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ORIGINAL ARTICLE

Mountain Pine Beetle (*Dendroctonus ponderosae*) Outbreak Triggers Growth Release in Small Whitebark Pine (*Pinus albicaulis*)

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Abstract

Whitebark pine (*Pinus albicaulis,* WBP) is an important high-elevation conifer in the Western USA that was listed as ''threatened'' under the Endangered Species Act in 2023. Consequently, land managers are tasked with ensuring the long-term viability of WBP populations through conservation and restoration efforts. The effects of mountain pine beetle (*Dendroctonus ponderosae*, MPB) outbreaks on WBP dynamics are poorly understood, especially for smaller-diameter trees that typically escape attack due to their size, allowing for persistence in the understory through outbreak events. Here, we assess growth responses for 10–25 cm diameter WBP trees growing in areas within the Greater Yellowstone Ecosystem that suffered substantial overstory mortality (impacted by MPB) and locations that experienced little to no mortality (unimpacted by MPB) during a MPB outbreak spanning from the 1970s through the early 1980s (peaking in 1981). In the 31 years following the outbreak, surviving WBP in the impacted units exhibited a significant growth release (61% increase in basal area increment; $cm^2\ year^{-1}$) compared to WBP in the unimpacted units (8% increase in basal area increment). Additionally, in the post-outbreak period we found strong, positive relationships between WBP growth and minimum temperature in the impacted units only, suggesting that the outbreak may have altered canopy structure in ways that increased growth potential for surviving WBP. Collectively, our findings suggest that the presence of smaller-diameter trees in WBP forests can offer resilience to beetle impacts and emphasizes the importance of maintaining multi-aged forest structures to buffer outbreak effects.

Key words: Ecosystem resilience; growth response; competition; mountain pine beetle; *Dendroctonus ponderosae*; outbreaks; dendroecology.

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Author's contribution NEK was involved in data curation, formal analysis, investigation, methodology, writing—original draft, and writing—review and editing; EKS took part in conceptualization, methodology, investigation, resources, data curation, writing—review and editing, and funding acquisition; SMH was responsible for conceptualization, methodology, investigation, resources, supervision, project administration, and funding acquisition.

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Highlights

- Small whitebark pine grew faster after a mountain pine beetle outbreak.
- Whitebark pine growth was strongly, positively related with climate post-outbreak.
- Multi-aged whitebark pine forests are more resilient to bark beetle outbreaks.

Introduction

High-elevation forests provide numerous ecological functions (Kräuchi and others 2000) yet face numerous threats from biotic and abiotic disturbances and climate change (Lu and others 2025). Whitebark pine (*Pinus albicaulis* Engelm.; WBP) is an important high-elevation species that contributes multiple ecological benefits across subalpine environments throughout the northern Rocky Mountains, USA (Tomback and others 2001). At upper treeline and alpine margins, WBP stabilizes soils, reduces erosion, intercepts moisture, and promotes snowpack accumulation and retention (Arno and Hoff 1989; Tomback and others 2001). Once established, WBP ameliorates harsh site conditions and facilitates establishment of other plant species, forming tree islands that enhance understory development and ecosystem heterogeneity. In addition, its large, energy-rich seeds are a critical food resource for a variety of wildlife, including grizzly bears (*Ursus arctos horribilis*). However, WBP forests have faced substantial mortality, as has been documented in other high-elevation forest ecosystems (Andrus and others 2021; Bryant and others 2024), due to changing climate and associated shifts in insect pressures. Over the last century, several factors have caused mortality in WBP forests, including the introduction of the nonnative pathogen *Cronartium ribicola* J.C. Fisch. that causes white pine blister rust (WPBR), native mountain pine beetle (*Dendroctonus ponderosae* Hopkins; MPB) outbreaks, climate change, and alterations in historical fire regimes (Tomback and others 2001, 2016). Consequently, it is listed as ''endangered'' in Canada and ''threatened'' in the USA to provide federal protection and encourage recovery efforts. Given these numerous threats, as well as unfavorable forecasts for future establishment under a changing climate (Parks and others 2025), it is crucial to understand the demographics of WBP populations and the impacts of biotic and abiotic disturbances on tree growth and establishment. With this data-driven knowledge, land managers will be better equipped to determine appropriate treatment options and prioritize treatment areas that can be extrapolated to other landscapes.

While high mortality rates in WBP forests have been observed following MPB outbreaks (Macfarlane and others 2023), there is relatively limited research quantifying how resulting changes in stand structure and density affect WBP establishment, age structure, and growth of surviving trees (Amberson and others 2018; Goeking and Izlar 2018). Additionally, even under outbreak scenarios, there are often trees that escape attack, survive, and go on to produce seed that contribute to future WBP forests (Six and others 2018; Maher and others 2020). MPB have historically acted as a natural biotic agent for thinning pine forests, whereby MPB typically select and kill larger diameter trees (e.g., > 15–18 cm diameter at breast height; DBH), while smaller, subhost-sized WBP escape (Safranyik and Carroll 2006; Shanahan and others 2016). Over extended time periods, and in the absence of large, high-severity fires, MPB can act as an evolutionary filter on WBP populations. By preferentially killing trees with lower defenses, beetle outbreaks can increase the prevalence of defensive traits and other genetic characteristics that promote survival (Six and others 2018; Kichas and others 2020). This process has allowed WBP to persist for thousands of years despite substantial biotic and abiotic pressures, with its range and abundance fluctuating in response to climatic variability (Iglesias and others 2015; Pederson and others 2025).

WBP forests, similar to other high-elevation forest ecosystems, exhibit highly variable responses to disturbance, reflecting differences in stand structure, composition, and successional dynamics across environmental gradients (Larson and Kipfmueller 2012; Seidl and others 2014; Holtmeier and Broll 2018; Thom and Seidl 2022). MPB outbreaks can cause substantial shifts in stand structure, as medium to large trees are disproportionately killed and seedling and sapling densities increase (Meyer and others 2016). Other research has documented sustained regeneration, moderate cone production, and structurally diverse stands following MPB outbreaks, as well as a lack of successional replacement by more shade-tolerant species despite prolonged mortality from multiple stressors (Amberson and others 2018; Meyer and others 2023). These findings suggest that WBP forests may exhibit low resistance but high resilience to MPB outbreaks and underscore the importance of structural and compositional diver-

sity in shaping post-disturbance stand development and long-term ecosystem recovery (DeRose and Long 2007; Windmuller-Campione and others 2017).

