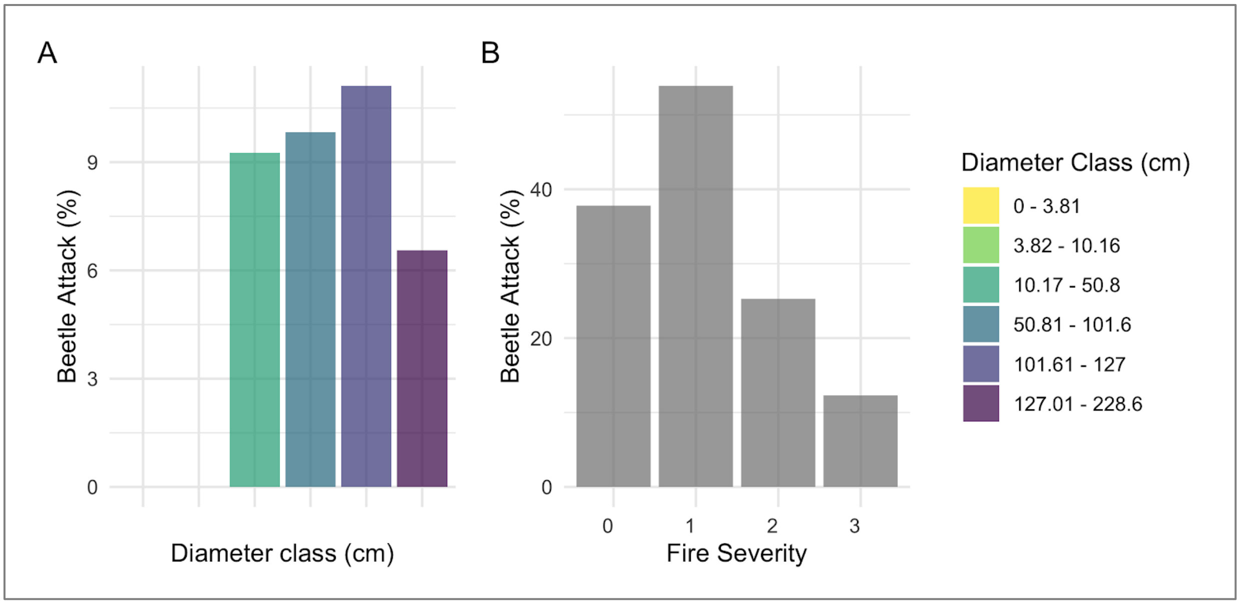

Figure 4. Variation in MPB attacks across diameter class and fire severity. A) MPB attacks (percent; number attacked stems/total live stems) across diameter class (DBH class). B) MPB attacks on live sugar pine stems across fire severity (0 = no fire, 1 = low, 2 = moderate, 3 = high). NPS

Estimated standing dead trees across diameter class, fire, and VPDmax

Overall, Rim Fire plots were associated with higher mortality compared to primary plots (Figure 5A) and high severity plots were associated with the highest number of standing dead sugar pine stems (Figure 5C). There was a hump-shaped relationship between standing dead trees and diameter class, with the highest levels of standing dead peaking at the 50–100 cm DBH range (Figure 5B). The relationship between VPDmax and mortality was also relatively hump-shaped, with the lowest levels of standing dead trees occurring in the hottest, driest plots (Figure 5D). Further research is needed to determine which factors, including tree age, fire severity, WPBR, and MPB, are the strongest correlates of recent mortality.

