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Research Article

Whitebark pine persistence potential highly variable following disturbance in the Intermountain West, USA

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Abstract

Widespread mortality poses a major conservation challenge for foundation species whitebark pine (*Pinus albicaulis* Engelm.). We assessed whitebark pine forest structure, composition, and persistence potential in Idaho and Nevada, USA following mountain pine beetle (MPB), wildfire, and no recent disturbance by comparing overstory and regeneration relative abundances, classifying postdisturbance communities, and gauging persistence via residual mature trees and seedlings. Wildfire mortality spanned all species and sizes and exceeded MPB mortality, which was limited to larger pines. Disturbance regulated competing canopy species, with subalpine fir trees decreasing following fire and rising following MPB; however, subalpine fir relative regeneration abundance was disproportionately greater following fire and MPB. Non-native white pine blister rust disproportionately impacted small trees in 48% of plots. Whitebark pine persistence metrics of live overstory for cone production (basal area $\geq$ 5 $m^2 \cdot ha^{-1}$) and successful regeneration ($\geq$250 seedlings$\cdot ha^{-1}$) occurred on 23% of plots. A subset (14%) exceeded overstory but not seedling metrics, while 33% exceeded seedling but not overstory metrics. Roughly 30% of plots did not meet minimum persistence thresholds. Sufficient overstory was predominantly on undisturbed sites, with satisfactory seedling densities after MPB. Consideration of forest composition and persistence metrics will be valuable for prioritizing conservation efforts.

Key words: fire, bark beetles, white pine blister rust, five-needle pines, foundation species, Intermountain West

Introduction

Conservation planning in an era of rapid climate change requires a keen focus on species threatened by or vulnerable to extirpation. Tracking demographic changes in species of concern as well as shifts in community composition after disturbance will be critical to identifying vulnerable populations and determining restoration priorities. Many forest tree species have experienced widespread mortality in recent decades (Hammond et al. 2022) due to heightened climate-driven disturbances, including insect outbreaks, wildfire, and extreme weather events (Anderegg et al. 2022). Non-native, invasive pathogens and pests have further impacted climate-stressed forest communities by, for example, exploiting a tree's weakened defenses during and after drought stress (Anderegg et al. 2015). Of particular conservation concern are foundation tree species—those that delineate ecological communities, provide critical ecosystem services, and determine ecosystem functioning and stability (Ellison et al. 2005).

Whitebark pine (*Pinus albicaulis* Engelm.) is a foundation tree species of western North America that is of increasing conservation concern (Arno 2001; Tomback et al. 2001; Ellison et al. 2005) and was recently designated as "Threatened" under the US Endangered Species Act (US Fish and Wildlife Service 2022). Whitebark pine is characterized as a climate and edaphic specialist that has the ability to establish and survive in extreme conditions and on poor soils at treeline (Maher et al. 2021), and its occurrence plays a foundational role in structuring harsh treeline environments. The species is snowpack-dependent (Hankin et al. 2021) and, by way of its occurrence, further increases snowpack deposition and retention that drive ecosystem composition and function (Tomback et al. 2011) and facilitate the establishment and survival of less tolerant plant species by creating favorable microsite conditions (Tomback et al. 2016*a*). Whitebark pine forests also support diverse wildlife communities, and whitebark pine seeds are an essential food source for the grizzly bear (*Ursus arctos horribilis* Ord) (Felicetti et al. 2003) and Clark's nutcracker (*Nucifraga columbiana* Wilson), the latter of which plays an important role in seed dispersal (Hutchins and Lanner 1982; Tomback 1982, 2022). While the species can dominate on drier sites, it is more widespread as a co-dominant or seral species with subalpine fir (*Abies lasiocarpa* Hook.) and lodgepole pine (*Pinus contorta* Dougl.

ex Loud.) on sites with greater moisture availability and at lower elevations (Arno 2001; Goeking and Izlar 2018). Overstory mortality in this species is particularly concerning because of its keystone status and potential negative consequences to hydrologic, edaphic, and ecological processes and associated plant and animal communities (Tomback et al. 2016*b*).

Whitebark pine forests have faced widespread mortality and declining forest health for many decades (e.g., Keane and Arno 1993; Macfarlane et al. 2013; Shanahan et al. 2016; Goeking and Izlar 2018), but severity and extent have risen under recent warming and drying trends (Young et al. 2023; Airey and Taylor 2024). Acute causes include native mountain pine beetle (MPB) outbreaks (*Dendroctonus ponderosae* Hopkins; Gibson et al. 2008*)*, spread of the non-native fungal pathogen causing white pine blister rust (*Cronartium ribicola* J.C. Fisch., hereafter WPBR; Schoettle et al. 2022), seral densification and competitive exclusion stemming from historical fire suppression policies (Airey and Taylor 2024), and high-severity burning in areas where ladder fuels and/or high fuel loads have developed (Leirfallom et al. 2015). Disturbance processes play an important yet diverse role in stand development depending on community composition and site characteristics. For example, low- to moderate-severity wildfire can foster whitebark pine success by removing competing species such as subalpine fir and fostering Clark's nutcracker seed caching behavior. Conversely, the likelihood of MPB damage in whitebark pine is greater when it co-occurs with lodgepole pine, the MPB's preferred host (Howe et al. 2021; Raffa et al. 2013). Rising mature tree mortality from wildfire and other disturbance agents is likely to diminish seed availability, limit future tree establishment, and potentially, when severe, lead to local extirpation of whitebark pine (Leirfallom et al. 2015).

Collaborative multi-agency and multipartner conservation and restoration efforts are thus underway to ensure the persistence of the species and maintain ecosystem function in impacted stands (e.g., Jenkins et al. 2022; Tomback et al. 2022); however, the scale of these actions has so far fallen short of the magnitude and extent of whitebark pine population decline. Restoration efforts are concentrated in the Northern and Rocky Mountain Regions of the western United States (Montana, Wyoming) and the Canadian Rockies, where rising WPBR incidence (Shanahan et al. 2016; Shepherd et al. 2018) coincided with several large-scale MPB outbreaks in the late 20th and early 21st centuries (Gibson et al. 2008; Cardinal et al. 2022). More recently, whitebark pine mortality from MPB has been a widespread phenomenon in portions of the Pacific Northwest, Intermountain, and Pacific Southwest Regions of the species' range (Oregon, Washington, Idaho, Nevada, California), where incidence of WPBR continues to expand (Goeking and Izlar 2018; Meyer et al. 2023). In more xeric regions of the species' distribution, summer temperature stress has also been identified as a driver of canopy mortality (Wong and Daniels 2017; Young et al. 2023), while regeneration success has been strongly linked to snowpack dynamics (Hankin et al. 2021, 2023). Ongoing climatic warming and variable moisture extremes (IPCC 2022) will continue to interact with biotic mortality agents and shift fire behavior and regimes to progressively threaten whitebark pine persistence (Keane et al. 2017). Restoration of the species will therefore require varying approaches, and application of appropriate management will depend upon matching desired outcomes with the local composition, structure, and disturbance context.