Rising temperatures have been linked to increased bark beetle activity, particularly in high-elevation forests (Bentz and others 2016; Buotte and others 2016), but warming may also enhance tree growth and establishment where temperature currently limits productivity (Harsch and others 2009), potentially creating both risks and opportunities for forest development in coming decades. For instance, WBP trees have responded positively to regional warming, exhibiting increased growth and defense (Kichas and others 2023), suggesting that warming temperatures may promote enhanced vigor and resilience within high-elevation WBP populations. Similar temperature-driven growth increases have been observed in WBP populations in the Sierra Nevada (van Mantgem and others 2023) and in high-elevation bristlecone pine (*Pinus longaeva* D.K. Bailey) populations in California and Nevada since the late twentieth century (Salzer and others 2009; Bunn and others 2018). However, WBP growth is also governed by lagged moisture availability and temperature variability, with controls shifting from temperature limitation to drought stress under changing climate regimes (Wong and Daniels 2017). These shifts can increase susceptibility to pathogens and bark beetles, elevating mortality. Collectively, these findings underscore that climate–disturbance interactions shape long-term dynamics in high-elevation forests and highlight the importance of understanding how surviving trees mediate post-disturbance trajectories across subalpine ecosystems.

We examined how a MPB outbreak, spanning from the 1970s through the 1980s, affected WBP growth and recruitment within the Greater Yellowstone Ecosystem (GYE), USA. Given that MPB typically target larger trees (those over 20–25 cm DBH) (Safranyik and Carroll 2006), our study aimed to: (1) assess whether live small-diameter (< 25 cm DBH) WBP experienced a growth release following the subsequent changes in canopy structure, and (2) compare relationships between stand structure, climate, and WBP growth in MPB-impacted stands to those in adjacent unimpacted stands. We hypothesized that MPB outbreaks act as a natural thinning agent and that surviving WBP trees would experience a release in radial growth with a concomitant increase in WBP recruitment, due to reduced intraspecific competition and increased resource availability stemming from changes to the canopy structure. Results provide much needed information on the potential for WBP forests to be resilient to naturally occurring MPB outbreaks via triggering growth release in smaller-diameter WBP, which is particularly important for forest managers tasked with conserving and restoring WBP ecosystems in the GYE and throughout WBP's native range.

Methods

Study Area Description and Site Selection

Data were collected in 2012 across five different sites in the Custer Gallatin National Forest, Montana, USA (Figure S1), approximately 31 years after an MPB outbreak affected the area. The broader region experienced extensive MPB activity from the 1970s through the 1980s (Harley and others 2019) and additional bark beetle activity in the early 2000s (Buotte and others 2016). Using historic Forest Health Protection aerial survey imagery collected between 1971 and 1990 (obtained from the US Forest Service Bozeman District Office), we identified five sites along the Gallatin Crest that exhibited substantial canopy change over approximately a ten-year period attributable to MPB-caused mortality. The five identified sites contained multiple stands of pure or mixed WBP along with subalpine fir (*Abies lasiocarpa* (Hook.) Nutt), Engelmann spruce (*Picea engelmannii* Parry ex Engelm.), and lodgepole pine (*Pinus contorta* Dougl. var. *latifolia* Engelm). Each of the five sites is approximately 16 hectares, covering roughly 80 hectares total across the study region. Within each site, we defined an unimpacted unit (no overstory mortality; ''unimpacted'') and an impacted unit (MPB-caused mortality; ''impacted'') for a total of ten units (five unimpacted units and five impacted units). The impacted/unimpacted units were generally around eight hectares in size but varied across sites depending on topography and WBP availability (Table S1). While bark beetle outbreaks typically occur over several years, we identified 1981 as the peak year of the outbreak based on aerial imagery of the study region. Over this time period, we observed a majority of trees in the red needle phase with complete defoliation by the late 1980s/early 1990s.

Data Collection and Sample Preparations

At each of the five sites, up to 25 of the visibly healthiest live WBP trees between 10 and 25 cm

DBH were randomly sampled in both unimpacted and impacted units. To determine tree age and growth rate, we collected two 4.3 mm increment cores from each sample tree, with the first core collected at breast height (~ 1.37 m) and the second core collected approximately 30 cm below the first. To evaluate potential growth release of residual trees following the MPB outbreak, we focused on trees 10–25 cm DBH and hypothesized that these individuals could have recruited into this size class during the ~ 30 years since disturbance. Trees in this intermediate size class are ecologically and operationally important: They often function as replacement or recruitment trees in silvicultural treatments and contribute to post-disturbance resilience by buffering mortality of older cohorts, thereby maintaining population continuity following disturbance (Long and others 2018; Schoettle and others 2018; Seidl and Turner 2022; Tomback and others 2022). In choosing the healthiest trees, we tried to minimize confounding variables that might affect tree growth, including WPBR, irregular growth form, broken tops, or clear signs of insect or animal damage. Additional measurements included the height at which the increment cores were collected, diameter at core height, growth form (isolated single stem versus clumped stems), and WPBR infection status. Clumps were defined as multiple stems fused at the root collar, a growth form characteristic of establishment from Clark's nutcracker (*Nucifraga columbiana*) seed caching behavior in which multiple seedlings germinate in close proximity and fuse as they grow. WPBR infection status was recorded as the number of cankers, their location on branches or bole, and whether infections were classified as active or inactive.

To characterize neighborhood structure and composition, at every fifth sampled WBP tree, we established a 15.24 m × 0.91 m belt transect plot oriented along a randomly selected azimuth, with the sampled tree marking the back edge of the plot. Within each belt transect, we tallied all live trees by height class (< 10 cm; 10–49.9 cm; 50–99.9 cm; 100–140 cm; and > 140 cm, including overstory trees). At the center of the belt transect, 7.62 m from the sampled WBP tree, we recorded species and DBH information for neighboring live and dead trees (both WBP and non-WBP) using a basal area factor (BAF) 20 angle gauge to estimate neighborhood competition and also estimated canopy cover using a spherical densiometer, averaging measurements taken in four cardinal directions. This approach was chosen to efficiently characterize the local neighborhood structure and competitive environment under the logistical constraints of small field crews, distances hiked to selected sites, processing of samples in the field, and unreliable site access during active fire seasons. Narrow belt transects anchored at the base of randomly selected live WBP trees provided a targeted and repeatable measure of immediate neighborhood conditions within areas where live WBP occurred, which were often patchy and irregularly distributed across stands. A broader, stand-level sampling design may not have intersected areas containing live WBP, whereas the focal-tree-based belt transects ensured that neighborhood structure was quantified in ecologically relevant locations while requiring substantially less time and effort than fixed-area plots, concentric designs, or distance-based competition indices.

