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Verbenone and Green-Leaf Volatiles Reduce Whitebark Pine Mortality in a Northern Range-Expanding Mountain Pine Beetle Outbreak

Etienne Cardinal¹

Brenda Shepherd¹

Jodie Krakowski²

Carl James Schwarz³

John Stirrett-Wood¹

¹Parks Canada Agency, Jasper National Park.

²Independent consultant

³StatMathComp Consulting by Schwarz

Corresponding author: Brenda Shepherd, Brenda.shepherd@canada.ca

ABSTRACT

This is the first study testing effectiveness of semiochemical treatments to protect individual trees from a range-expanding mountain pine beetle (MPB, *Dendroctonus ponderosae* Hopkins) attack into newly exposed host populations of endangered whitebark pine (*Pinus albicaulis* Engelmann). We investigated the effectiveness of a combination of verbenone and Green-Leaf Volatiles (GLV) to protect rare and valuable disease-resistant trees during a MPB epidemic from 2015 to 2018 in Jasper National Park, Canada. Treatments reduced the proportion of trees attacked by MPB for all diameter classes, across all stands, from 46 to 60%. We also evaluated the effect of the exotic disease white pine blister rust (caused by the fungus *Cronartium ribicola* J.C. Fisch), the species' other main regional threat. MPB were less likely to attack large, rust infected trees than healthy trees, emphasizing the value of the semiochemical treatment. Protecting large, cone-bearing disease-resistant whitebark pine trees is fundamental to whitebark pine recovery. Maintaining reproductive trees on the landscape increases the frequency and diversity of rust-resistant genotypes more effectively than just planting seedlings to replace MPB-killed trees, because this slow-growing species takes over 80 years to reproduce. Our study confirmed protecting large rust-resistant trees with verbenone and GLV is a proactive and effective treatment against MPB for whitebark pine in naïve populations.

KEYWORDS

Whitebark pine, white pine blister rust, verbenone, Green-leaf Volatiles, mountain pine beetle, insect range expansion, forest pest management

INTRODUCTION

Insect outbreaks have become a major challenge in forest management and conservation of forest ecosystems (e.g. Ramsfield et al. 2016). The mountain pine beetle (MPB, *Dendroctonus ponderosae* Hopkins) is an indigenous insect found throughout pine forests of western North America, historically occurring in Canada in the southern half of British Columbia and southwest Alberta (Safranyik and Carroll 2006; Taylor et al. 2006), extending to a small endemic population in Jasper National Park, west-central Alberta (Figure 1). Increasing winter minimum temperatures facilitated unprecedented levels of MPB population growth and northward range expansion in western Canada (Carroll et al. 2006; Safranyik et al. 2010, Taylor and Carroll 2004). A marked increase in the MPB infestation of lodgepole pine (*Pinus contorta* var. *latifolia* Engelmann) in 2014–2015 led to a large MPB outbreak in the park (Parks Canada Agency 2016), including a significant range expansion into higher elevations (Safranyik and Carroll 2006), threatening recovery efforts for endangered whitebark pine (*Pinus albicaulis* Engelmann) forests (Gibson et al. 2008; Shepherd et al. 2018).

FIGURE 1 - Map of JNP, study sites

Whitebark pine grows in the mountainous regions of western North America. It is listed as endangered under Canada's *Species at Risk Act* (SARA) due to impacts from the disease white pine blister rust (WPBR, caused by the introduced fungus *Cronartium ribicola* J.C. Fisch), epidemics of MPB, altered fire cycles and climate change (COSEWIC 2010). Whitebark pine has declined dramatically, including over the past 10 years in the Canadian Rocky Mountains, primarily due to its high susceptibility to WPBR, suffering nearly 100 percent mortality in the southern portion of the Canadian range (Shepherd et al. 2018). North American trees have only been exposed to this Eurasian disease for approximately one generation and are not yet adapted to it, so blister rust-resistant trees are extremely rare (Snieszko et al. 2011). The most effective method to recover slow-growing, long-lived whitebark pine is to increase the population level of genetic resistance to WPBR (Keane et al. 2012). It is therefore essential to identify and protect whitebark pine trees that are naturally resistant to WPBR (Mahalovich et al. 2006). Since 2010, Parks Canada has assessed tens of thousands of whitebark pine trees in Jasper National Park and identified several hundred putatively rust-resistant trees ("plus trees"), which are tested through a multi-

year process to confirm expression of heritable resistance. Each plus tree embodies an investment worth thousands of dollars to the recovery program.

From the 1970s to the 1980s, a MPB outbreak in the USA Northern Rocky Mountains and adjacent Waterton Lakes National Park in Canada resulted in “ghost forests” of dead whitebark pine (Arno and Hoff 1989). In the Greater Yellowstone Ecosystem, MPB killed more than 700,000 whitebark pines in 2004 alone (Gibson et al. 2008). Monitoring in Jasper National Park from 2004 to 2014 indicated MPB was absent in whitebark pine stands, but was spreading in lodgepole pine forests to the west and south. An outbreak was declared in Jasper National Park in 2015, fuelled by subsequent in-flights from the west (Trevoy et al. 2018). Ground and aerial surveys confirmed MPB range had expanded to some high-elevation whitebark pine stands starting in 2016, killing whitebark pine plus trees (Shepherd et al. 2018). Productive plus trees are often older and larger trees, which may make them more susceptible to MPB attack than smaller trees (Safranyik and Carroll 2006; Shanahan et al. 2016). Warming temperatures have been linked with MPB northward range expansion as well as into higher elevations (Powell and Bentz 2009; Safranyik and Carroll 2006). Lodgepole pine stands that had not co-evolved with MPB, but were attacked during range-expanding epidemics, had higher MPB reproductive success than co-evolved stands, suggesting naïve pine stands may be more susceptible to MPB attack if they had not evolved adaptive expression of constitutive or induced defense mechanisms (Cudmore et al. 2010). Studies have also shown variable and complex relationships between WPBR occurrence in whitebark pine trees and MPB attack, ranging from protective to detrimental effects of WPBR against MPB (Bockino and Tinker 2012; Shanahan et al. 2016).