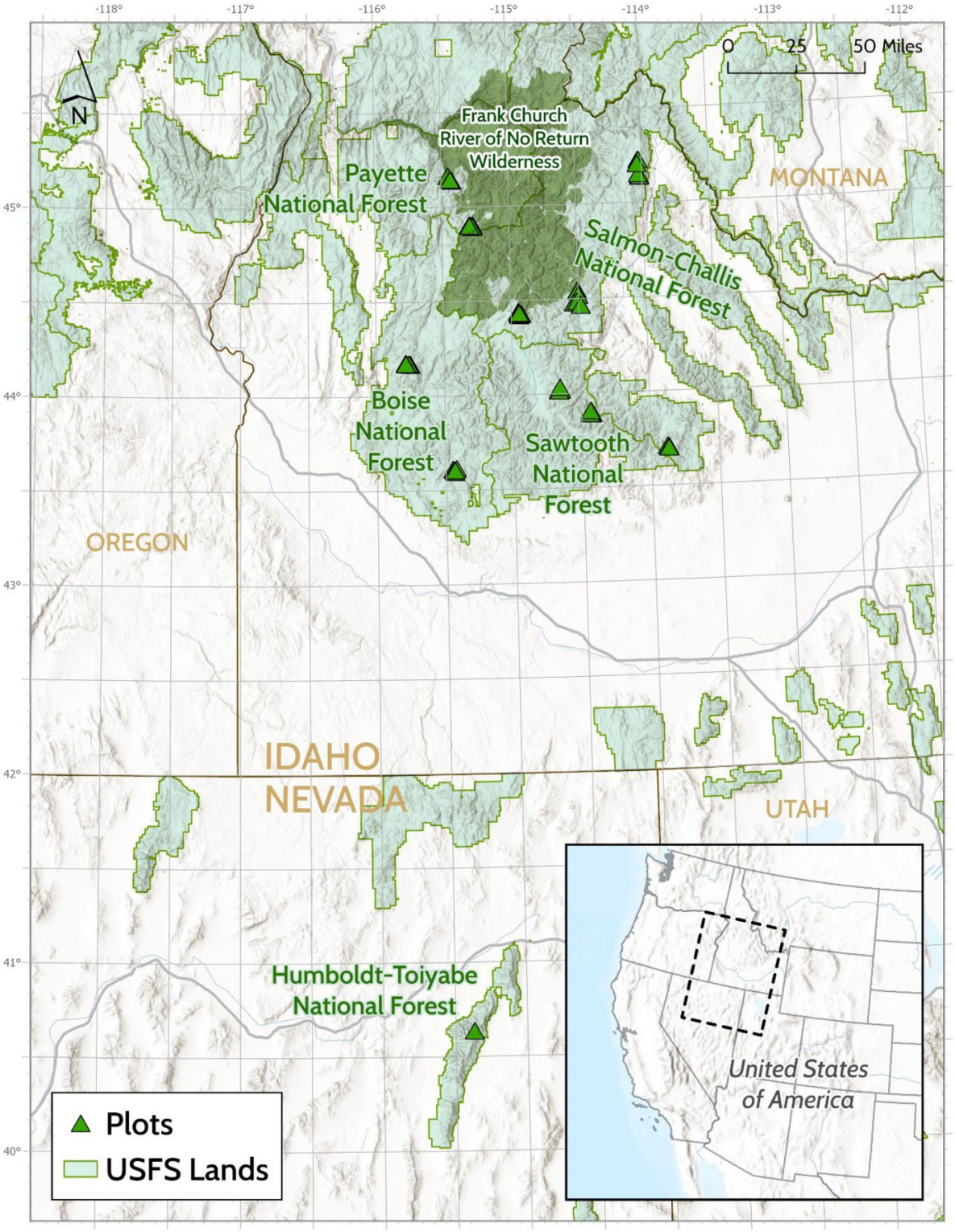
We established a network of forest health monitoring plots in areas disturbed by MPB and wildfire to (1) assess whitebark pine forest structure, composition, and demography, and determine rates of WPBR infection in stands impacted by fire and MPB, and (2) evaluate patterns of whitebark pine persistence among whitebark pine forest communities representative of those in central Idaho and northern Nevada. Conservation of the species is dependent on stands retaining mature reproductively viable trees in sufficient numbers for cone production (McKinney et al. 2009) and to attract Clark's nutcracker (Hutchins and Lanner 1982; Barringer et al. 2012), which are each critical for successful regeneration and recruitment. We applied thresholds representing mature live tree basal area (Mahalovich et al. 2006; McKinney et al. 2009) and regeneration (Keane et al. 2012) to evaluate potential for persistence and continued ecological function in whitebark pine forests. This information will further support conservation prioritization efforts and targeted restoration of impacted stands.

Materials and methods

Site selection

In 2018, we established 64 plots in the whitebark pine forest type (>2440 m in elevation) across six study sites in five US National Forests and one wilderness area in the Intermountain Region (Region 4) of the United States (Fig. 1; Table 1). Whitebark pine stands were delineated using the Vegetation Classification, Mapping, and Quantitative Inventory (2018) and Forest Inventory and Analysis Individual Tree Species Parameter Maps (2012). Within this forest type, plot locations were stratified by potential evapotranspiration (1 km resolution; low [120–265 mm], medium [265–289 mm], and high [289–433 mm]), topographic position index (1 km resolution; low [−125–0 m], medium [0–39 m], and high [39–233 m]), fire occurrence [0, 1], MPB occurrence [0, 1], and placed in individual subwatershed United States Geological Survey (USGS) hydrologic units (Seaber et al. 1987). Geospatial polygon data that represented these unique criteria were assigned sequential random numbers and sorted to prioritize sampling by strata. Plots were stratified across the full population (i.e., the region), and a minimum of five plots were located in each administrative unit (except on the Humboldt-Toiyabe National Forest due to time constraints). Sampling within each administrative unit was not balanced by disturbance category, and scaling differences in the MTBS and Aerial Detection Survey (ADS) data further led to a sampling imbalance as plots were reclassified based on field observations (Table 1). Fire occurrence data were obtained from the Monitoring Trends in Burn Severity database (Eidenshink et al. 2007; data downloaded: 1 November 2018; 2012–2017), and presence of burning was confirmed during field data collection using evidence

Fig. 1. Study sites included five USDA National Forests and one wilderness area in the Intermountain Region of the western United States. Figure was created using Environmental Systems Research Institute (ESRI) ArcGIS Pro version 3.6.0 and assembled from the following data sources: World Terrain Basemap (ESRI, USGS, and NOAA), 3DEP Hillshade (USGS), land ownership, and administrative unit (USDA Forest Service).



of charcoal, litter consumption, and/or tree bole charring and crown scorch. MPB outbreak occurrence data were obtained from the US Forest Service ADS Program in polygons classified as moderate or severe cumulative damage (Johnson and Wittwer 2006; data downloaded: 1 November 2018; Surveys: 1999–2015).

Table 1. Sampling intensity by National Forest administrative unit and disturbance type.

	Disturbance				
	Fire	MPB	Fire + MPB	No fire or MPB	Total
Boise National Forest	4	4	0	4	12
Salmon-Challis National Forest	0	10	1	7	18
Payette National Forest	5	4	1	1	11
Sawtooth National Forest	0	3	1	8	12
Frank Church River of No Return Wilderness	2	0	5	1	8
Humboldt-Toiyabe National Forest	0	0	0	3	3
Total	11	21	8	24	64

Note: MPB: mountain pine beetle.