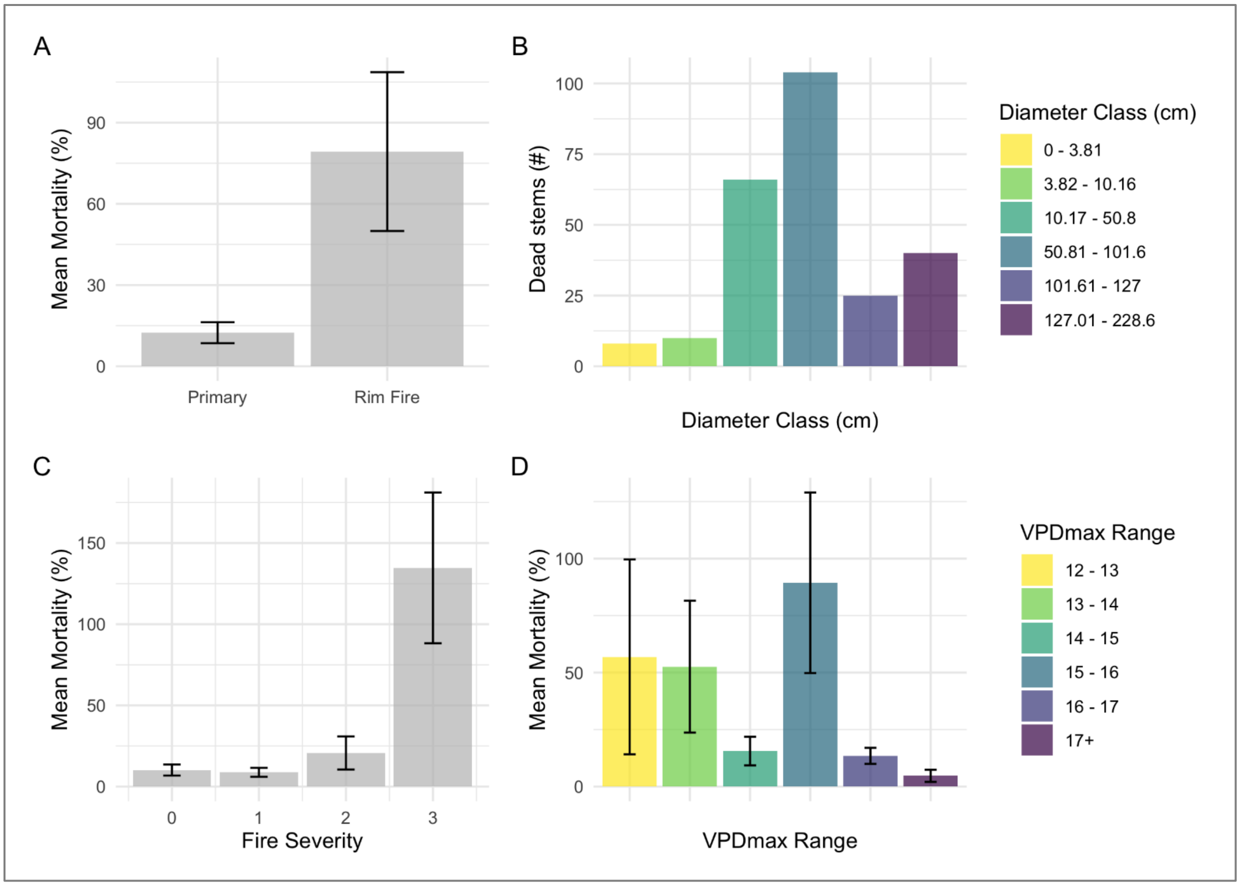

Figure 5. Estimated plot-level sugar pine mortality. A) Estimated mortality in primary compared to Rim Fire plots. B) Count of standing dead stems across a range of diameter classes. C) Mean plot-level mortality across fire severity classes. D) Mean mortality across a range of maximum VPDmax (kPa) values, where higher values of VPDmax indicate hotter, drier conditions. Figures with error bars show standard error. NPS

Estimated recruitment across WPBR, fire, and VPDmax

In contrast to mortality, there was not a significant difference between primary and Rim Fire plots with respect to recruitment (Figure 6A). However, mortality increased with increased fire severity whereas recruitment decreased with increased fire severity (Figure 6B). Interestingly, greater recruitment was found in the hottest, driest regions of the sugar pine range in Yosemite (Figure 6C). Finally, average recruitment was lower in plots with the highest number of infections (Figure 6D), suggesting that high levels of WPBR may limit recruitment. Further research is needed to understand the most important drivers of sugar pine recruitment in Yosemite.