To support alpine ecosystem integrity in Jasper National Park and whitebark pine communities, a key conservation action is, “*where protection from mountain pine beetle is required, protect high-value individual whitebark pine trees*” (Parks Canada Agency 2017, p.15). In 2014 Parks Canada began applying a semiochemical treatment to valuable plus trees in anticipation of MPB spread into nearby whitebark pine stands. Verbenone is a MPB antiaggregation pheromone effective at protecting single high-value trees. It sends a chemical signal to MPB that the trees are fully occupied, deterring attacks and

colonization (Fettig et al. 2012; Gillette et al. 2014). Green-leaf volatiles (GLV) are molecules which are produced by almost all green plants and they play an important role in plant defenses. Up to 40% more trees escape attack and over 75% of trees survive MPB mass attacks when verbenone and GLV are applied together during outbreaks (Kegley and Gibson 2004; Bentz et al. 2005; Perkins et al. 2015), compared to verbenone alone (Fettig et al. 2012; Gillette et al. 2014; Seybold et al. 2018).

Despite semiochemical protection, some whitebark pine plus trees in Jasper were killed by MPB (Parks Canada Agency, unpublished data). This prompted our study, whose objective was to determine how effective single-tree verbenone and GLV treatment was in protecting high-value whitebark pine trees from MPB during a recent outbreak (2015–2018) in a population not previously exposed to MPB.

MATERIALS AND METHODS

Study area

Extending over 11,000 square kilometers along the eastern slopes of the Rocky Mountains, Jasper National Park is the largest park in the UNESCO Canadian Rocky Mountain Parks World Heritage site (Figure 1). Conifer forests in the montane and subalpine zones are largely composed of lodgepole pine, a common MPB host in western Canada (Safranyik and Carroll 2006). After a century of fire suppression, most lower-elevation forests in Jasper National Park have shifted from a mosaic of patches of varying ages and lower-density stands to support large, dense, continuous stands of old lodgepole pine that are highly susceptible to MPB (Achuff et al. 2001, Schindler et al. 2000; Tande 1979). The recent MPB outbreak spread rapidly in Jasper from 123 ha affected in 2013, growing to over 229,000 ha of forested area at the peak of the outbreak in 2018 (Canadian Forest Service 2019). In 2019, a very cold winter killed approximately 98% of overwintering MPB, considerably slowing down their spread (Canadian Forest Service 2019) and this was considered the end of the MPB expansion phase of the outbreak in our study.

Study stands

Whitebark pine trees generally grow at higher elevations than lodgepole pine stands, forming the treeline forests along alpine ridges. Exposure to nearby infested lodgepole pine and landscape position influenced the variable MPB infestation rates we observed in whitebark pine throughout Jasper National Park. As prescribed in the proposed recovery strategy for whitebark pine (Environment and Climate Change Canada 2017), we surveyed the health of whitebark pine stands. High-value stands containing plus trees were targeted for seed collection, and they were visited annually to monitor individual tree health (e.g. alive/dead, WPBR resistance/infection levels) and MPB status (Table 1). Smaller and remote stands were visited less frequently. In 2020, we revisited 9 stands that included plus trees protected with semiochemicals during the MPB outbreak (1600 m to 2050 m average elevation; Table 2). Stands were surveyed in one to four subsections based on previous field visits conducted to locate whitebark pine trees. We did not have complete annual data on beetle pressure within each stand and thus treated the 2020 surveys as post-outbreak results.

TABLE 1 - annual MPB trees protected & ha affected

TABLE 2 - characteristics, incl. elevation, and DBH x MPB attack of stands assessed

Semiochemical Protection Treatment and Tree Surveys

We applied one high-dose Synergy Shield verbenone pouch (7.85 g *trimethyl-bicyclo-heptenone*, CAS-No 80-57-9) combined with one Synergy Shield GLVM pouch (3.84 g leaf alcohol *1-hexanol*, CAS-No 11-27-3, hexyl alcohol *Z3-hexanol*, CAS-No 928-96-1) on the shady side of each plus tree approximately 2 m above the ground. GLV was used under a research authorization exemption via Health Canada – Pest Management Regulatory Agency. We started protecting whitebark pine plus trees from MPB with semiochemicals in 2014 in stands at highest risk of attack based on tree DBH and proximity to MPB source populations. As the MPB population spread, we protected plus trees in more stands until an outbreak was declared in 2017–2018 (Canadian Forest Service 2019), after which we applied single-tree protection to high value trees throughout whitebark pine stands. We visited these trees every year from 2014 to 2020 between May and early July to monitor health condition, including MPB, and re-apply semiochemicals. MPB attacks were recorded where we observed characteristic pitch tubes, feeding galleries, and bark peeling (Burleigh et al. 2014).

We assessed survival and MPB attack signs of protected trees in 2020 at the end of the outbreak. We considered attacked trees to be alive if some green needles were present, and dead if all remaining needles were orange and started shedding. We also recorded GPS coordinates and diameter at breast height (DBH) of each tree. For this study, we included 193 trees that had been consistently protected annually since MPB arrived in the area of the stand, and were protected by 2018, at the peak of the outbreak. Trees that died of causes other than MPB were excluded.

During 2020, we also assessed the health status of unprotected control trees within the same stands against which we compared the effectiveness of the semiochemical treatment. Since there was no MPB in whitebark pine stands prior to this outbreak, we assume attacked control trees were attacked during the 2015–2018 outbreak. Rather than attempting to determine the attack year post-hoc, we classified trees as healthy or attacked, dead or alive, by the end of the outbreak. We selected control trees in representative local conditions by conducting stand surveys near the protected trees. Since the pheromone plume radius is 4–5 m (Miller 2002), we only included control trees at least 7 m away from protected plus trees. Unless fewer trees were available in the stand, we aimed to find ten control trees with similar DBH within 100 m of each protected tree, or a minimum of 100–120 control trees per stand, whichever was greater (total 1808 control trees; Table 3). We only included trees with a minimum DBH of 15 cm since trees smaller than that have a lower likelihood of being attacked by MPB (Shanahan et al. 2016). For control trees, we recorded GPS coordinates, DBH, live/dead, presence/absence of MPB attack, and presence/absence of WPBR based on visible infections and symptoms (Burleigh et al. 2014).