The combination of fire and MPB disturbance histories resulted in the following categories: wildfire ("fire"), mountain pine beetle ("MPB"), wildfire and MPB ("fire + MPB"), and no recent fire or MPB disturbance ("no fire or MPB"). Stands designated as "no fire or MPB" were confirmed during field data collection (see Field sampling section) and in datasets of disturbance but were likely influenced by disturbance at some point in the past and many were impacted by WPBR. WPBR was not considered in site stratification and selection but was recorded when present during data collection. Administrative units included the Boise National Forest ($n = 12$), Frank Church River of No Return Wilderness ($n = 8$), Humboldt-Toiyabe National Forest ($n = 3$), Payette National Forest ($n = 11$), Salmon-Challis National Forest ($n = 18$), and Sawtooth National Forest ($n = 12$). To ensure that our sample represented stands that were potentially suitable for restoration management activities, plots were restricted to within 1 km of roads or trails or within 10 km of roads in the Frank Church Wilderness Area.

Field sampling

Sampling protocols were adapted from whitebark pine monitoring protocols developed by the Greater Yellowstone Whitebark Pine Monitoring Working Group (2011) and US Forest Service Region 5 to allow for cooperative use of these data for broader scale analyses and assessments (Meyer et al. 2016; Slaton et al. 2019). Plot locations were deemed suitable for sampling if whitebark pine was dominant or co-dominant in the stand and enough whitebark pine trees were available to characterize stand conditions (i.e., ~10–25 stems within the plot). In locations where these criteria were not met, crews established a random compass bearing and traveled in increments of 100 m until a suitable location was identified. In each plot, we inventoried all seedlings (<1.37 m in height), saplings (<7.6 cm diameter-at-breast height (DBH; 1.37 m height) but >1.37 m height), and trees (>7.6 cm DBH) in a 0.05 ha circular fixed-radius plot (radius: 12.6 m). Individuals were sampled for species, DBH, mortality status (dead or alive), and signs of damage from fire, MPB infestation, and WPBR. Fire damage was indicated by bole charring and (or) crown scorch in plots with known recent fire activity. MPB infestation was indicated by pitch tubes and frass, and trees were scored for time since mortality using the following scale: *red*—pitch tubes and frass present on >50% of the bole, crown yellow to red with 0%–10% needles lost, *gray*—pitch tubes and frass present, crown red to brown, 10%–100% of needles lost, *older*—pitch tubes present, 100% needles lost, fine branch wood broken but medium and larger branch wood retained (Keen 1955). Within-plot incidence of WPBR was restricted to live whitebark pine seedlings, saplings, and trees due to the difficulty of positively identifying WPBR in trees killed by fire or bark beetles. WPBR infection was indicated for whitebark pine by having (1) aecial sacs (WPBR fruiting body) or (2) two or more signs including cankers on the stem or branches, branch flagging, branch swelling, yellow to orange discoloration of bark, or rodent chewing (Hoff 1992). Trees that exhibited branch swelling or chewing in combination with dwarf mistletoe were considered false positives if no other trees in the plot exhibited additional definitive signs of WPBR (i.e., aecial sacs, e.g., Lamoille Canyon, Nevada).

Data processing and analysis

Pre- and postdisturbance overstory stand densities, mortality, quadratic mean diameter (QMD), and species composition were calculated for each plot. Observed species were recorded as whitebark pine, lodgepole pine, subalpine fir, and "other". The "other" species group represented all species occurring in low abundance and included Engelmann spruce (*Picea engelmannii* Parry ex Engelm.), mountain hemlock (*Tsuga mertensiana* (Bong.) Carrière), Douglas-fir (*Pseudotsuga menziesii* (Mirbel) Franco), and aspen (*Populus tremuloides* Michaux (Michx.)). Diameter distributions for pre- and postdisturbance structures were produced by averaging tree density in 5 cm DBH bins across all plots within a given species and disturbance type. Predisturbance metrics were computed by aggregating live and dead standing trees, with disturbance-associated mortality represented by standing dead. Postdisturbance regeneration was assessed as seedling and sapling densities, although due to the unknown timing of MPB outbreak and unknown age of seedlings and saplings, some regeneration may predate the disturbance. Here and throughout, "predisturbance" refers to before the most recent fire, MPB, or both occurred, and "postdisturbance" refers to after fire, MPB, or both occurred in a given plot. Incidence of WPBR was assessed as a secondary disturbance agent across all plots, regardless

of primary disturbance type, and could be present in "no fire or MPB" plots.

To assess persistence potential of whitebark pine, plots were categorized based on stand metrics indicative of species persistence: presence or absence of live whitebark pine basal area $\geq$5 $m^2 \cdot ha^{-1}$ (Mahalovich et al. 2006; McKinney et al. 2009) and healthy whitebark pine seedling densities $\geq$250 stems$\cdot ha^{-1}$ (i.e., recommended planting density assuming 50% survival; Keane et al. 2012). These persistence metrics characterize the ability of a stand to continue to produce cones through remnant live tree cover and regenerate successfully to produce a juvenile cohort sufficient for recruitment into larger reproductively mature trees. Plots were tallied within each category and summarized by National Forest administrative unit and disturbance type. Healthy seedlings were those lacking signs of disturbance, including WPBR infection.

Differences in mortality rate, live tree density, dead tree density, sapling density, and seedling density were evaluated across disturbance types for each species using generalized linear mixed effects models and by comparing marginal means. Models predicting proportional tree death (mortality rate) were fit using logistic regression with a binomial distribution and logit link function and weighted with total tree density (live and dead). Models predicting tree density response variables were fit using a Poisson distribution and log link function. Due to the imbalance in our sampling design, models were implemented in a bootstrapping framework (5000 reps) that included resampling at two levels (observation and administrative unit). Marginal means, contrasts, and 95% confidence intervals were computed after nonconvergent models were removed from the bootstrap sample. Statistical significance was judged using 95% confidence intervals of contrasts based on the distribution of samples collected.

Change in overstory species composition following disturbance was assessed by taking the difference between postdisturbance and predisturbance overstory species relative densities. Differences in generational composition were computed by taking the difference between species relative densities in the postdisturbance regeneration (i.e., seedlings and saplings) and postdisturbance live overstory tree size classes. Significant differences in species composition were tested using a bootstrapped two-sided *t*-test (9999 reps; $\alpha = 0.05$), and *p* values were adjusted for multiple tests using the false discovery rate method (Benjamini and Hochberg 1995).

Postdisturbance forest community types were identified using a hierarchical agglomerative cluster analysis based on a species-size class community matrix that included live seedling, sapling, small tree (<25 cm DBH), and large tree ($\geq$25 cm DBH) abundances for each species. Twenty-five centimeter DBH was chosen as an approximate threshold between small and large diameter tree size classes due to the documented size minimum for lodgepole and whitebark pine susceptibility to MPB mortality (Perkins and Roberts 2003; Meyer et al. 2016). The dissimilarity matrix was generated using the Bray-Curtis index, and clustering was computed using Ward's method. The optimal number of clusters was identified using the "elbow method", and differences in community types were confirmed using permutational multivariate analysis of variance (PERMANOVA) and pair-wise PERMANOVA tests ($\alpha = 0.05$).