We collected 412 increment cores from 109 WBP in unimpacted units and 107 WBP in impacted units (216 WBP total) and established 41 belt transect plots (3–5 belt transect plots/unit). At each of the five sites, we also collected one increment core from approximately six overstory trees (WBP and non-WBP) to support chronology development, resulting in an additional 31 cores. All cores were air-dried, prepared, and processed using standard dendrochronological techniques (Cook and Kairiukstis 1990; Stokes and Smiley 1996). Ring widths were measured to the nearest 0.001 mm using a Velmex measuring stage interfaced with the recording software Measure J2X (Voortech Consulting 2005). Tree-ring series were crossdated visually and graphically using ring width patterns and frost rings and were statistically checked using COFECHA (Holmes and others 1986).

Although observed WPBR was relatively low across the unimpacted and impacted units in 2012, we identified 35 pairs of trees with and without WPBR symptoms (35 diseased trees and 35 disease-free trees of similar size) and looked for differences in tree growth. Trees were paired based on diameter (< 3 cm difference) and distance (within the same impacted or unimpacted unit) to control for potential differences in ontogeny and microsite variability. Lastly, from the forest structure and competition data, we calculated metric stand density index (SDI) (Reineke 1933) and evaluated relationships between SDI, basal area (total, live, dead, inter- and intraspecific basal area), canopy cover, competitor height class, and WBP growth.

Monthly climate data were obtained from the parameter-elevation regressions on independent slopes model (PRISM) in the absence of instrumental weather records at the study sites (Daly and

others 1994; Kipfmueller and Salzer 2010). We extracted monthly minimum, mean, and maximum air temperature (°C) and total precipitation (mm) at a 4 km spatial resolution using the PRISM AN dataset (Abatzoglou and others 2017). Monthly climate data were aggregated into annual and seasonal windows to evaluate tree growth responses to seasonal variability. For temperature, seasonal groupings included a warm season (May–September), spring (March–May), and summer (June–August). For precipitation, we additionally considered a cool season (prior-year October–April), and water year (prior-year October-September), which better capture snowpack accumulation and soil moisture availability relevant to high-elevation forests. To assess climate-growth relationships in relation to MPB disturbance, climate data were divided into two time periods: a pre-outbreak period (1950–1980) and a post-outbreak period (1982–2012). These intervals correspond to the 31 years preceding and following the peak MPB outbreak year (1981) and align with the temporal extent of available tree-ring data used in subsequent growth analyses.

Data Analysis

To address our two primary research objectives, first we determined whether live small-diameter (< 25 cm DBH) WBP trees were present during the MPB outbreak or established in subsequent decades, using dendrochronology to estimate tree age and establishment dates. Results of these preliminary analyses are provided in the supplemental information (Text S1, Figures S2-S4, Table S2).

All statistical analyses were conducted in R (version 4.5.0) (R Development Core Team 2008). We used correlation analyses, analysis of variance (ANOVA), multivariate techniques, and *t*-test analyses to examine differences in tree growth between unimpacted and MPB-impacted units. To quantify the influence of the MPB outbreak on WBP growth, we calculated a growth ratio defined as the mean difference between the 31-year pre-outbreak period (1950–1980) and the 31-year post-outbreak period (1982–2012), centered on the 1981 outbreak peak. Tree growth was quantified using basal area increment (BAI; $cm^2\ year^{-1}$), calculated with the *bai.out* function in the *dplR* package (version 1.75), and a standardized, unitless ring width index (RWI). The RWI chronologies were developed using interactive detrending with the *i.detrend* function to remove age-related growth trends while preserving climate-related variability (Bunn 2008). For RWI, each tree-ring series was fitted with a negative exponential curve or a flexible spline with a frequency response of 75% of the series length to remove geometric growth trends (Fritts 1976). Conservative detrending methods were applied to preserve multi-decadal variability in the ring width series (Cook and Kairiukstis 1990; Cook and Peters 1997), as such low-frequency signals may capture important climate influences, disturbance response, and stand dynamics (Briffa and others 1992). Climate analyses were performed using the detrended RWI series and the *seascorr* and *dcc* functions in the *treeclim* package (version 2.0.6) and the *monthly_response_seascorr* function from the *dendroTools* package (version 1.2.10).

We used generalized linear mixed models (GLMM) with a Gamma distribution and log link function to evaluate predictors of post-outbreak tree growth (BAI). All continuous predictors were standardized (mean = 0, SD = 1) to improve model convergence and interpretability. Site (e.g., GTL, PCR, SHL) was treated as a random effect. To assess collinearity among candidate predictors, we examined Pearson correlation coefficients and variance inflation factors. Height-class variables were highly correlated, so we used principal component analysis and retained the first two principal components for modeling. Model selection was based on AICc (*MuMIn::dredge*) to identify a parsimonious subset of predictors. Model fit was evaluated using marginal and conditional R^2 values, representing variance explained by fixed effects alone and by both fixed and random effects, respectively. Residual diagnostics were conducted using the *DHARMa* package; the final models passed all key checks (Kolmogorov–Smirnov, quantile deviation, and outlier tests), indicating good model fit.

Results

Effects of Mountain Pine Beetle Outbreaks on Tree Growth

WBP tree growth was relatively similar across MPB-impacted and unimpacted units from 1608 through around 1780, at which point growth in impacted units declined relative to unimpacted units and remained lower through 1980. However, post-1981 growth in the impacted units increased substantially relative to the unimpacted units and remained higher through the end of the sampling period in 2012 (Figure 1). When comparing tree growth from the 31 years pre-outbreak (1950–1980) to the 31 years post-outbreak (1982–2012), we found that impacted WBP experienced a 61%