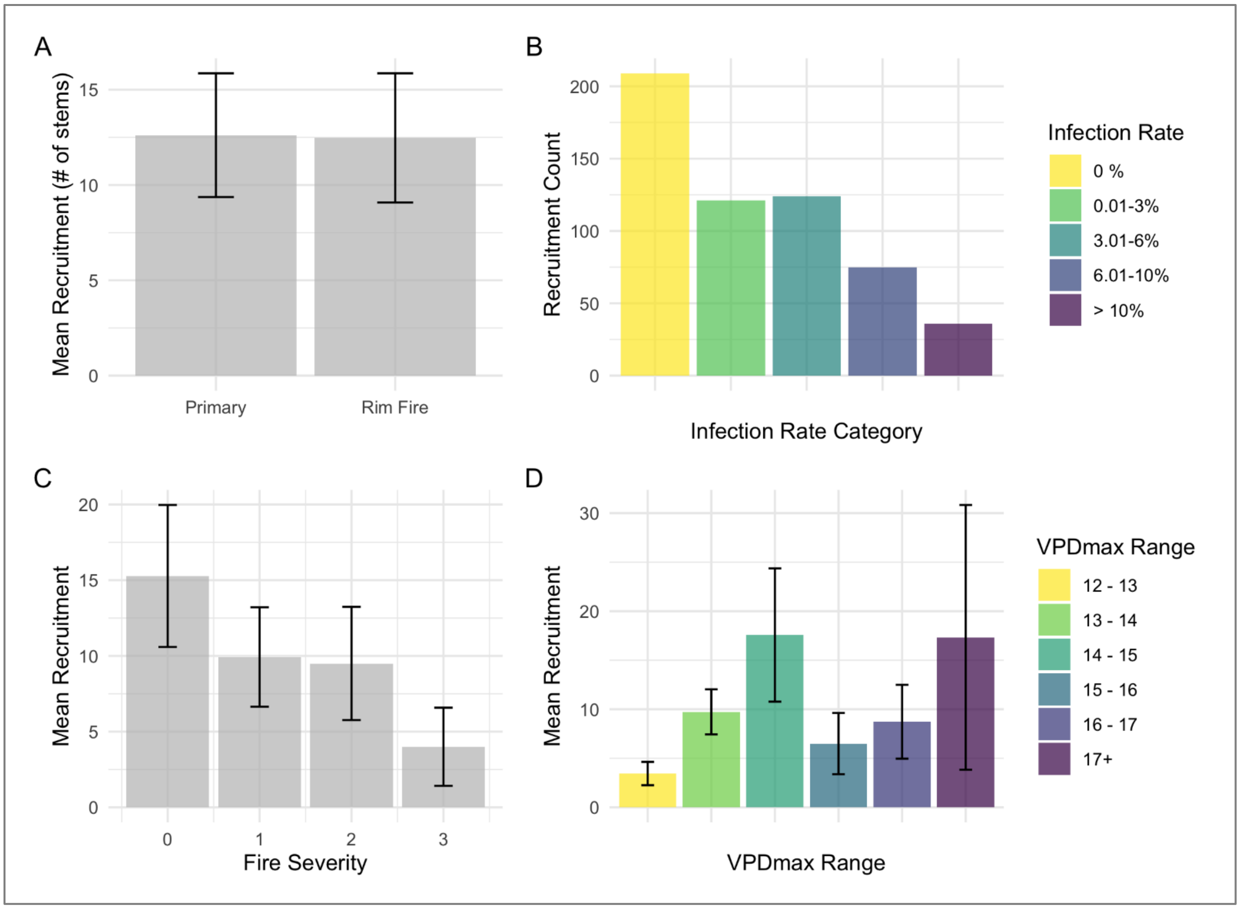

Figure 6. Estimated sugar pine recruitment. A) Mean number of recruits (estimated first at the plot-level) between primary and Rim Fire plots. B) Mean recruitment across infection rate. C) Mean recruitment across plots that fall in four severity classes (0 = no fire, 1 = low severity, 2 = moderate severity, 3 = high severity). D) Mean recruitment across maximum VPDmax for plots that fall within the six VPDmax ranges, where higher VPDmax indicates hotter, drier conditions. All error bars are estimated standard errors. NPS

Discussion

Our results suggest that white pine blister rust (WPBR) is widespread throughout the sugar pine range in Yosemite. Mean extent outside of the Rim Fire footprint was 64%, which is higher than the extent—53.1%—recently documented in SEKI (Dudney et al., 2020). However, the average infection rate outside of the Rim Fire footprint (4.4%) was slightly lower than the infection rate observed in SEKI (6.4%). These patterns suggest that infection dynamics are fairly similar in both Parks and long-term trends identified in SEKI may also be relevant in YOSE. For example, in SEKI, climate change and drought are suppressing WPBR infections in lower elevation sugar pine hosts, which has contributed to declines in infection rates over the past 20 years (Dudney et al., 2021). The declining trend in WBPR, however, coincides with concerningly high mortality in sugar pine, underscoring that lower disease pressure does not necessarily correlate with population health and persistence (Dudney et al., 2021). These results suggest that WPBR continues to threaten sugar pine persistence in Yosemite and identifying rust-resistant individuals will be critical to support future restoration efforts.