We further conducted a redundancy analysis to evaluate associations between forest communities, disturbance types, and established gradients of elevation and climatic moisture deficit (Arno 2001). Historical climatic moisture deficit was extracted using plot locations as scale-free point estimates generated using ClimateNA v6.00 software (Wang et al. 2016). Arithmetic means ($\pm$1 standard error) were computed for elevation, climatic moisture deficit, overall mortality rate, and WPBR occurrence rate, and differences among community types were tested. To accomplish this, the species-size class community matrix was standardized using the Hellinger method (Legendre and Gallagher 2001), and continuous explanatory variables were centered and scaled using a root-mean-square transformation. The significance of axes and explanatory variables were tested at $\alpha = 0.05$. The frequency of plots in each community type was tallied by National Forest administrative unit and disturbance type to show the geographic distribution of community types. The frequency of plots (ratio of total sampled) in each community type was further tallied by presence or absence of live whitebark pine basal area $\geq$5 $m^2 \cdot ha^{-1}$ and healthy whitebark pine seedling densities $\geq$250 stems$\cdot ha^{-1}$.

All analyses were conducted in R 4.3.2 (R Core Team 2024) using the following packages: base, boot.pval (Thulin 2025), cluster (Maechler et al. 2025), dendroextend (Galili 2015), emmeans (Lenth and Piaskowski 2025), ggdendro (de Vries and Ripley 2024), lmersampler (Loy et al. 2023), tidyverse (Wickham et al. 2019), and vegan (Oksanen et al. 2013).

Results

Disturbance-driven changes in stand structure and composition

Disturbances were generally moderate in severity based on overstory tree mortality (Table 2). Mortality was greatest in plots that experienced fire, but mortality in plots that experienced fire alone did not differ from those with fire + MPB (Table 2). QMD of dead trees was greater in plots impacted by MPB over other disturbances. Nearly all trees (~93%) that exhibited signs of MPB had lost their needles and were thus likely killed more than 3–4 years prior to sampling. Fire, MPB, and fire + MPB reduced live tree density and live basal area (Table 3). The greatest reductions in stand density were in plots impacted by fire or fire + MPB. Fire reduced subalpine fir density more than whitebark pine, lodgepole pine, and "other" species, while whitebark pine density decreased the most in MPB plots (Table 3). Live tree density did not change significantly for any species in plots with no fire or MPB. On sites with no fire or MPB, tree density was significantly greater and QMD was lower ($p > 0.05$) in plots that recorded presence of WPBR than plots where WPBR was absent (Table 4).

Persistence metrics varied widely among regions and disturbance types. Over all plots sampled, whitebark pine was found to have $\geq$5 $m^2 \cdot ha^{-1}$ live basal area in 24 of 64 plots

Table 2. Mean (±1 standard error) mortality rate (%), live tree density (stems·ha^{-1}), and dead tree density (stems·ha^{-1}) by species in each disturbance type.

	Disturbance			
	Fire	MPB	Fire + MPB	No fire or MPB
Mortality rate (% of density)				
Whitebark pine	46.2 ± 11.7%^{a}	30.8 ± 6.5%^{b}	43.2 ± 13%^{ab}	9.9 ± 3.3%^{c}
Subalpine fir	59.6 ± 12.5%	–	64 ± 11.9%	19.4 ± 6.6%
Lodgepole pine	42.3 ± 14.2%	27.2 ± 5.9%	58 ± 11.1%	0.3 ± 0.3%
Other	19.7 ± 10.7%^{ab}	–	39.6 ± 17.8%^{b}	0.7 ± 0.7%^{a}
Live trees (stems·ha^{-1})				
Whitebark pine	35 ± 11^{a}	337 ± 66^{b}	90 ± 38^{b}	376 ± 87^{b}
Subalpine fir	84 ± 44^{ab}	180 ± 39^{a}	38 ± 16^{b}	78 ± 24^{ab}
Lodgepole pine	107 ± 38	135 ± 34	160 ± 60	32 ± 16
Other	5 ± 4	23 ± 9	8 ± 8	52 ± 27
Dead trees (stems·ha^{-1})				
Whitebark pine	131 ± 69^{a}	211 ± 57^{a}	88 ± 26^{b}	30 ± 8^{c}
Subalpine fir	165 ± 52	–	198 ± 80	34 ± 19
Lodgepole pine	65 ± 28	89 ± 26	205 ± 52	1 ± 1
Other	13 ± 8^{a}	–	22 ± 10^{b}	5 ± 5^{ab}

Note: Estimates are specific to each disturbance agent and nonhost species (e.g., subalpine fir, other species) are not included in mountain pine beetle (MPB) mortality estimates. Background mortality is represented in the "no fire + MPB" category. Letters denote statistical differences between disturbances and were omitted in cases of nonsignificance ($\alpha = 0.05$).

Table 3. Mean (standard error) tree density, basal area, and quadratic mean diameter before and after disturbance.

	Tree density (stems·ha^{-1})		Basal area (m^2·ha^{-1})		Quadratic mean diameter (cm)	
	Pre	Post	Pre	Post	Pre	Post
Fire						
PIAL	171 (64)	34.5 (11.5)	5.4 (1.3)^{a}	1.7 (0.6)^{b}	19.6 (2.8)	15.1 (4.1)
ABLA	267 (58)^{a}	83.6 (44.3)^{b}	7.5 (1.5)^{a}	1.6 (0.8)^{b}	20.3 (1.5)^{a}	10.1 (2.7)^{b}
PICO	175 (41)	107.3 (37.8)	6.7 (2.2)	3.3 (1.3)	22.4 (5.5)	11.5 (3.4)
Other	20 (11)	5.5 (3.9)	2.8 (2.4)	0.4 (0.3)	11.4 (5.5)	5.7 (3.8)
Total	158 (27)^{a}	57.7 (15.6)^{b}	5.6 (0.9)^{a}	1.7 (0.4)^{b}	18.4 (2.1)^{a}	10.6 (1.8)^{b}
MPB						
PIAL	603 (111)^{a}	337.1 (65.9)^{b}	23.4 (4.4)^{a}	7.4 (1.6)^{b}	23.9 (3.1)^{a}	15.7 (1.5)^{b}
ABLA	213 (51)	180.0 (39.3)	5.6 (1.5)	4.6 (1.2)	13.7 (1.7)	13.6 (1.7)
PICO	233 (56)	135.2 (34.0)	9.4 (2.2)^{a}	3.9 (1.3)^{b}	17.1 (2.6)	13.1 (2.1)
Other	40 (17)	22.9 (9.3)	4.6 (2.3)	2.7 (1.5)	11.6 (4.5)	11.2 (4.8)
Total	272 (40)^{a}	168.8 (24.1)^{b}	10.8 (1.6)^{a}	4.6 (0.7)^{b}	16.6 (1.6)	13.4 (1.4)
Fire + MPB						
PIAL	208 (74)	90 (37.6)	6.5 (2.2)	2.1 (1.3)	19.1 (2.4)	11.3 (2.7)
ABLA	253 (85)^{a}	37.5 (15.8)^{b}	7.8 (2.7)^{a}	0.9 (0.5)^{b}	18.9 (1.2)^{a}	9.9 (3.3)^{b}
PICO	400 (92)^{a}	160.0 (59.8)^{b}	11.8 (1.5)^{a}	3.4 (1.1)^{b}	20.8 (1.4)	16.1 (2.9)
Other	35 (16)	7.5 (7.5)	3.7 (2.6)	1.5 (1.5)	15.6 (6.5)	6.4 (6.4)
Total	224 (42)^{a}	73.8 (20.2)^{b}	7.5 (1.2)^{a}	2.0 (0.6)^{b}	18.6 (1.7)^{a}	10.9 (2.0)^{b}
No Fire or MPB						
PIAL	406 (92)	375.8 (87.4)	20.9 (4.1)	15.2 (3.0)	27.9 (4.2)	23.5 (2.7)
ABLA	113 (38)	78.3 (24.0)	3.8 (1.7)	2.0 (0.7)	14.7 (2.7)	11.6 (2.5)
PICO	33 (17)	31.7 (16.0)	1.6 (0.8)	1.6 (0.8)	5.8 (2.4)	5.8 (2.4)
Other	58 (32)	52.5 (27.1)	3.2 (1.1)	3.1 (1.0)	15.3 (5.0)	15.3 (5.0)
Total	152 (30)	134.6 (27.7)	7.4 (1.4)	5.5 (1.0)	15.9 (2.0)	14.0 (1.8)