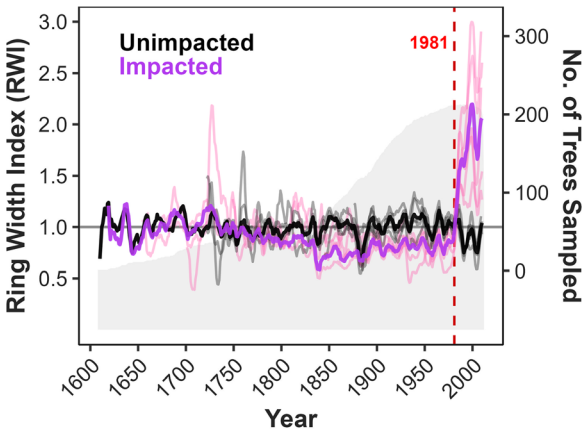

Figure 1. Time series of the ring width index (RWI) from 1608 to 2012. The RWI series were developed from 216 WBP trees sampled across unimpacted units (black) and impacted units (purple), with light black lines corresponding to the five separate unimpacted units and light purple lines corresponding to the five separate impacted units. The gray horizontal line represents average growth for the RWI series. The dashed red line reflects the 1981 peak outbreak year identified through aerial imagery. Gray background shading reflects sample depth over time.

increase in BAI (54% increase for RWI), while unimpacted trees experienced an 8% increase in BAI (9% reduction in RWI). This pattern of increased growth (both RWI and BAI) in the impacted units relative to the unimpacted units held across all five sites (Figures 2A, S5). Tree size was positively related to growth release, but not age, in the impacted units, while growth ratio was unrelated to both size and age for trees in the unimpacted units (Figure 2B, C). Data from the overstory trees indicate that some non-WBP individuals exhibited increased growth (positive BAI ratio values) during the 31-year post-outbreak period, although the sample size was small (31 cores) and substantial variability was observed both within and among sites (Figure S6).

We noticed subtle differences in the relationships between tree growth (RWI and BAI), tree size (DBH), and tree age between impacted and unimpacted WBP. RWI and BAI were positively related to tree size in impacted trees, but in unimpacted trees only BAI was related to size (Figure 3). Total, pre-outbreak, and post-outbreak RWI and pre-outbreak BAI were positively related to tree age in impacted units but unrelated in unimpacted units (Figure 3).

Factors Influencing WBP Tree Growth

Competition and Stand Structure

Live tree basal area was higher in unimpacted units 31 years post-outbreak, whereas impacted units had higher basal area of dead trees (Table 1). Mortality was substantially higher in impacted units (68%) compared to unimpacted units (29%). Impacted units had lower stand densities of live trees, as indicated by Reineke's stand density index (SDI) and trees per hectare, with lower canopy cover (47%) relative to unimpacted units (76%; Table 1).

Pre-outbreak BAI and condition (impacted vs. unimpacted) were the strongest predictors of post-outbreak growth (Table 2). These variables were consistently statistically significant across all top models. Across the unimpacted and impacted units, differences in BAI between the pre- and post-outbreak periods alone explained considerable variance ($\sim$ 85%) in the tree-ring record (Figures 4, S7).

Two competing models were identified within ΔAICc < 2 of the top-ranked model, incorporating the additional structural predictors of mortality (ΔAICc = 0.84) and PC2 (ΔAICc = 0.88). Among these, mortality exhibited the highest relative variable importance across the top model set but was not statistically significant in its best-supported model ($p = 0.298$). In contrast, PC2 was a significant negative predictor ($p = 0.017$; Table S3). PC2 was derived from a principal component analysis of height-class structure, with positive loadings corresponding to larger conspecific trees and negative loadings associated with the smallest height class, reflecting a gradient in vertical structure. The GLMM including mortality had a conditional R^2 of 0.729 and a marginal R^2 of 0.674, while the PC2 model had a conditional R^2 of 0.715 and a marginal R^2 of 0.682, indicating that most of the explained variance was attributable to fixed effects (Tables 2, S3; Figure S8).

Ecological variables of SDI, trees per hectare, canopy cover, interspecific basal area, and tree age showed only modest associations with post-outbreak BAI in exploratory models, and none consistently improved model performance or appeared in top-ranked candidate models based on AICc. This suggests that pre-disturbance growth and competitive pressure from conspecific neighbors were more influential drivers of post-treatment growth than stand structure or species composition alone.

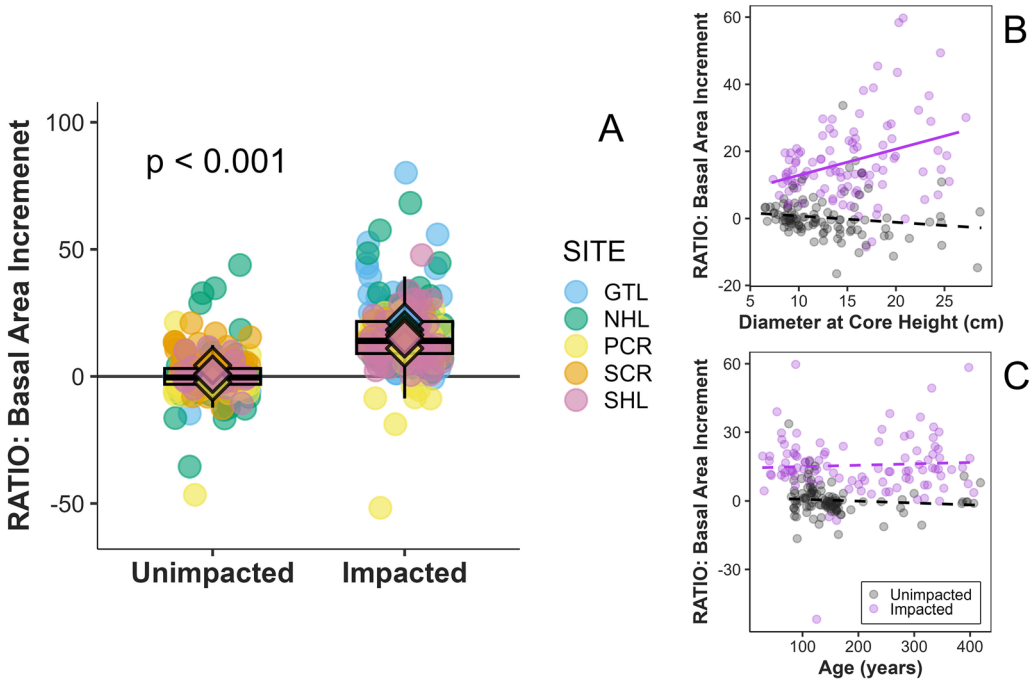

Figure 2. (**A**) Boxplot comparison of the ratio of tree growth (31 years post-outbreak—31 years pre-outbreak) for basal area increment (BAI; cm^2 $year^{-1}$) across the unimpacted (left) and impacted (right) units, with the different sites represented by different colors and the mean age for each unimpacted and impacted unit depicted as a diamond (colored by site). Positive values indicate greater growth in the post-outbreak period. Boxes denote first and third quartiles, lines the median, and whiskers the 1.5 interquartile range. The reported *p*-value is from the nonparametric Wilcoxon rank-sum test comparing the ratio of tree growth (BAI) across the unimpacted and impacted units. Scatterplot panels (right) show relationships between the ratio of tree growth (BAI) and (**B**) diameter at core height (cm), and (**C**) tree age (years). Solid lines denote significant regression relationships ($p < 0.05$), while dashed lines denote nonsignificant relationships based on linear models.