Important predictors of WPBR infections in YOSE sugar pine were alternate host species presence (the most commonly observed genus was *Ribes*) and pine host density. These results are consistent with previous surveys in the southern Sierra Nevada, which showed positive effects of alternate host occurrence on white pine infections (Dudney et al., 2020). Though alternate host abundance was important for infections, the density of pine hosts was negatively correlated with WPBR. This surprising result is also consistent with previous findings (Dudney et al., 2020) and underscores that alternate host species are more important than pine host density for WPBR infections. High pine host density may also be associated with unknown environmental variables that suppress infections, and future research that seeks to disentangle the mechanisms of these density effects would provide useful insights into disease risk.

Though previous research did not find significant effects of fire on WPBR infection (van Mantgem et al., 2011; Dudney et al., 2020), our results indicate that the effects of fire are strongly negative, at least within ten years post-fire. There are likely three important mechanisms that explain these results. First, fire reduces live host density, which removes active infections and suppresses the disease risk in that region. Second, WPBR spreads during wave years and fire may reduce the number of wave year events by limiting WPBR reproduction when more suitable climate windows occur. Third, moderate and high severity fire often opens the canopy and increases aridity, which can limit spore spread, as well as pine host establishment. Similar mechanisms have also been identified in sudden oak death, where the presence of fire removed hosts and lowered environmental suitability for disease (Simler-Williamson et al., 2021). Additionally, though previous research did not detect fire effects, these studies were spatially limited and underpowered (i.e., fewer plots were impacted by moderate-high severity fire) (van Mantgem et al., 2011; Dudney et al., 2020).

Though climate variables were not significantly correlated with WPBR infections, microclimates may be playing an important role that our study was unable to capture. For example, WPBR infection rates were very high (approximately 60–70%) in specific stands outside of our study plots within

Yosemite that were often co-occurring with giant sequoias. Giant sequoia groves are typically close to perennial water sources and their canopy may trap more moisture compared to other mixed conifer species. These microclimates may be more suitable for WPBR infections, though this hypothesis has never been tested. Future research that explores possible mechanisms leading to the dramatic differences in infection rates in these specific stands would provide valuable insight into future disease risk in Yosemite's sugar pine.

There are two important caveats to highlight in this report. First, because we did not find a relationship between climate variables and WPBR, we could not develop a disease risk map related to climate. These results, however, are not surprising as they are consistent with spread dynamics in SEKI's sugar pine— there is not enough climate variation across the sugar pine range to detect a climate-WPBR relationship (Dudney et al., 2020). If YOSE expands the WPBR surveys into western white and whitebark pine, we expect that a climate relationship could be identified, which would enable researchers to develop a WPBR risk map. Second, our mortality estimates are coarse because we only have data from one survey and we likely underestimated mortality in small-stemmed trees that decompose quickly. Our approach was able to capture recent mortality, however, in larger stemmed individuals. The drivers of mortality included fire, MPB, drought, and WPBR, though the proximate cause of death was impossible to determine in situ. Interestingly, the hottest driest regions were not associated with the highest level of mortality, suggesting that these sugar pine stands may be more resilient to drought and MPB. This pattern was consistent with recruitment, which was still relatively high in hotter, drier regions—variability in recruitment, however, increased with increasing VPD. This variability suggests that microsite suitability may become an increasingly important determinant of sugar pine recruitment in hotter, drier regions.

To identify potentially rust-resistant individuals, we needed to find stands with at least one healthy stem surrounded by many infected individuals. This would increase the likelihood of identifying rust-resistant individuals. Because none of the plots within the stratified random sampling design had infection rates above 16.7%, we searched for higher infections rates in stands with more suitable microclimates. Anecdotally, higher infection rates were also found outside of monitoring plots in Giant Sequoia Groves. Thus, crew surveyed Mariposa Grove, Tuolumne Grove, and Merced Grove and found much higher infection rates (> 30.0% of stems expressed infections). The infection rates were visually estimated after walking through a stand. Some areas may have had infection rates as high as 70–80%, but due to time limitations, crew were unable to measure the exact infection rate. Crew also found similarly high infection rates at Crane Flat and Goat Mountain Snow Play Area, which was a happy accident—they camped and drove through these regions and coincidentally observed the higher infection rates. Crew selected 52 healthy stems in these stands in 2023 and 67 stems in 2024 (154 total). This enabled the Ancient Forest Society to collect cones from 20 candidate trees across the park including Mariposa Grove, Crane Flat, and Tuolumne Grove that are undergoing genetic testing at the Placerville nursery.