TABLE 3 - characteristics of MPB live/dead comparison stands

DATA ANALYSIS

Semiochemicals Effectiveness in Protecting Whitebark Pine

To assess the effectiveness of the semiochemical treatment in protecting whitebark pine from MPB, we used logistic regressions to model the probability (p) of MPB attack as a function of the treatment

(Hosmer Jr. et al. 2013). Because over 90% of trees attacked by MPB were dead (Table 3), we used *MPB_Attack* as the response variable:

$$MPB_Attack_i \sim Binomial(p_i) \quad (1)$$

Where *MPB_Attack_i* is a 0/1 variable indicating if tree *i* is alive and not attacked by MPB (0), or attacked or dead from MPB (1), and *p_i* is the probability that tree *i* is attacked or killed by MPB. The following logistic transformation then applies for the model:

$$\theta_i = \log\left(\frac{p_i}{1-p_i}\right) \quad (2)$$

We accounted for geographic variation in the intensity of MPB infestation across the park by including *Stand* as a random effect in a generalized linear mixed model (*glmm*) logistic regression. The primary predictor variable is the treatment (*Semiochem*). The most basic model for the log-odds θ_i that contains the fixed effect of *Semiochem* (0,1) and the random effect (*R*) of *Stand i* as a proxy for the local intensity of MPB attack is:

$$\theta_i = Semiochem_i + Stand(R)_i \quad (3)$$

We subsequently fit additional models testing effects of the tree-level covariates *DBH*, *Elevation*, and their interactions, keeping in mind that *Stand*, *DBH*, and *Elevation* are not completely independent variables because of stand and habitat dynamics (Figure 2). While stands vary in elevation and DBH, the nature of stand dynamics is such that the effects of DBH and elevation must be interpreted as marginal within each stand; the *Stand* random effect incorporates differences in mean DBH and elevation between stands. We used this approach to distinguish single-tree treatment effects from possible confounding effects at the stand level within which single trees are nested. While there may be a negative relationship of $p(MPB_Attack)$ with *DBH* or *Elevation* for single trees, we tested tree- and stand-level models to ascertain whether this reflected a population-wide response.

FIGURE 2 - Graph of DBH vs Elevation

WPBR and MBP Interaction

Because our protected trees were all considered rust-resistant and showed little to no sign of WPBR, presence of WPBR could not be used as a covariate in this analysis. To discriminate relationships between WPBR and MPB, we proceeded to a second analysis exclusively using control trees surveyed in

2020 (n=1808) because *BlisterRust* presence was only assessed on untreated control trees. This also removed potential confounding effects of rust resistance in all treated trees. We used the same approach to analyze the effectiveness of the treatment, substituting *Semiochem* with *BlisterRust* as the primary predictor variable, *Stand* was included as a random effect in the *glmm*, and we subsequently fit additional models that included effects of the covariates *DBH*, *Elevation*, and their interactions using the same model selection, averaging, and assessment approach:

$$\theta_i = \text{BlisterRust} + \text{Stand}(R)_i \quad (4)$$

We used an information theoretic approach (Burnham and Anderson 2002), fitting models with the base effect of *Stand*, followed by combinations of *Semiochem*, *DBH*, *Elevation* and their interactions. Models were compared using AICc and then weighted by the difference in AICc (ΔAICc) from the best-fitting model. To improve numerical stability of the fitting process, we standardized *DBH* to variable *DBH.s* by subtracting 30 cm and standardized *Elevation* to variable *Elevation.s* by subtracting 2000 m, distributing the values around a mean approaching 0. This standardization had no impact on the model selection process or the estimated coefficients, except for the intercept.

We analysed data and produced figures using R v.4.0.3 (R Core Team 2021). We assessed model fit based on residual diagnostic plots from the *DHARMA* package in R (Hartig 2020) based on Q-Q plots, rank transformations, and standardized residuals. No deviation from goodness-of-fit was observed for the models testing *MPB_Attack* for *Semiochem* or *BlisterRust*.

SPATIAL AUTOCORRELATION

Visual inspection of the data led us to test for potential clusters of MPB-attacked trees. We used a two-step approach to test for spatial correlation of the probability of a tree to be attacked or killed by MPB. First, we performed a coarse large-scale analysis to explore spatial correlation between stands in the study area. We only included control trees to eliminate variability or bias associated with the treatment. We determined the proportion of control trees attacked or killed by MPB for each stand and computed Moran's *I* statistics based on mean stand Easting and Northing, which divides spatial covariation between

points into total variation (Moran 1948). We also computed those values at the stand subsection level. To investigate spatial correlation between individual trees, we conducted a second analysis comparing results between our *glmm* treatment analysis and a logistic regression with explicit spatial autocorrelation using individual tree coordinates (Anderson and Ward 2019). Spatial autocorrelation usually generates unbiased estimates, but may underreport the true uncertainty, increasing false positive rates (Beale et al. 2010). By comparing the estimates and their standard errors, we assessed the approximate increase in uncertainty due to spatial autocorrelation. To compare with our initial *glmm* using stands as a random factor, we used the *glmmfields* package from *R* (Anderson and Ward 2020) to fit the spatially explicit logistic regression model:

$$p(\text{MPB_Attack}) = \text{DBH} + \text{Elevation} + \text{Semiochem} \quad (5)$$

RESULTS

MPB Impacts on Tree Mortality

Nearly all of the plus trees attacked by MPB ($n=44$), protected or not, died within two years of being attacked: 85% were dead after one year, and only five attacked trees were still alive after two years. Among the 193 trees protected with verbenone and GLV in 2020 and included in the analyses, 23 were killed by MPB (11.9%) and 13 were attacked and still alive (6.9%). Given the mortality rate observed in all plus trees in the park after two years, we expect most of the trees recently affected by MPB would be dead by 2021 or 2022. Total mortality rate in combined attacked control and protected trees was 92% (Table 3).