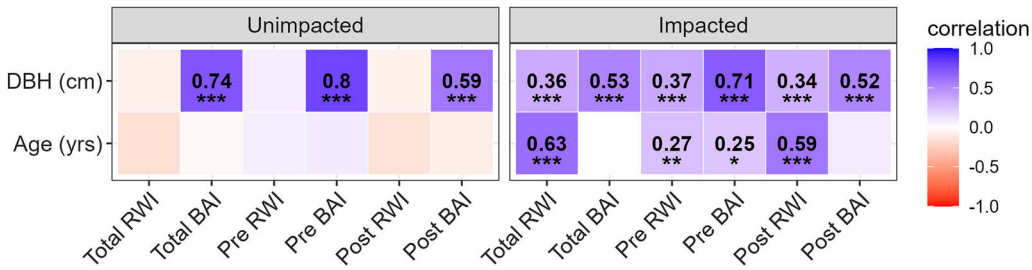

Figure 3. Spearman correlation coefficients for WBP tree growth (RWI; unitless ring width index and BAI; basal area increment; cm^2 $year^{-1}$), tree size (DBH; cm) and tree age (years). Total RWI and Total BAI reference the full time series, while Pre RWI and Pre BAI encompass the 31 years prior to the mountain pine beetle outbreak (1950–1980) and Post RWI and Post BAI encompass the 31 years post-outbreak (1982–2012). Correlations are only displayed if statistically significant at the $\alpha < 0.05$ level.

Blister Rust (WPBR) and Tree Growth Form (Isolated Stems versus Clumped Establishment)

In 2012, 17% of sampled WBP trees had signs or symptoms of WPBR (37 out of 216 trees; 19 trees in the impacted units and 18 trees in the unimpacted units) with active symptoms on 24 trees and inactive symptoms on 13 trees. For the 35 pairs of diseased and disease-free WBP trees, we did not detect any difference in growth rate pre- and post-outbreak (Figure S9; RWI $p = 0.981$; BAI $p = 0.7$). However, when considering growth form (e.g., WBP trees growing in clumps and those growing as isolated single stems), we found that WBP tree growth was 33% greater in the post-outbreak period for trees growing in clumps relative to single

Table 1. Summary of Average Stand-Level Structural Metrics Derived from Neighborhood Competition Measurements Collected in Belt Transects Established at Every Fifth Sampled WBP Tree

Metric	Unimpacted	Impacted	*p*-value
Basal Area (m^2 ha^{-1})	**49.5** (± 2.1)	38.7 (± 1.2)	*< 0.001* ***
Basal Area (non-WBP)	**18.9** (± 0.9)	5.2 (± 0.7)	*< 0.001* ***
Basal Area (WBP)	**20.1** (± 2)	6.8 (± 0.4)	*< 0.001* ***
Basal Area (Live)	**39** (± 2.2)	11.9 (± 0.6)	*< 0.001* ***
Basal Area (Dead)	10.6 (± 0.5)	**26.6** (± 1.4)	*< 0.001* ***
Mortality (%)	29 (± 2.4)	**68** (± 1.5)	*< 0.001* ***
SDI (Metric)	1,775 (± 113.9)	1,431 (± 46.8)	0.729
Canopy Cover (%)	**76** (± 1)	47 (± 1.4)	*< 0.001* ***
Trees per Hectare (Total)	**1,733** (± 138)	809 (± 38)	0.017 *
Trees per Hectare (non-WBP)	**779** (± 46)	157 (± 30)	*< 0.001* ***
Trees per Hectare (WBP)	940 (± 94)	652 (± 35)	0.899

Reported values include total basal area (m^2 ha^{-1}), basal area attributed to interspecific (non-WBP) and intraspecific (WBP) competition, live and dead trees, percent mortality, Reineke's stand density index (SDI; metric), canopy cover (%), and tree density (trees ha^{-1}). P-values indicate statistically significant differences between unimpacted and impacted units ($\alpha < 0.05$) based on Wilcoxon rank-sum tests; bold text indicates the larger value between groups.

Table 2. Top Three Generalized Linear Mixed Models Predicting Post-Outbreak Basal Area Increment (BAI; cm^2 $Year^{-1}$) for WBP

Rank	Model	logLik	AICc	ΔAICc	Weight	R^2
1	Post_BAI ~ Pre_BAI + Condition	−179.65	369.6	0	0.291	0.691
2	Post_BAI ~ Pre_BAI + Condition + Mortality	−179.01	370.4	0.84	0.191	0.729
3	Post_BAI ~ Pre_BAI + Condition + PC2	−179.03	370.5	0.88	0.187	0.715

Models were ranked using Akaike's information criterion corrected for small sample sizes (AICc). Shown are model parameters, log-likelihood (logLik), AICc score, ΔAICc (difference from the top model), Akaike weight (model support), and conditional R^2 (proportion of variance explained by both fixed and random effects). Condition = unimpacted (0) or impacted (1) by MPB. PC2 was derived from a principal component analysis of height-class structure.

stem trees for both RWI ($p = 0.016$) and BAI ($p = 0.012$; Figure S10).

Climate Relationships

Following the MPB outbreak, trees in the impacted units were more sensitive to temperature (particularly minimum temperature) and precipitation. We observed a significant shift in the relationship between tree growth and temperature, with growth negatively correlated with annual, summer, and warm-season temperatures during the pre-outbreak period (1950–1980), but strongly positively correlated with those same seasonal temperatures in the post-outbreak period (1982–2012; annual average: $r = 0.53$; $p = 0.002$ / warm season: $r = 0.52$; $p = 0.003$ / summer: $r = 0.42$; $p = 0.019$; Figure 5). August, September, and October minimum temperatures exhibited the strongest positive relationship with WBP growth ($r = 0.42$; $p = 0.019$, $r = 0.53$; $p = 0.002$, and $r = 0.36$; $p = 0.049$, respectively), whereas we observed weak to negative relationships for all monthly and seasonal temperatures in the unimpacted units (Figure 5). These same patterns were present, albeit weaker when considering average and maximum temperature, with September continuing to exhibit the strongest positive relationship with tree growth in the impacted units (Figure 5).