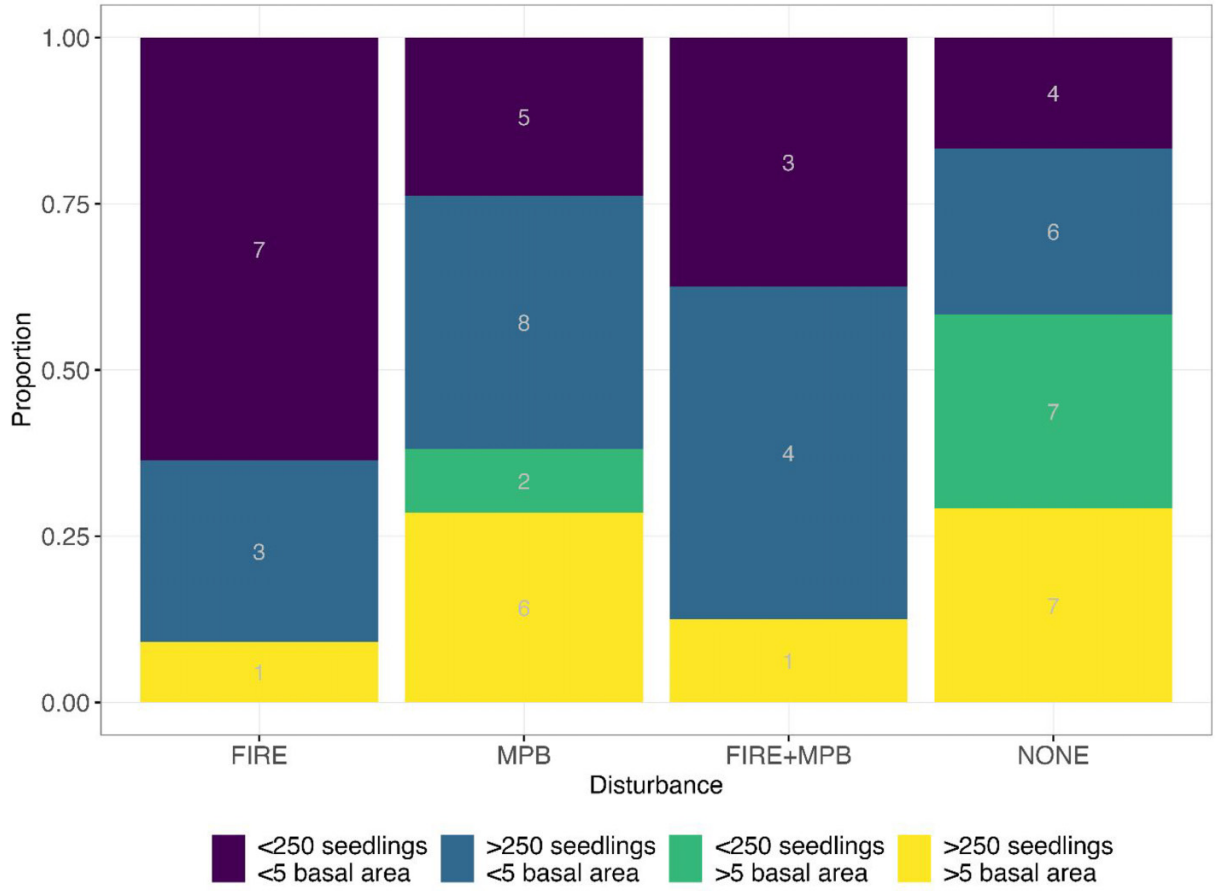
Note: Plots lacking fire and (or) mountain pine beetle (MPB) (i.e., "no fire or MPB") include background mortality. Species abbreviations include ABLA—Subalpine fir (*Abies lasiocarpa*), PIAL—Whitebark pine (*Pinus albicaulis*), PICO—Lodgepole pine (*Pinus contorta*), and other—species of low abundance. Letters denote statistically significant differences before and after disturbance and were omitted in cases of nonsignificance ($\alpha = 0.05$).

Table 4. Mean (±1 standard error) tree density, basal area, and quadratic mean diameter for whitebark pine in plots with and without white pine blister rust (WPBR) on sites with no fire or mountain pine beetle disturbance ($n = 24$).

	WPBR present	WPBR absent
Tree density (stems·ha^{-1})	645 (155)[a]	167 (25)[b]
Basal area (m^2·ha^{-1})	21.5 (4.9)	20.4 (6.8)
Quadratic mean diameter (cm)	21.3 (2.4)[a]	34.4 (7.7)[b]
Quadratic mean diameter (cm, *dead trees only*)	16.0 (4.2)	28.8 (13.5)

Note: Mean incidence of trees with WPBR was 13% in plots with WPBR present. Letters denote statistically significant differences in means and were omitted in cases of nonsignificance ($\alpha = 0.05$).

Fig. 2. Stacked bar chart showing the proportion of plots sampled per disturbance type that fall within four categories representing contrasting low and high seedling density and low and high tree basal area, respectively. Numbers denote the number of plots in each group. MPB: mountain pine beetle.



(~37%) and healthy whitebark pine seedlings exceeded 250 individuals·ha^{-1} in 35 of 64 plots (~56%) (Table A1). Taken in combination, 23% of plots exceeded both seedling and basal area metrics, 14% of plots exceeded the basal area metric but not the seedling metric, 33% plots exceeded the seedling metric but not the basal area metric, and 30% of plots fell below both seedling and basal area metrics (Fig. 2). Plots with ≥5 m^2·ha^{-1} live basal area were most frequently found on sites with no recent disturbance (70% of plots with no fire or MPB) and less frequently on sites with recent disturbance: 33% of plots impacted by MPB, 13% of plots impacted by fire + MPB, and 9% of plots impacted by fire (Fig. 2; Table A1). Plots with ≥250 seedlings·ha^{-1} were most frequently found following MPB (66% of plots), fire + MPB (62% of plots), no fire or MPB (50% of plots), and were least frequently found following fire (36% of plots). Persistence metrics for individual National Forest administrative units can be found in Table A1.