Model Selection and Variable Importance

We found the strongest support for models that included the effect of *Semiochem* or *BlisterRust*, highlighting the significance of the semiochemicals and WPBR with respect to probability of MPB attack. All but one model with $\Delta\text{AICc} < 10$ included *Semiochem* or *BlisterRust*, *Elevation.s*, and *DBH.s* (Table 4). Variable importance is measured as the sum of weights of every model (n) including each of the variables. Based on the sum of weights of each model, there was no support for models excluding any of these terms; the models including them ($n=14$) accounted for 100% of the total sum of weights (Table 4).

Model support was also split among several models that involved interactions between the effect of *Semiochem* or *BlisterRust* and the other covariates (Table 4). In the pheromone treatment analysis, the interaction between *Elevation.s* and *Semiochem* was included in all models with $\Delta AICc < 2$, with models including this term ($n=6$) accounting for 96% of the sum of weights, showing strong support for this interaction (Table 4). The interaction between *DBH.s* and *Semiochem* had more marginal support with models including this term only accounting for 70% of the sum of weights. In the WPBR analysis, the interaction between *DBH.s* and *BlisterRust* was included in all of the best models, and models including this term ($n=6$) accounted for 100% of the sum of weights (Table 4). The top three models all contained the interaction between *Elevation.s* and *BlisterRust*, and models including this term ($n=6$) accounted for 89% of the sum of weights (Table 4).

TABLE 4 - glmm model selection results

Semiochemical Treatment Effectiveness Against MPB

The semiochemical treatment reduced the probability of MPB attack or death; the model averaged effect of *Semiochem* on the response variable *MPB_Attack* was negative and the 95% CI excluded 0 (95% CI: -2.26, -0.73; Table 5). Table 6 summarizes the predicted log-odds of MPB attack or death with and without protection, for *DBH* and *Elevation* set to the 25th, 50th, and 75th percentiles for an “average” stand. For all *DBH* and *Elevation* levels, semiochemicals appear to protect against MPB. However, because *DBH* and *Elevation* are inversely related (Figure 2), the full range of *DBH* may not be present within any *elevation* class, and vice versa. Additionally, a stand only occurs within a limited *elevation* range, therefore the model varying the full range of *elevation* within an “average” stand in Table 6 may not represent a realistic scenario. Interactions between *Semiochem*, *Elevation.s*, and *DBH.s* indicate that the level of protection increased with larger trees and at lower elevations. Model coefficients indicate that the probability of *MPB_Attack* decreased with increasing *Elevation* (Table 5). *MPB_Attack* probability decreased faster for protected trees than for unprotected trees (Figure 3). The probability of *MPB_Attack* increased with greater *DBH* in unprotected trees more rapidly than in protected trees (Figure 4). However, both of these interactions were weak, with confidence limits including or approaching zero. Though the 95% confidence

intervals are wide, a treatment effect may still be detected even if the 95% CI for treated and untreated stands overlap (Figure 3, Figure 4).

TABLE 5 - Model averaging for Semiochem and BlisterRust

TABLE 6 - Predicted log-odds with DBH and Elevation set to the 25th, 50th, and 75th percentiles for an "average" stand **possibility to delete as per text note

FIGURE 3 - logistic graph between DBH & MPB attack/death

FIGURE 4 - logistic graph between Elevation and MPB attack/death

WPBR Infection and MPB Attack Interaction

All stands had trees with and without WPBR. All models with $\Delta AICc < 10$ that explored the impacts of covariates included *Stand* as a random effect and contained the binary variable *BlisterRust* (Table 4). Models including all three main explanatory variables (*BlisterRust*, *Elevation.s*, *DBH.s*) accounted for nearly 100% of the total sum of weights (n=14 models). The interaction between *Elevation.s* and *BlisterRust* was included in models with $\Delta AICc < 3$. Two-factor interactions of *Elevation.s* x *BlisterRust* and *DBH.s* x *BlisterRust* were also included in the best models. Models including the interaction between *DBH.s* and *BlisterRust* (n=6) accounted for nearly 100% of the sum of weights, while models including the interaction between *Elevation.s* and *BlisterRust* accounted for 89% of the sum of weights (Table 4). Although the effect of elevation and its interaction with other covariates were included in the best models, none of the estimates including *Elevation.s* as a single factor or in interactions had large model weights for model averaging (Table 5). On the other hand, the effect of DBH and its interaction with WPBR had model averaged estimates whose CI excluded 0 (Table 5). The effect of WPBR infection on the likelihood of MPB attack or death mostly varies with tree size, and marginally with elevation. Three explanatory variables had 95% confidence intervals that excluded zero when accounting for variation in the probability of MPB attack or death (Table 5). The positive coefficient for *DBH.s* indicates MPB is more likely to impact larger trees, as observed in the semiochemical treatment analysis, and the negative coefficient of the interaction between *DBH.s* and *BlisterRust* indicates that MPB are less likely to impact large trees infected by WPBR than uninfected large trees (Table 5); *BlisterRust* made no difference in smaller trees (Figure 5). Reflecting the inverse relationship between *Elevation.s* and *DBH.s*, the probability of MPB

attack or death of all trees (infected or healthy) decreased slightly with increasing *Elevation* (i.e., trees with smaller DBH), the effect size (estimate) was very small and non significant (Table 5).

FIGURE 5 – logistic graph of MPB attack/death vs DBH for WPBR

Stand Effects and Spatial Autocorrelation

Models including stand variability as a random factor showed no evidence of lack of fit using any metric (KS test: $p < 0.001$ (both analyses); dispersion test: $p = 0.7$ (both analyses); outlier test: $p = 0.6$ (semiochemical treatment), $p = 1.0$ (WPBR infection)). Moran's I tests indicated no evidence of spatial partitioning of variation between stands ($p = 1.0$) and there was a weak trend between sections within stands ($p = 0.1$). The spatially explicit model (eq. 5) and the *glmm* using *Stand* as random factor and the same variables produced very similar estimates and standard errors (Table 7).