Finally, our results have important implications for the management and restoration of sugar pine. Specifically, developing climate change-focused strategies should be a focus given current rates of mortality that have been, in part, driven by warming temperatures (Dudney et al., 2021). Holistic, win-win solutions that focus on multiple stressors, including drought, WPBR, fire, and MPB, will greatly enhance success. These strategies could include identifying drought-resistant and WPBR-resistant individuals through further field- and lab-based research, followed by larger-scale nursery production of targeted genotypes. Trees growing in the hottest, driest regions, for instance, may be more drought-resistant and suitable for seed collection for future restoration. However, if they are not resistant to WPBR, planting efforts of drought-resistant trees may result in failure. Furthermore, our findings suggest that allowing smaller patches of high severity fire to burn through sugar pine stands may help suppress disease pressure, which could be an effective restoration tool if implemented carefully. Further research, however, is needed to understand exactly how long the fire effects last and the ideal patch sizes that might otherwise limit sugar pine recruitment and threaten their persistence. Planting rust-resistant seedlings in high severity patches could be an effective strategy to help mitigate the negative effects of high intensity fire.

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Appendix A

Tables 2–6 show details of model results.

Table 2. Environmental correlates of WPBR infections. Generalized linear mixed model results predicting tree-level presence/absence of white pine blister rust (WPBR). Explanatory variables are listed under "Predictors." The table provides the coefficient estimate ("Estimates"), the 95% confidence intervals (C.I.), and the P-values for each predictor variable.

Predictors	Estimates	CI	P-value
(Intercept)	0.04	−0.08 to 0.16	0.508
VPD (max)	0.00	−0.01 to 0.01	0.858
Alternate hosts	0.04	0.01 to 0.06	**0.016** [A]
MPB occurrence	−0.01	−0.03 to 0.02	0.580
Live PILA density	−1.61	−2.96 to −0.26	**0.019** [A]
Low severity fire	−0.04	−0.07 to −0.00	**0.036** [A]
Moderate severity fire	−0.05	−0.08 to −0.01	**0.009** [A]
High severity fire	−0.07	−0.12 to −0.02	**0.005** [A]
DBH (cm)	0.00	0.00 to 0.00	0.050

[A] Bolded P-values indicate significance.

Table 3. Random effects of WPBR infections. Summary of the random effects from the generalized linear mixed model. The table includes the residual variance (σ^2), the variance attributed to the grouping factor (e.g., "Plot Number"), the intra-class correlation coefficient (ICC), the number of plots (N Plot Number), total observations, and the marginal and conditional R^2 values.

Title of column	Estimates
σ^2	0.04
$\tau_{00\ \text{Plot Number}}$	0.00
ICC	0.02
$N_{\text{Plot Number}}$	53
Observations	1405
Marginal R^2 / Conditional R^2	0.022 / 0.037

Table 4. Environmental correlates of MPB attacks. Generalized linear mixed model results predicting tree-level MPB attacks. Explanatory variables are listed under "Predictors." The table provides the coefficient estimate ("Estimates"), the 95% confidence intervals (C.I.), and the P-values for each predictor variable.

Predictors	**Estimates**	**CI**	**P-value**
(Intercept)	0.99	0.79 to 1.19	**<0.001** [A]
VPD (max)	−0.04	−0.05 to −0.03	**<0.001** [A]
Live PILA density	3.01	0.12 to 5.89	**0.041** [A]
Low severity fire	0.27	0.21 to 0.33	**<0.001** [A]
Moderate severity fire	0.01	−0.05 to 0.08	0.675
High severity fire	−0.35	−0.42 to −0.29	**<0.001** [A]
Slope	0.00	−0.00 to 0.00	0.118
DBH (cm)	−0.00	−0.00 to −0.00	1.000

[A] Bolded P-values indicate significance.

Table 5. Random effects of MPB attacks. Summary of the random effects from the generalized linear mixed model. The table includes the residual variance (σ^2), the variance attributed to the grouping factor "Plot Number" (τ_{00}), the intra-class correlation coefficient (ICC), the number of plots (N Plot Number), total observations, and the marginal and conditional R^2 values.