In the impacted units, precipitation–growth relationships shifted toward more negative correlations following the outbreak, with statistically significant reversals from positive to negative correlations occurring in July and September (July: $r = -0.46$; $p = 0.009$ / September: $r = -0.50$; $p = 0.004$). Although annual, warm-season, and water-year precipitation also showed similar directional shifts, these relationships were not statistically significant. No comparable patterns were observed in the unimpacted units (Figure 5).

Discussion

Effects of Mountain Pine Beetle Outbreaks on Tree Growth

Across the five sites, we observed a significant release in WBP radial growth in units that were im-

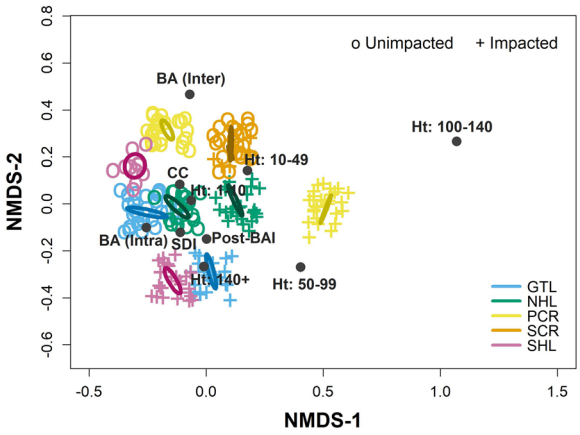

Figure 4. Nonmetric multi-dimensional scaling (NMDS) ordination of tree growth (basal area increment, BAI) during the post-outbreak period (1982–2012) for impacted (+) and unimpacted (O) units, based on 216 live WBP trees. Black dots represent forest structural and compositional variables positioned in ordination space relative to tree growth. Variable abbreviations: BA (Inter) = interspecific basal area (m^2 ha^{-1}); BA (Intra) = intraspecific basal area; CC = canopy cover; SDI = stand density index (metric). Height-class variables (Ht) correspond to live WBP tree counts in the following ranges: Ht 1–10 (1–10 cm), Ht 10–49 (10.1–50 cm), Ht 50–99 (50.1–100 cm), Ht 100–140 (100.1–140 cm), and Ht 140 + (> 140 cm). Ellipses are 95th percentile CIs for each grouping. Stress = 0.141; two-dimensional solution.

pacted by a MPB outbreak event (peaking in 1981), which persisted for 31 years to our sampling in 2012 (Figures 1, 2). Reduced intraspecific competition within the MPB-impacted units, as well as altered canopy characteristics, including mortality of larger diameter dominant and codominant trees, increased access to resources promoting enhanced growth following the MPB outbreak (Kichas and others 2020). It is probable that greater sunlight availability was also beneficial to competing Engelmann spruce and subalpine fir and that, over time, these more shade-tolerant species may overtop and outcompete WBP in the absence of additional disturbance.

The vast majority (> 99%) of the sampled smaller-diameter WBP (< 25 cm DBH) were already established before the outbreak (Text S1, Figure S2). These smaller trees survived or escaped the outbreak that killed larger trees (> 25 cm DBH) and subsequently experienced a significant release in growth in the following decades. Interestingly, WBP trees in the impacted units were growing more slowly over the majority of the record, relative to similarly sized trees in the unimpacted units, and these impacted areas were most notably affected by the MPB outbreak event (Figure 1). This suggests that forest stands with slower growing trees were more susceptible to MPB. One explanation is that smaller, subhost size WBP in impacted units escaped attack and persisted through the outbreak, but were inherently slower growing than the larger trees that were preferentially killed. Alternatively, impacted units may have supported higher pre-outbreak densities of large, dominant WBP, which both increased host availability (i.e., more resources to sustain MPB populations) and suppressed growth of subordinate trees through competition and overstory shading. Under this scenario, greater host abundance would help explain the high mortality observed in aerial imagery, while reduced pre-outbreak growth rates would reflect resource limitation in more densely structured stands. Our data are not designed to directly test how growth affected MPB susceptibility, as we did not assess growth rates in larger-sized trees that were killed in the MPB outbreak, nor record site-level mortality data, in terms of number and size of trees that were killed during the outbreak, relative to the live trees that were sampled. While it is difficult to fully ascertain from our tree-ring records, the fact that we sampled trees randomly throughout the unimpacted and impacted units does indicate that stands of slower growing trees were more susceptible to bark beetle activity, but surviving trees in these stands were capable of significant growth releases in the years following the outbreak (Figures 1, 2). Although the sampled WBP were relatively small in diameter (< 25 cm DBH), most individuals (78%) were more than 100 years old and nearly one-third (30%) exceeded 200 years, yet still exhibited substantial growth release in impacted units (Figure 2). This finding is consistent with evidence that even physiologically mature trees can respond strongly to reductions in competition (Keane and others 2007; Kichas and others 2024). While younger individuals are often assumed to show greater release due to higher trait plasticity (Retzlaff and others 2018), the pronounced release observed among these older trees highlights the capacity of WBP to respond dynamically to disturbance even at advanced ages (Figure 2C). Within the impacted units, however, growth release increased with tree size (DBH), indicating that larger stems, independent of chronological age, experienced greater post-disturbance growth responses (Figure 2B).

Growth rate is a complicated metric for assessing WBP susceptibility to beetle-related mortality, and other traits may be more informative. Several studies have documented a range of growth rate