TABLE 7 – Spatial model vs glmm, SE comparison

DISCUSSION

Effectiveness of Semiochemical Treatment

Similar to findings in regions with established MPB populations (Seybold et al. 2018), our results support the effectiveness of the antiaggregation pheromone verbenone, in combination with GLV, in protecting whitebark pine from MPB attack. Our study confirmed this treatment was effective in a host population that had never been exposed to this threat before: whitebark pine stands in a northern range expansion of MPB. Our treatments always included the combination of two semiochemicals, so it is not possible, and we did not intend, to discriminate between the effectiveness of verbenone and GLV from this study.

Effects of Diameter, Elevation, and Health on Trees and Stands

MPB is known to prefer larger diameter trees, typically attacking trees above 15 cm DBH, where attack rates increase with diameter, which is a proxy for age (Safranyik and Carroll 2006). In this study area, DBH is also inversely correlated with elevation, where higher-elevation trees tend to be smaller as growing seasons are shorter and sites tend to be nutritionally poorer and more xeric due to mesotopography. The nutritional value of the phloem varies between whitebark and lodgepole pine host

trees; faster-growing trees with less nutritional stress can support larger MPB broods and overwinter success (Six and Adams 2007). Typically, whitebark pine can support MPB populations, but their ecologically marginal habitats in colder habitats with short growing seasons and nutrient-poor sites may not support the population density and bioenergetic capacity to sustain epidemic populations under most circumstances except during extreme MPB pressure (Amman 1982; Cerezke 1995).

Accounting for distance between individual trees in the spatially explicit logistic regression model made no meaningful difference to parameter estimates and had only slightly larger standard errors compared to the *glmm* model including the same main effects (semiochemical treatment, elevation, DBH; Table 7). This suggests that the random effect of *Stand*, as used in the *glmm*, captures most of the spatial variability in attack rates that is primarily caused by MPB progression through the study area (Jasper National Park) driven by host tree size and elevation, rather than where individual trees are in relation to one another on a large geographic scale. The marginal effect of elevation within stands, evident in *glmm* results, may also have captured part of the spatial variability within stands rather than an actual effect of elevation; trees closer to each other share more elevation similarity than trees further apart. The results from the simpler *glmm* models are robust to ignoring the small effect on standard error caused by the minor within-stand spatial autocorrelation. Inferences about the effects of semiochemical treatment therefore can be applied broadly, which indicates this treatment should be effective at protecting whitebark pine stands in the region, including other northern and high-elevation areas with new range expansions of MPB.

This was the first MPB epidemic in the region so it is reasonable to assume that MPB signs and symptoms were accurately characterized and could not have indicated old attacks. While it is more difficult to accurately detect WPBR infection on dead than living trees, field staff indicated underreporting WPBR infection in MPB-killed trees was not a significant source of bias, given their expertise in forest health assessments and the relatively recent MPB mortality. While attacked trees in old MPB outbreaks may slough off bark with characteristic indications of WPBR, trees attacked during the 2015–2018 MPB

outbreak retained diagnostic indicators of infection by 2020 such as co-located swelling and cracking bark, sap, and rodent chewing.

Comparison with other studies

As Bockino and Tinker (2012) observed in Yellowstone and Larson (2010) found across several states, our study confirmed WPBR infection and DBH were both significant factors affecting MPB impact potential. MPB preferentially selected larger whitebark pine in Yellowstone, and trees with heavy WPBR infection over less severely infected trees, regardless of their relative abundance in a stand (Bockino and Tinker 2012). Dooley and Six (2015) observed significantly more uninfected trees were attacked, and at higher densities than infected trees, although more heavily infected trees had far higher MPB emergence rates and may have required fewer attacks to kill them. Six and Adams (2007) noted that more severe WPBR infection predisposed whitebark pine trees to MPB attack and mortality through triggering drought stress that may send a biochemical signal influencing MPB preference. Jules et al. (2016) found whitebark pine trees in Oregon infected with WPBR were several times more likely to be attacked and killed by MPB than uninfected trees; annual survivorship for attacked trees was 65%, much higher than in our study area, where well over 90% of attacked trees died (Table 3).

Some studies found opposite trends. Shanahan et al. (2016) observed no interaction between WPBR and MPB in Yellowstone in a long-term study, where MPB killed most attacked trees within two years, similar to this study, but the probability of mortality in their study was lower for larger trees in stands with higher evapotranspiration (a site-specific effect) - this effect may also contribute to the variability across stands we observed. Based on a multi-year study in Idaho, Schwandt and Kegley (2004) suggested that at low population levels during a regional epidemic, MPB may select trees with more severe WPBR infections, but this pattern was reversed at epidemic MPB pressure (Kegley and Gibson 2004). Their results suggested there may be a point where increasing MPB populations switch from attacking WPBR-weakened trees to apparently healthy trees, but small sample sizes precluded statistically significant findings. Our study found a similar result in trees with DBH above 25 cm (Figure 5).

WPBR infection significantly influenced MPB attack rates across all stands in our study area, reflected in its strong significance as a model term alone, and interacting with *DBH* and *Elevation*. Its primary effect is that trees with WPBR were less likely to be attacked by MPB: the protective effect was stronger in larger trees that typically are more susceptible to MPB attack. This implies that high-value uninfected plus trees are more susceptible to MPB attack in the same stand as infected trees of the same size. Protecting plus trees with semiochemicals was highly effective in all elevations and tree sizes, both at the individual tree and the stand levels.

Based on average responses by DBH class, we found that protection with verbenone and GLV reduced the probability of MPB attack for all whitebark pine trees, especially those larger than ~35 cm DBH, by 46 to 60% (Figure 3). Using a similar approach, Perkins et al. (2015) applied verbenone annually to whitebark pine during a recent MPB outbreak in Idaho over seven years and found that treatment doubled the proportion of all size classes of surviving trees from 34 to 68%. Gillette et al. (2014) found 30% of control trees, 80% of trees with verbenone, and 83% of trees with verbenone and GLV in Montana were not attacked by MPB, indicating little incremental gain from GLV (Seybold et al. 2018). They also found the probability of MPB mass attack (likely leading to death) for whitebark pine was reduced by 58 to 100% for treated whitebark pine trees. Fettig and Munson (2020) suggested verbenone alone may be just as effective protecting lodgepole pine at the individual tree and the stand level as the two semiochemicals combined. Bentz et al. (2005) found verbenone pouches deterred MPB attacks in whitebark pine at one of two sites, and treatment was more consistently effective in lodgepole pine stands.