Title of column	**Estimates**
σ^2	0.00
τ_{00} Plot Number	0.01
ICC	1.00
$N_{\text{Plot Number}}$	52
Observations	1376
Marginal R^2 / Conditional R^2	0.852 / 1.000

Table 6. Plot-level summary statistics. Includes the summary statistics for the 56 surveyed plots, including plot number, fire severity classification, counts of live and dead sugar pines, occurrence of *Ribes* spp., and the occurrence of WPBR and MPB.

Plot Number	Fire Severity	Alive Trees	Dead Trees	Total Trees	MPB Present	*Ribes* Present	WPBR Present	Infection Rate %
1	0	20	2	22	Present	Absent	Absent	0.000
2	0	37	0	37	Absent	Present	Present	8.108
3	0	32	17	49	Present	Present	Present	2.040
4	1	32	2	34	Absent	Absent	Present	2.941
5	3	0	1	1	Absent	Absent	Absent	0.000
6	1	32	1	33	Present	Present	Absent	0.000
7	0	36	3	39	Present	Present	Present	15.384
8	0	21	1	22	Present	Present	Present	4.545
9	0	32	1	33	Absent	Present	Present	9.090
10	0	39	1	40	Absent	Absent	Present	2.500
11	3	27	14	41	Present	Present	Absent	0.000
12	3	1	4	5	Absent	Present	Absent	0.000
13	3	7	11	18	Absent	Present	Absent	0.000
14	1	52	10	62	Present	Present	Absent	0.000
15	3	6	25	31	Absent	Present	Absent	0.000
16	1	31	0	31	Present	Present	Present	6.451
17	2	41	1	42	Present	Absent	Absent	0.000
18	2	34	5	39	Present	Present	Present	7.692
19	1	30	4	34	Present	Absent	Absent	0.000
20	2	57	6	63	Absent	Present	Present	3.174
21	3	37	2	39	Absent	Present	Absent	0.000
22	0	33	3	36	Absent	Present	Present	5.555
23	3	9	3	12	Absent	Present	Absent	0.000
24	3	8	1	9	Absent	Absent	Absent	0.000
25	2	13	0	13	Absent	Present	Present	7.692
26	2	30	9	39	Present	Present	Present	2.564
27	0	38	3	41	Present	Absent	Present	7.317
28	0	102	3	105	Absent	Present	Present	0.952
29	3	0	1	1	Absent	Present	Absent	0.000
30	0	43	4	47	Present	Present	Absent	0.000
31	0	4	0	4	Absent	Absent	Absent	0.000
32	2	13	2	15	Absent	Absent	Absent	0.000
33	3	6	2	8	Absent	Present	Absent	0.000
34	0	43	1	44	Absent	Present	Present	13.636
35	0	16	0	16	Absent	Absent	Present	12.500

Table 6 (continued). Plot-level summary statistics. Includes the summary statistics for the 56 surveyed plots, including plot number, fire severity classification, counts of live and dead sugar pines, occurrence of *Ribes* spp., and the occurrence of WPBR and MPB.

Plot Number	Fire Severity	Alive Trees	Dead Trees	Total Trees	MPB Present	*Ribes* Present	WPBR Present	Infection Rate %
36	0	34	5	39	Present	Present	Present	5.128
37	3	4	0	4	Absent	Present	Absent	0.000
38	0	30	4	34	Absent	Absent	Present	8.823
39	1	39	12	51	Present	Present	Absent	0.000
40	0	31	13	44	Present	Absent	Absent	0.000
41	3	0	6	6	Absent	Absent	Absent	0.000
42	1	35	8	43	Present	Present	Present	4.651
43	2	18	1	19	Absent	Present	Absent	0.000
44	2	27	0	27	Absent	Present	Present	3.703
45	0	10	0	10	Absent	Absent	Absent	0.000
46	3	21	0	21	Absent	Present	Absent	0.000
47	3	7	26	33	Absent	Present	Present	3.030
48	1	30	0	30	Present	Present	Present	16.666
49	2	23	25	48	Present	Present	Absent	0.000
50	1	30	0	30	Present	Absent	Present	3.333
51	1	21	0	21	Present	Present	Present	4.761
52	2	29	5	34	Absent	Absent	Present	2.941
53	1	31	6	37	Present	Absent	Absent	0.000
54	1	40	2	42	Present	Present	Present	2.380
55	1	18	0	18	Absent	Absent	Absent	0.000
56	1	33	1	34	Absent	Present	Absent	0.000

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