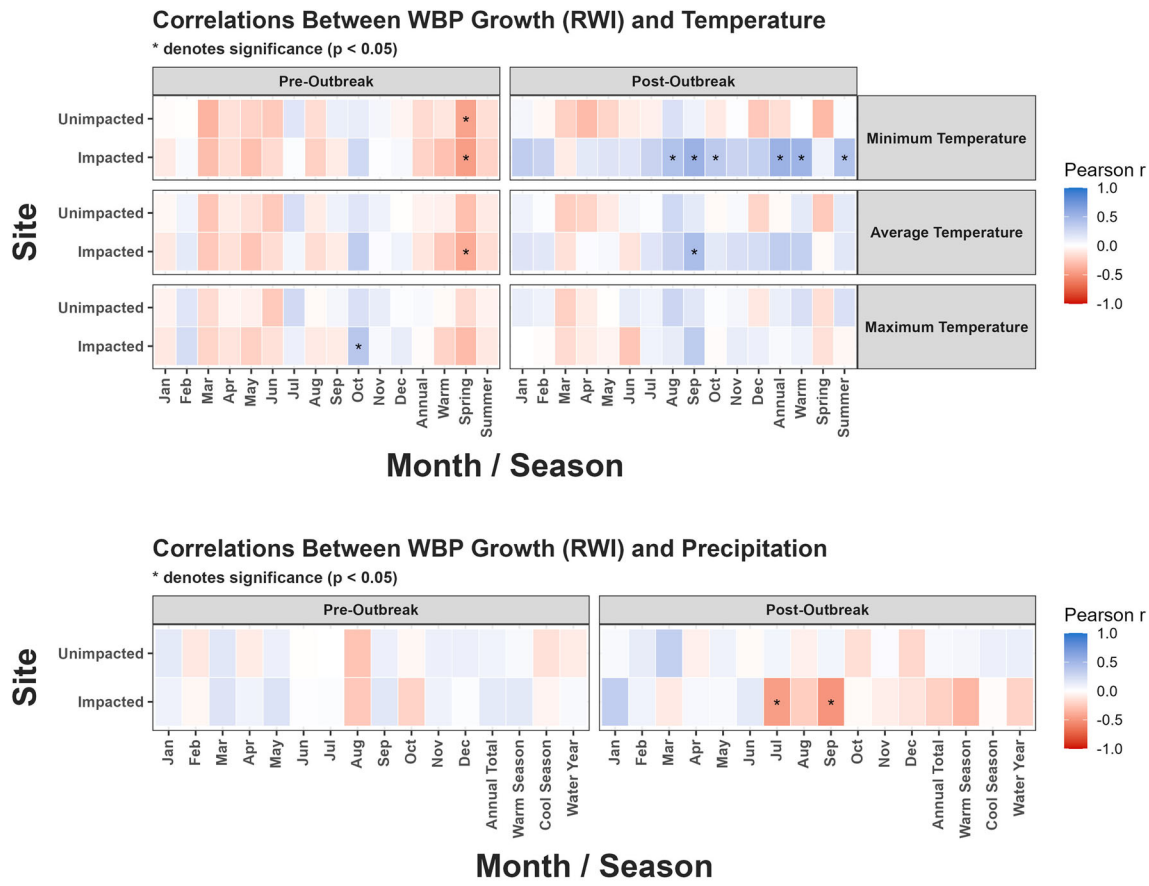

Figure 5. Pearson correlation coefficients for tree growth (unitless ring width index; RWI) and monthly and seasonal climate values for [top] temperature (minimum, average, and maximum °C), and [bottom] precipitation (mm) during the pre-outbreak (1950–1980) and post-outbreak (1982–2012) periods. Unimpacted sites experienced little overstory mortality during the outbreak, while impacted sites had extensive mortality. Blue shading indicates positive correlations while red shading indicates negative correlations. The asterisk (*) indicates significance at $\alpha < 0.05$ from Pearson correlation tests (*t*-test of the correlation coefficient).

configurations, both prior and up to MPB outbreaks, with no clear indicator for predicting tree survivability. For example, Kichas and others (2020) found that WBP trees persisting through MPB outbreaks had lower growth rates compared to trees that died over the full ~ 100 year chronology. However, 20 years prior to mortality, these residual live trees demonstrated greater growth than trees that had died. Similar investigations (Six and others 2021; Margoles 2011) where MPB-killed trees displayed initial rapid ring growth that later slowed or was equal to surviving trees further highlight the spectrum of growth rate potentials. Consequently, the nuance of these relationships emphasizes our inability to establish generalizable associations in tree growth preceding mortality and warrants ongoing research to better understand these correlations over a diverse array of species and environments, particularly in light of changing biotic and abiotic pressures. WBP resistance to MPB may also be more related to tree defenses than growth rates. For instance, Kichas and others (2020, 2021, 2023, 2024) found positive relationships between WBP tree growth and resin duct defenses, suggesting that trees bilaterally invest in both growth and defense. Notably, resin duct defenses were more important in predicting WPB survival than growth (Kichas and others 2020). Additionally, Six and others (2018) found that WBP trees that persisted through MPB outbreaks had a distinct genetic structure, suggesting that survivability is a heritable trait and that beetles select against such trees even under outbreak scenarios. As such, it is imperative to maintain within-stand genetic diversity insomuch as possible when considering restoration treatments in WBP and other forest ecosystems, as trees persisting through bark beetle outbreaks or other environmental

stressors are best adapted to withstand future disruptive pressures and pass on these genetic characteristics to their progeny.

Factors Influencing WBP Tree Growth

Competition and Stand Structure

Understanding how stand-level factors influence WBP growth is critical for informing effective restoration strategies. Pre-outbreak growth and stand condition (impacted vs. unimpacted) were the most consistent and significant predictors of post-outbreak tree growth (Tables 2, S3; Figures S7-S8), indicating that faster-growing WBP were better able to capitalize on release following disturbance. Although this pattern has been observed in other tree species (Roberts and Harrington 2008; Moreau and others 2022; Ara and others 2023), it has rarely been demonstrated in WBP, underscoring the importance of promoting healthy, structurally diverse WBP stands, comprised of multiple age and size classes, to enhance both resistance to MPB and recovery following disturbance or management intervention. Among structural variables, overstory mortality exhibited high relative importance across the top growth predicting model set and had a positive effect estimate, suggesting that beetle-induced mortality may enhance post-outbreak growth by reducing competition and increasing resource availability. While mortality was not statistically significant in its best-supported model ($p = 0.298$), its consistent inclusion in top models supports its role as a potentially influential driver of post-disturbance growth dynamics. PC2, derived from a principal component analysis of height-class structure, was a significant negative predictor ($p = 0.017$), suggesting that the presence of taller conspecific trees may suppress growth of surviving individuals, likely through competition for light and other resources. This highlights the complex role of competition in shaping post-outbreak trajectories. In unimpacted units, greater total basal area, reflecting higher competition from both conspecific and interspecific trees, was associated with reduced WBP growth. Conversely, in impacted units, lower canopy cover and reduced tree densities appeared to alleviate competitive pressures and promote increased growth rates in residual WBP following the outbreak event (Table 1, Figures 1, 2). It should be noted that we did not sample stand density or record any competition metrics prior to the MPB outbreak event, so it is possible that pre-outbreak densities and competition dynamics within the impacted areas could have influenced the response of surviving trees to changes in stand structure, as has been found in other research (Keane and others 2007; Maher and others 2018). Such observations are perhaps unsurprising for a shade-intolerant species but are important considerations for understanding WBP dynamics over time and with fluctuating pressures from MPB. Though investigating within-stand competition dynamics was not a direct objective of this study, future research should consider stand characteristics and the growth response of a range of species to MPB outbreaks in WBP ecosystems and establish repeat monitoring to better understand these dynamics over longer time periods.