These findings support Parks Canada in continuing applying this treatment to high-value whitebark pine plus trees when there is an appreciable likelihood of MPB attack. Given the slow growth and maturation rate of these trees, replacing each tree takes a century or more, so protecting them from mortality is a proactive way to expedite recovery and provide a source of seeds with increased rust resistance for restoration planting. These plus trees are unique and irreplaceable as they contribute pollen and seeds with increased resistance to natural regeneration that is absent from unselected wild trees.

Study Limitations

Ecological and environmental factors governing MBP outbreaks mainly consist of host tree properties and distribution, beetle pressure, and weather factors (Kunegel-Lion and Lewis 2020; Safranyik and Carroll 2006). Individual host tree properties influence susceptibility to beetle outbreaks. For example, a better investment in defense structure development increases a tree's capacity to resist beetle attack (Kichas et al. 2020), despite the general trend of large trees being preferred hosts for MPB (Safranyik and Carroll 2006). Our results indicate that larger DBH increased susceptibility to MPB, while WPBR decreased it. The relationship between WPBR and MPB susceptibility is also influenced by site level factors including drought stress (Larson 2010), climatic factors (Safranyik and Carroll 2006), and host plant distribution (Powell and Bentz 2014), and at the tree level by tree vigour and genetic disease resistance (Kegley and Gibson 2004). We did not include a climate or weather assessment in our analysis, instead focusing on testing the effects of treatments and WPBR on MPB impacts. Stratifying our data at the stand level controlled most of the variability in MPB pressure and weather factors at the study area scale in our analyses, as those factors have minimal variability at the individual tree scale.

A more statistically robust design to test treatment effectiveness, if resources were unlimited, would have been to monitor a large number of trees twice a year from 2014, just before the beginning of the MPB outbreak, to 2020, using a before-after control-impact approach. In spring, while applying semiochemicals, crews would assess the health status of each tree and exposure to MPB over the course of the previous year for each tree. In fall, re-assessments would monitor the progress of the MPB outbreak. Verbenone and GLV would have been applied to a geographically distributed sample of rust-susceptible trees to provide a more robust test at the tree level of the potential effect of blister rust on MPB susceptibility.

Management Implications

Canada is a signatory to the *Convention on Biological Diversity* (United Nations 1992) which supports measuring, sustaining, and mitigating impacts to biological diversity. Protecting keystone species against MPB mortality and invasive pathogens is a measurable way to help achieve this goal. As a keystone, the

decline of whitebark pine below a threshold where its unique ecosystems would no longer be able to sustain themselves would negatively affect numerous associated wildlife species including black bears (*Ursus americanus* Pallas), grizzly bears (*Ursus arctos* L., special concern status, western population), whitebark pine's obligate disperser Clark's nutcracker (*Nucifraga columbiana* Wilson) and many other birds, small mammals, as well as ecosystem processes (Kendall and Arno 1990). Maintaining ecological integrity of functioning stands, and restoring ecological function in impaired stands, requires effectiveness monitoring of status and stand dynamics, and targeted treatments based on local risks and stand conditions. Increasing rates of WPBR infection and mortality (Shepherd et al. 2018), combined with recent range expansion of MPB into whitebark pine stands of Jasper National Park, mean that larger rust-resistant trees with the highest reproductive capacity may be more at risk of MPB attack than average trees in a stand. The most robust restoration approach for this species includes a key objective of increasing the frequency of WPBR resistance genes in populations (Environment and Climate Change Canada 2017; Keane et al. 2012). Protecting these high-value plus trees from MPB attack, and collecting their seeds to produce seedlings for restoration both advance this objective (Parks Canada Agency 2017).

Parks Canada has made significant investments over the past five years across all mountain parks to help recover whitebark and limber pine (*P. flexilis* James), and has further committed five more years of funding. Much of this work focused on identifying WPBR-resistant trees and growing and planting their seedlings. This study confirms the effectiveness of supporting specific recovery activities in current plans. Protecting 250 trees would cost approximately \$20,000 CAD annually, for the combination of semiochemicals used in our study, or over \$120,000 CAD for a sustained five-year MPB outbreak. Further research is required to compare the effectiveness of verbenone alone in protecting trees, versus in combination with GLV, as using verbenone alone may improve cost effectiveness. Whitebark pine stands with MPB-killed mature rust-resistant trees will take 80 to 100 years to recover as seedlings from rust-resistant parent trees begin to produce cones and replace the ecosystem function lost to MPB. If recovery of the species hinges on the survival and reproduction of WPBR-resistant trees, proactive

protection with verbenone and GLV where there is a MPB risk is critical, considering nearly all unprotected trees that were attacked by MPB died in our study.

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COMPETING INTERESTS STATEMENT

The authors declare there are no competing interests.

CONTRIBUTOR'S STATEMENT

EC: conceptualization, methodology, investigation, formal analysis, writing - original draft and review & editing.

BS: supervision, conceptualization, methodology, project administration, funding acquisition.

JK: writing - review & editing.

CJS: methodology, formal analysis, writing - review & editing.

JSW: investigation.

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DATA AVAILABILITY STATEMENT

Data and conditions of use may be requested directly to the corresponding author.

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TABLES

Table 1. Cumulative number of whitebark pine plus trees attacked by mountain pine beetle (MPB), and annual area affected by MPB in Jasper National Park. Attacked trees counted each year reflect MPB attack that happened during the previous year.

Year	2013	2014	2015	2016	2017	2018	2019	2020
No. of study trees attacked	0	1	1	5	7	21	38	44
Hectares affected	123	6 251	21 600	48 600	93 156	162 700	229 176	3 568

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Table 2. Mean tree elevation and DBH of whitebark pine study stands surveyed in 2020 in Jasper National Park.