Tree size distributions indicated differential whitebark pine tree mortality and survival depending on disturbance type (Fig. 3). In stands that experienced fire, mortality affected all species and was skewed toward smaller size classes, resulting in a flattened surviving tree size class distribution. In stands with MPB activity, mortality was skewed toward larger whitebark pine and lodgepole pine host trees, and the

Fig. 3. Mean whitebark pine tree size distributions predisturbance (i.e., all standing) and postdisturbance (i.e., residual live standing) in plots exposed to various disturbance types including fire ($n = 11$), mountain pine beetle (MPB; $n = 21$), fire + MPB ($n = 8$), and no fire or MPB ($n = 24$).

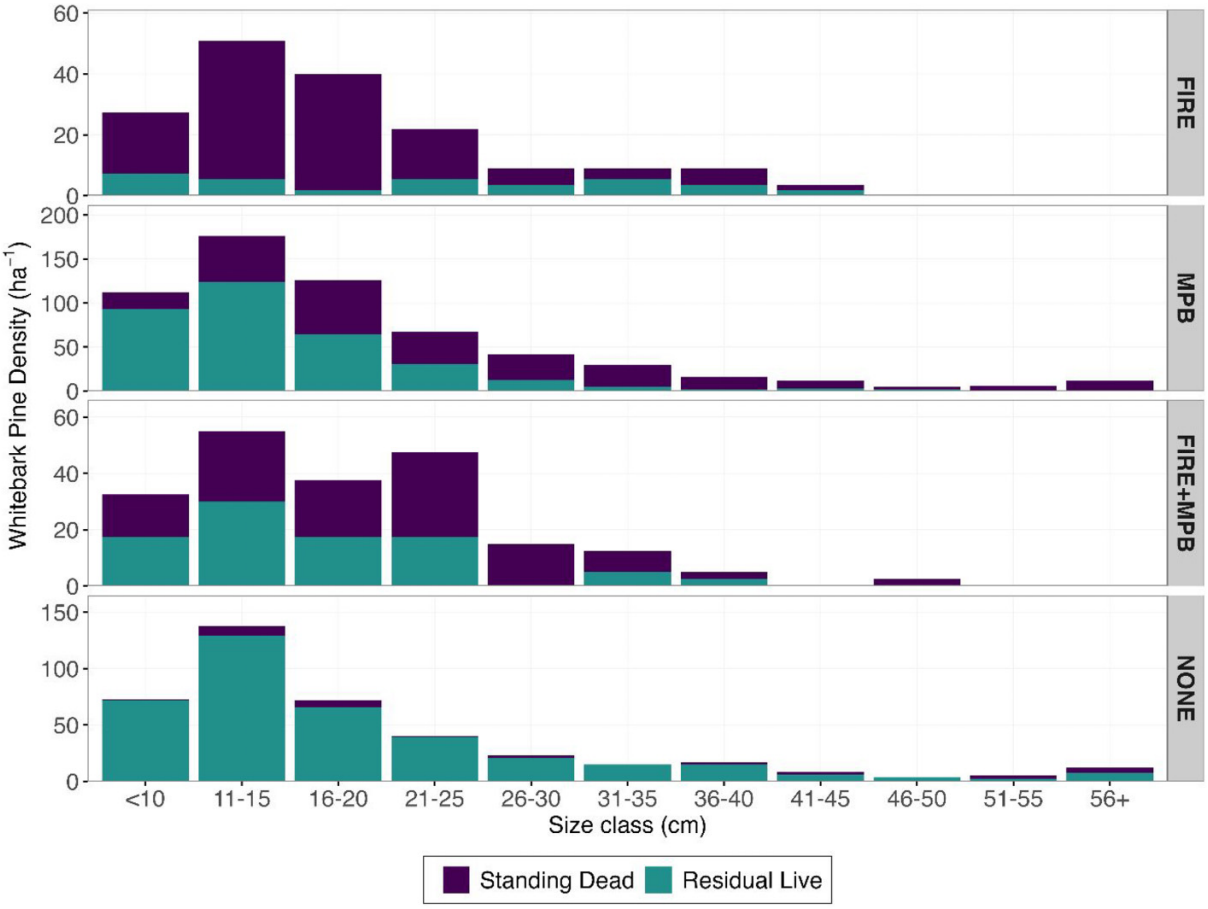


Table 5. Live seedling and sapling density (stems·ha^{-1}) by species in each disturbance type (mean ± 1 standard error).

	Disturbance			
	Fire	MPB	Fire + MPB	No fire or MPB
Seedlings (stems·ha^{-1})				
Whitebark pine	325 ± 107^{a}	890 ± 258^{b}	372 ± 98^{c}	298 ± 70 cd
Subalpine fir	689 ± 242^{a}	1711 ± 519^{b}	448 ± 257^{c}	1692 ± 1034^{d}
Lodgepole pine	255 ± 118^{a}	248 ± 72^{ab}	485 ± 122^{b}	58 ± 48^{c}
Other	25 ± 14	46 ± 19	25 ± 20	42 ± 21
Saplings (stems·ha^{-1})				
Whitebark pine	89 ± 27^{a}	313 ± 65^{b}	118 ± 33^{a}	311 ± 66^{b}
Subalpine fir	156 ± 78^{a}	300 ± 83^{b}	110 ± 31^{a}	166 ± 50^{a}
Lodgepole pine	84 ± 28^{a}	64 ± 18^{a}	168 ± 54^{b}	11 ± 8^{c}
Other	4 ± 2	5 ± 5	2 ± 2	28 ± 17

Note: Letters denote statistically significant differences among disturbance types and were omitted in cases of nonsignificance ($\alpha = 0.05$). MPB: mountain pine beetle.

distribution of surviving trees was skewed toward smaller size classes and greater dominance of nonhost species in larger size classes. MPB targeted larger whitebark pine individuals, with QMD of standing dead trees greater in plots affected by MPB (mean = 24.0 cm) than all other disturbance categories (fire = 15.4 cm, fire + MPB = 17.8 cm, no fire or MPB = 13.8 cm); however, differences were not statistically significant (p values > 0.05). In stands exposed to fire + MPB, mortality encompassed a broader size distribution than either disturbance alone. Incidence of WPBR in plots with no fire or MPB was greatest in whitebark pine trees in small-to-medium-size classes (Fig. A1).

Postdisturbance live seedling and sapling densities varied widely by species and disturbance type (Table 5). In general,

seedlings were abundant and more prevalent than saplings, though time since disturbance was not included in analysis and would likely influence the distribution of regenerating size classes. Seedling density was highest in plots impacted by MPB. In these plots, seedling and sapling densities did not differ between whitebark pine and subalpine fir, but both species were greater in density than lodgepole pine and the "other" species group. In fire plots, whitebark pine seedling and sapling densities did not differ from subalpine fir and lodgepole pine densities but were greater than the "other" species group. Seedling and sapling species composition were similar between plots affected by fire alone and fire + MPB. In stands with no fire or MPB, both whitebark pine and subalpine fir seedling density were significantly higher than lodgepole pine and "other" species. Mean whitebark pine seedling density was less than subalpine fir seedling density (298 vs. 1692 stems·ha^{-1}); however, these differences were not statistically significant due to high variability among plots ($p > 0.05$).