Blister Rust (WPBR) and Tree Growth Form (Isolated Stems versus Clumped Establishment)

We did not detect any differences in WBP tree growth in the 31 years following the MPB outbreak for WPBR diseased/disease-free trees (Figure S9). This suggests that WPBR did not readily influence tree growth or tree vigor prior to our 2012 sampling. However, we do not know when WPBR infection occurred relative to our sampling, so we cannot quantify how infection may influence growth in trees also impacted by MPB outbreaks. In addition, while WPBR prevalence was relatively low across our sample sites in 2012, Thoma and others (2019) found prevalent WPBR infection in cone-bearing WBP trees throughout the GYE from 2000 to 2018 and reported that larger WBP trees were more likely to be infected under warmer August/September temperatures and more humid conditions. Ongoing monitoring of WPBR, particularly in areas that have also experienced MPB activity, will be critical in prioritizing areas for management and evaluating the success of conservation and restoration programs under changing climate and disturbance regimes.

Regarding growth form, we observed a greater post-outbreak growth release in WBP growing in clumps relative to trees growing as isolated stems (Figure S10). The increased growth could be due to increased canopy cover and enhanced photosynthesis promoting increased production and storage of carbohydrates. This contrasts with Kichas and others (2024), who reported no difference in growth responses between clumped and isolated WBP stems during the nine years following mechanical thinning treatments in eastern Idaho. While we observed a greater growth release in these clumped trees, managers should strive to retain most WBP, regardless of growth form, in restoration treatments where feasible (Kichas and

others 2024). More importantly, preserving within-stand genetic diversity and high-vigor cone-bearing trees is the best strategy for increasing adaptability of WBP forests to future disruptions.

Climate Relationships

We found that WBP trees growing in areas affected by the MPB outbreak showed increased sensitivity to minimum temperature in the 31 years following the outbreak (Figure 5). WBP in the impacted units exhibited strong positive relationships with tree growth, annual average minimum temperature, and warm season/spring minimum temperature, whereas WBP trees growing in the unimpacted units showed weak but negative relationships. We speculate that the positive response of WBP to increased minimum temperatures in the stands affected by the MPB outbreak reflects increased availability of sunlight and resources conducive to photosynthesis facilitating enhanced growth of surviving trees. These findings suggest that changes in canopy structure following MPB outbreaks boost the growth response of trees to climate, particularly warm-season (May–September) temperature. Other research has found similar temperature-driven increases in WBP radial growth, indicating that these are largely energy-limited ecosystems (Dudney and others 2023; Kichas and others 2023). Interestingly, we did not detect such relationships within the unimpacted units, which suggests that MPB-mediated changes in stand structure are important for adapting WBP stands to changing abiotic conditions. Following the outbreak, tree growth in impacted units shifted to a negative correlation with July and September precipitation. We interpret this counterintuitive pattern as reflecting the energy-limited nature of high-elevation WBP forests, where growth is constrained more by temperature and solar radiation than by water availability. The positive response to warm-season temperature indicates that high-elevation WBP forests benefit from warm, sunny conditions that enhance photosynthesis and growth. Conversely, periods of elevated precipitation in the warm season are typically associated with cooler, cloudier weather that constrains photosynthesis. This could be useful for managers in prioritizing treatment areas, as WBP trees growing within sites previously affected by MPB outbreaks are naturally and positively responding to enhanced warm-season temperature. However, future studies should continue to investigate relationships between climate and WBP growth throughout the full range of WBP habitat, particularly across changes in latitude, to ensure maximum compatibility between treatment prescriptions and shifting environmental conditions. For instance, it is possible that declining regional snowpack in the northern Rocky Mountains (Pederson and others 2009, 2011, 2013; Schoenemann and others 2020) will intensify tree stress, as WBP and other high-elevation plants will deplete soil moisture earlier in the summer due to photosynthesis and transpiration, leading to increased drought stress in late summer. As temperatures continue to rise, more frequent and severe drought conditions in these high-elevation ecosystems will likely hinder WBP growth and heighten vulnerability to MPB infestations and WPBR.

Conclusion

Overall, we found strong evidence that MPB acted as a biotic thinning agent, by reducing intraspecific competition and altering canopy structure in ways that increased growth of surviving trees within stands affected by a MPB outbreak event. It is important to note that our results generally pertain to trees between 10 and 25 cm in diameter; however, it is likely that smaller trees persisting through bark beetle outbreaks will grow into this size class in the following years in the absence of repeat disturbance, as smaller-diameter WBP exhibit a remarkable capacity for growth release following disturbance (Kichas and others 2024). Trees within this size class are also more likely to begin producing cones and are thus desirable for resource managers to protect due to their importance in restoration efforts. Additionally, WBP that survived the MPB outbreak across our study region appear to be better adapted to changing climate, exhibiting a positive growth response to increasing minimum temperature. Managers tasked with conserving and promoting WBP could consider legacies of MPB activity in the designation of treatment areas and utilize footprints of previous outbreaks that have smaller sized WBP in conservation and restoration planning efforts. Our research suggests that areas with smaller WBP are more resilient to MPB outbreaks, as advanced regeneration can rapidly capitalize on increased resources made available by the mortality of larger individuals. In contrast, areas without smaller WBP would take decades longer to regenerate after severe outbreaks, underscoring the importance of heterogeneous, mixed-age stands, as observed in other ecosystems (Windmuller-Campione and others 2017; Long and others 2018). This is particularly relevant in jurisdictions where management activities, including artificial planting

and prescription treatments, are less likely to occur, either due to agency philosophies limiting managerial interventions or in areas with complex topography where management activity is difficult and costly. Wherever possible, preserving within-stand genetic diversity is important, as trees that have persisted through outbreak events are best adapted to changing biotic and abiotic disturbance.

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DATA AVAILABILITY

The data used for this research are available in the ITRDB (International Tree-Ring Data Bank) at https://doi.org/10.25921/sajj-ex88.

Declarations

Conflict of interest The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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