Stand	Elevation ± SE (m)	DBH ± SE (cm)		
		All trees	Trees without MPB	Trees attacked by MPB
Astoria	1762 ± 2	31.8 ± 0.4	30.9 ± 0.5	33.8 ± 0.7
Beaver Lake	1902 ± 11	28.1 ± 1.0	26.6 ± 1.3	31.1 ± 1.6
Endless Chain	2003 ± 7	31.1 ± 0.7	30.4 ± 0.7	37 ± 2
Geraldine	1636 ± 2	39.0 ± 0.6	36.4 ± 0.8	42.1 ± 0.8
Hilda Gulch	2047 ± 1	22.4 ± 0.7	21.2 ± 0.6	26.9 ± 1.9
Lectern	1954 ± 3	32.8 ± 0.7	32.8 ± 0.7	32.4 ± 1.8
Miette Lakes	1960 ± 4	30.8 ± 0.8	28.6 ± 1	34 ± 1.2
Peveril	1949 ± 6	30.4 ± 1.1	30 ± 1.4	31.6 ± 1.5
Verdant	1997 ± 4	22.9 ± 0.9	21.3 ± 0.9	34.3 ± 1.9
Average	1846 ± 4	32.1 ± 0.3	30.2 ± 0.3	36.6 ± 0.5

Table 3. Mountain pine beetle (MPB) attack and tree mortality rates by stand, semiochemical protection treatment, and white pine blister rust (WPBR) incidence for whitebark pine trees surveyed in 2020 in post-outbreak conditions in Jasper National Park.

Stand	No. of trees by Treatment			No. of trees attacked by MPB by Treatment			No. of trees attacked by MPB	No. of control trees with WPBR	No. of control trees attacked by MPB	
	Protected	Control	Total	Protected	Control	Total	Total dead*	Total	WPBR	No WPBR
Astoria	39	464	502	6 (16%)	153 (33%)	159 (32%)	145 (91%)	309 (66%)	41 (27%)	70 (45%)
Beaver Lake	11	43	54	2 (18%)	17 (40%)	19 (33%)	19 (100%)	30 (70%)	5 (17%)	12 (92%)
Endless Chain	26	290	316	0	33 (11%)	33 (10%)	29 (88%)	263 (91%)	32 (12%)	2 (7%)
Geraldine	45	431	476	19 (42%)	202 (47%)	221 (46%)	201 (91%)	380 (88%)	19 (49%)	17 (33%)
Hilda Gulch	7	120	127	1 (14%)	25 (21%)	26 (20%)	24 (92%)	21 (18%)	1 (5%)	24 (24%)
Lectern	13	120	133	1 (8%)	21 (18%)	22 (17%)	21 (95%)	101 (84%)	13 (13%)	8 (42%)
Miette Lakes	40	183	223	6 (15%)	85 (46%)	91 (41%)	84 (92%)	164 (90%)	84 (51%)	2 (11%)
Peeveril	5	43	48	1 (20%)	12 (28%)	13 (26%)	13 (100%)	28 (65%)	10 (36%)	2 (13%)
Verdant	8	114	122	0	15 (13%)	15 (12%)	14 (93%)	62 (54%)	12 (19%)	3 (6%)
Total	193	1808	2001	36 (19%)	563 (31%)	599 (30%)	550 (92%)	1358 (75%)	217 (16%)	140 (47%)

* Mortality rate in MPB attacked trees: most trees affected by MPB in 2019-2020 will die within 2 years, after the completion of this study.

Table 4. Model selection results from *glmm* testing for the effects of a) semiochemical treatment (*Semiochem*), and b) presence of white pine blister rust (*BlisterRust*), on the probability of mountain pine beetle attack on whitebark pine trees, with covariates (elevation, DBH). All models where $\Delta AIC_c < 10$ are shown. The '+' symbol indicates where the binomial treatment variable was included in the model.

	Intercept	Treatment	Elevation.s (x 10 ⁻³)	DBH.s (x 10 ⁻²)	Elevation.s x Treatment	Elevation.s x DBH.s (x 10 ⁻⁵)	DBH.s x Treatment	Elevation.s x DBH.s x Treatment df	logLik	AICc	ΔAIC_c	Weight
Treatment												
a) Semiochem	-1.212	+	-1.71	4.46	+		+	7	-1089.42	2192.9	0.00	0.241
	-1.211	+	-1.81	5.36	+	4.14	+	8	-1088.50	2193.1	0.17	0.221
	-1.218	+	-1.90	5.62	+	5.47	+	9	-1087.51	2193.1	0.21	0.217
	-1.214	+	-1.78	4.19	+			6	-1090.81	2193.7	0.77	0.164
	-1.213	+	-1.88	4.87	+	3.39		7	-1090.15	2194.4	1.46	0.116
	-1.260	+	-2.06	4.10				5	-1094.37	2198.8	5.87	0.013
	-1.263	+	-2.03	4.33			+	6	-1093.58	2199.2	6.31	0.01
	-1.264	+	-2.12	5.01		3.28	+	7	-1092.97	2200.0	7.10	0.007
	-1.261	+	-2.14	4.55		2.27		6	-1094.05	2200.1	7.24	0.006
Sum of weights:		1 (14)	1 (14)	1 (14)	0.96 (6)	0.57 (6)	0.70 (6)	0.22 (1)				
b) BlisterRust	-0.4562	+	-0.44	12.88	+		+	7	-978.849	1971.8	0.00	0.468
	-0.426	+	-0.33	13.46	+	3.72	+	8	-978.263	1972.6	0.85	0.306
	-0.4338	+	-0.36	13.32	+	2.79	+	9	-978.258	1974.6	2.86	0.112
	-0.7642	+	-2.46	12.27			+	6	-981.653	1975.4	3.59	0.078
	-0.7671	+	-2.51	12.53		1.80	+	7	-981.506	1977.1	5.31	0.033
	-0.5581	+		12.29			+	5	-985.823	1981.7	9.92	0.003
Sum of weights:		1 (14)	1 (14)	1 (14)	0.89 (6)	0.45 (6)	1 (6)	0.11 (1)				

Table 5. Model averaging, including confidence intervals (CI), for model selection results from *glimm* testing for the effect of a) semiochemical treatment (*Semiochem*), and b) presence of white pine blister rust (*BlisterRust*), with covariates (elevation, DBH). Significant model terms are in bold font.