Disturbance-mediated forest communities

Changes in overstory species composition and differences in regeneration versus overstory species relative abundance were mediated by disturbance type (Fig. 4). Whitebark pine relative abundance in the overstory did not change significantly following disturbance; however, subalpine fir decreased in relative abundance following fire and increased in relative abundance following MPB. While not significant at the 95% confidence level, whitebark pine did exhibit trends of decline in overstory relative abundance following fire and MPB. When regeneration community composition was compared with surviving overstory composition, whitebark pine and subalpine fir had greater relative abundance in the regenerating community following fire than lodgepole pine. Following MPB disturbance, the relative abundance of subalpine fir was greater in the regenerating community compared to the overstory, while lodgepole pine (i.e., an MPB host species) decreased in relative abundance in the regenerating community. We did not observe a difference in species composition following fire + MPB disturbance. In plots with no fire or MPB, subalpine fir increased in relative abundance, whereas whitebark pine decreased in the regenerating community compared to the postdisturbance overstory community.

Cluster analysis identified four whitebark pine forest community types that differed in species abundances in live seedling, sapling, small tree, and large tree size classes (Fig. 5). Community types included (1) *whitebark and lodgepole pine co-dominant with sparse regeneration* (hereafter, "pine-low"), (2) mixed species with moderate regeneration (hereafter, "mixed-mod"), (3) mixed species with abundant regeneration (hereafter, "mixed-high"), and (4) whitebark pine dominant with moderate regeneration (hereafter, "whitebark-mod") (Fig. 5; Table A3). Composition of the *pine-low* forest community type included low densities of whitebark pine, lodgepole pine, and other species in large tree size classes with sparse seedlings and saplings in the understory. The *mixed-mod* forest community type included a moderately dense overstory mix of whitebark pine, subalpine fir, and lodgepole pine with an understory composed primarily of subalpine fir with whitebark pine and lodgepole pine in lower abundance. The *mixed-high* forest community type included a dense overstory dominated by whitebark pine with subalpine fir as an important associate and abundant seedlings and saplings dominated by subalpine fir with whitebark pine in lower abundance. Finally, the *whitebark-mod* forest community type was dominated by whitebark pine in all size classes with other species present in low abundances. The frequency of observed community types varied by National Forest administrative unit (Fig. 5; Table A2).

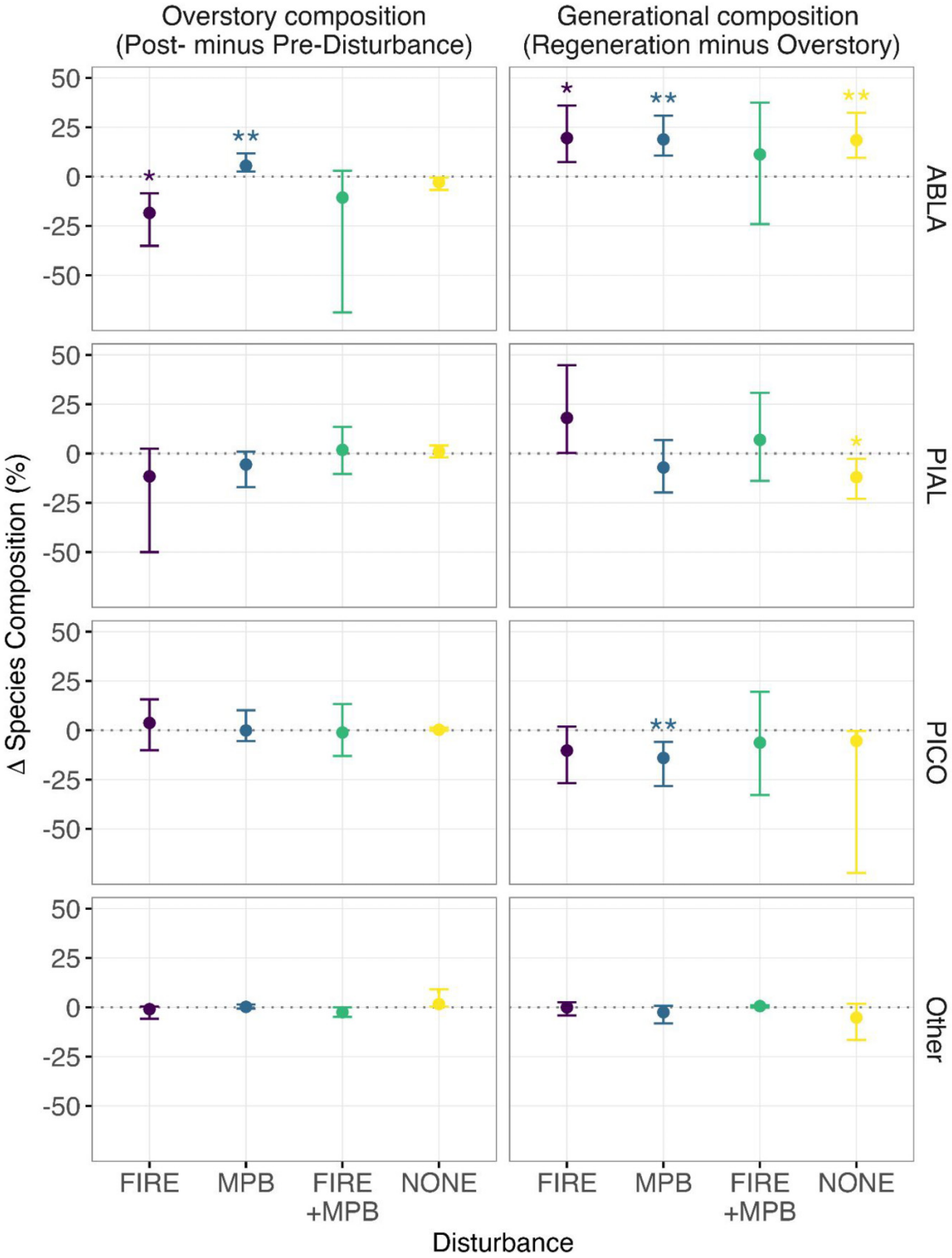
Redundancy analysis revealed that community structure and composition varied by disturbance type ($p = 0.002$) and across elevation ($p = 0.045$) and climate moisture deficit gradients ($p = 0.005$) (Fig. 6). Plots in the *pine-low* and *mixed-mod* community types were predominantly found at lower elevations with the greatest climatic moisture deficits (Table 6) and were associated with higher incidence of fire and fire + MPB disturbance types. Plots in the *mixed-high* community type occurred at intermediate elevations with the lowest climatic moisture deficit yet were associated with the highest incidence of MPB. Finally, plots in the *whitebark-mod* community type occurred at high elevations with high climatic moisture deficits and were associated with the highest number of plots that lacked impacts from fire or MPB (Fig. 6; Table 6).

Mortality rates were greatest in the *pine-low* type over other community types, whereas WPBR occurrence rates were greatest in the upper elevation *mixed-high* and *whitebark-mod* community types over low-elevation community types (Table 7). Whitebark pine was found to have ≥5 m^2·ha^{-1} live basal area in more than 55% of plots in the *mixed-high* and *whitebark-mod* community types, but 13% or fewer plots in the *mixed-mod* and *pine-low* community types (Table 7; Fig. A2). Healthy whitebark pine seedlings ≥250 stems·ha^{-1} were found in 84% of plots in the *mixed-high*, 61% of plots in the *whitebark-mod*, 50% of plots in the *mixed-mod*, and 0% of plots in the *pine-low* community types. WPBR was detected in 73% of plots in the *mixed-high*, 67% of plots in the *whitebark-mod*, 31% of plots in the *mixed-mod*, and was absent in the *pine-low* community type (0 of 11 plots).