	Model variables	Estimate	Std. Error	CI 2.5%	CI 97.5%
a)	Intercept	-1.21481	0.21607	-1.63830	-0.79133
	Semiochem	-1.49497	0.39194	-2.26315	-0.72678
	Elevation.s	-0.00181	0.00083	-0.00343	-0.00019
	DBH.s	0.04909	0.00885	0.031733	0.06644
	Elevation.s x Semiochem	-0.00368	0.00165	-0.00691	-0.00044
	Elevation.s x DBH.s	0.00003	0.00003	-0.00004	0.00008
	DBH.s x Semiochem	-0.02575	0.02644	-0.07757	0.02607
	Elevation.s x DBH.s x Semiochem	-0.00003	0.00008	-0.00019	0.00012
b)	Intercept	-0.47886	0.27992	-1.02750	0.06978
	BlisterRust	-1.01017	0.27441	-1.54801	-0.47233
	Elevation.s	-0.00062	0.00133	-0.00323	0.00199
	DBH.s	0.13046	0.01580	0.09949	0.16144
	Elevation.s x BlisterRust	-0.00234	0.00132	-0.00493	0.00025
	Elevation.s x DBH.s	0.00002	0.00003	-0.00005	0.00008
	DBH.s x BlisterRust	-0.09564	0.01654	-0.12806	-0.06322
	Elevation.s x DBH.s x BlisterRust	0.00000	0.00002	-0.00004	0.00004

Table 6. Predicted log-odds and estimates of MPB attack/death with and without semiochemicals, with DBH and elevation set to the 25th, 50th, and 75th percentiles for an "average" stand.

Semiochem	DBH (cm)	Elevation (m)	Predicted log-odds	Predicted estimate
0	23.0	1702.8	-0.9670	0.2755
1	23.0	1702.8	-1.2576	0.2214
0	30.5	1702.8	-0.6554	0.3418
1	30.5	1702.8	-1.0657	0.2562
0	39.0	1702.8	-0.3023	0.4250
1	39.0	1702.8	-0.8482	0.2998
0	23.0	1831.0	-1.2221	0.2276
1	23.0	1831.0	-1.9545	0.1241
0	30.5	1831.0	-0.8861	0.2919
1	30.5	1831.0	-1.7699	0.1456
0	39.0	1831.0	-0.5053	0.3763
1	39.0	1831.0	-1.5606	0.1736
0	23.0	1987.2	-1.5329	0.1776
1	23.0	1987.2	-2.8036	0.0571
0	30.5	1987.2	-1.1672	0.2374
1	30.5	1987.2	-2.6278	0.0674
0	39.0	1987.2	-0.7528	0.3202
1	39.0	1987.2	-2.4286	0.0810

Table 7. Estimated coefficients from both a logistic regression with explicit spatial autocorrelation using XY coordinates of individual trees, and a generalised linear mixed model (*glmm*) using *Stand* as a random factor accounting for spatial variability, where the probability of MPB attack is a function of tree diameter at breast height (DBH), elevation, or semiochemical treatment. Significant estimates with 95% confidence interval (CI) excluding zero are in bold font.

Term Model	Estimate		SE		95% CI	
	Spatial	glmm	Spatial	glmm	Spatial	glmm
Intercept	-3.02	1.64	1.40	1.54	-5.86, -0.38	-1.38, 4.66
Semiochem	-0.888	-0.885	0.211	0.204	-1.31, -0.48	-1.29, -0.48
Elevation	0.10×10^{-3}	-2.06×10^{-3}	7.33×10^{-4}	7.945×10^{-4}	$-1.28 \times 10^{-3}, 1.58 \times 10^{-3}$	$-3.62 \times 10^{-3}, 0.51 \times 10^{-3}$
DBH	5.44×10^{-2}	4.10×10^{-2}	5.34×10^{-3}	4.86×10^{-3}	$4.39 \times 10^{-2}, 6.48 \times 10^{-2}$	$3.15 \times 10^{-2}, 5.06 \times 10^{-2}$

FIGURES

Figure 1. Whitebark pine stands surveyed in 2020 in Jasper National Park, Alberta. Basemap from Esri, HERE, Garmin, (c) OpenStreetMap contributors, and the GIS user community (2021), World Light Canvas Gray Base Map (NAD83, Latitude-Longitude). Park boundary from Parks Canada Agency (unpublished shapefile).

Figure 2. Inverse correlation relationship (linear trend line: $R=0.34$) between tree diameter at breast height (DBH) and elevation in whitebark pine stands sampled in 2020 in Jasper National Park. Small circles represent individual trees ($n=2001$), unprotected (0) and protected with Verbenone and Green-Leaf Volatiles (1). The large circles indicate the mean tree DBH and elevation at each stand ($n=9$) with size scaled by the number of trees in each stand.

Figure 3. Trees protected with semiochemicals (1) were less likely to be attacked by MPB than control trees (0) as DBH increases. Predicted regression curves evaluated at average elevation and stand, with pointwise 95% confidence intervals are shown. Rug at bottom shows DBH values in the dataset.

Figure 4. Probability of attack by mountain pine beetle (MPB) decreased with elevation in whitebark pine trees. Protected trees (1) were increasingly less likely to be attacked than unprotected trees (0) at higher elevation. Predicted regression curves evaluated at average DBH and stand, with pointwise 95% confidence intervals are shown. Rug at bottom shows elevation values in dataset.

Figure 5. Probability of attack by mountain pine beetle (MPB) increases with DBH in unprotected whitebark control trees, but larger trees infected by white pine blister rust (WPBR) were less susceptible to MPB attack compared to healthy trees that showed no signs of WPBR infection. Predicted regression curves evaluated at average elevation and stand, with pointwise 95% confidence intervals are shown. Rug at bottom shows DBH values in dataset.