Discussion

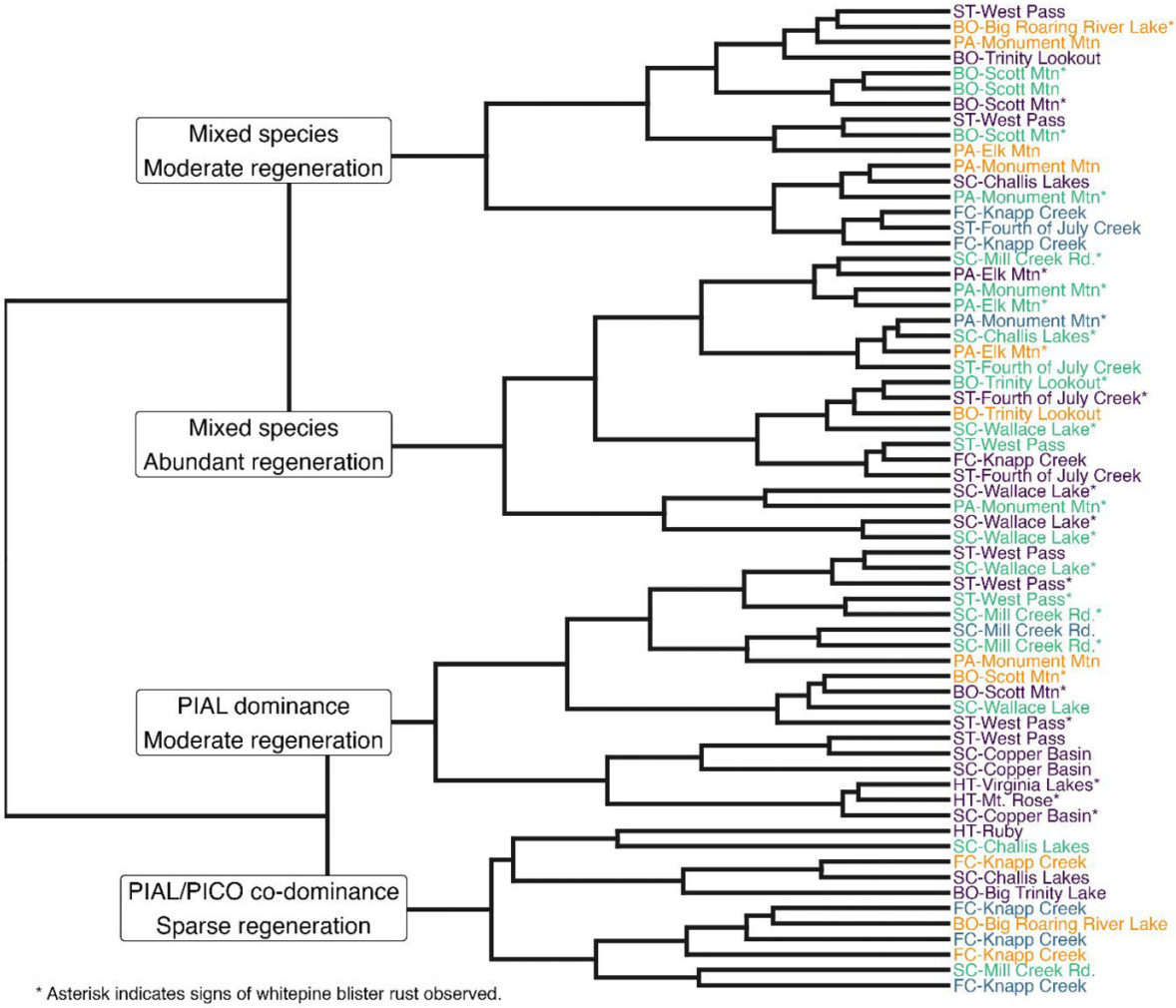
Whitebark pine was recently listed as "Threatened" under the Endangered Species Act (US Fish and Wildlife Service 2022), and ongoing mortality and corresponding declines in regeneration may erode the potential of this foundation tree species to maintain historical ecological function or persist across its current range (Tomback et al. 2011; Tomback et al. 2016*b*). Our study in central Idaho and northern Nevada documented overstory tree mortality and survival and characterized regeneration abundance and community composition following MPB and fire disturbance. We found that mortality was greatest at low elevations and following fire, and disturbance primarily regulated competing species. Subalpine fir declined in the overstory following fire but rose following MPB. Given differing rates of canopy survival and regeneration response following disturbance, subalpine fir exhibited

Fig. 4. Mean change in overstory species composition (%) and differences in generational species composition (%) following fire, mountain pine beetle (MPB), fire + MPB, or no fire or MPB disturbance ("none"). Change in overstory composition represents post- minus predisturbance species relative abundances. Difference in generational species composition (%) represents regeneration (i.e., seedlings and saplings) minus overstory tree species relative abundances. Error bars represent 95% confidence intervals based on bootstrapped *t*-test results and significances are denoted as follows: $*$ = adjusted p value < 0.05, $**$ = adjusted p value < 0.01, and $***$ = adjusted p value < 0.001.



greater dominance in the regeneration versus the overstory community in fire, MPB, or no fire or MPB settings, whereas whitebark pine was favored following fire and neutral following MPB or no recent fire or MPB. While whitebark pine persistence in both the canopy and regenerating communities offers an optimistic outlook for many postdisturbance stands,

Fig. 5. Dendrogram indicating plot associations with four whitebark pine forest community types identified using hierarchical cluster analysis. Labels identify the study area (i.e., USDA Forest Service national forest) and geographic location near each plot. USDA national forest abbreviations include BO—Boise National Forest, SC—Salmon Challis National Forest, PA—Payette National Forest, ST—Sawtooth National Forest, FC—Frank Church River of No Return Wilderness, and HT—Humboldt-Toiyabe National Forest. Label colors indicate disturbance type at each plot. Orange indicates fire, green indicates mountain pine beetle (MPB), blue indicates both fire and MPB, and purple indicates no fire or MPB. Asterisks indicate plots where signs of white pine blister rust were observed.



WPBR was present in nearly half of the sites we sampled, and ongoing expansion of the pathogen presents perhaps the greatest management challenge for long-term species persistence.

Concerns for whitebark pine populations generally arise due to three consequences of disturbance-driven canopy mortality. First, recent canopy mortality restricts the fecundity of whitebark pine populations through direct losses of mature cone-bearing trees, leading to reductions in whitebark pine regeneration (Leirfallom et al. 2015). We saw this effect pronounced in burned stands with high overstory tree mortality and in stands impacted by MPB where beetles targeted larger, reproductively mature whitebark pine. Second, as seen in this study, WPBR disproportionately impacts smaller size classes, which may ultimately prevent recruitment of mature seedbearing size classes (Burns et al. 2008). Third, high recruitment of shade-tolerant subalpine fir across all disturbance types and in some communities may direct forest trajectories away from whitebark pine dominance (Burns et al. 2008), although this pattern is variable and can depend on disturbance regimes, site productivity, and other environmental factors (e.g., Meyer et al. 2023; Airey and Taylor 2024; Campbell et al. 2024). Our findings provide additional evidence consistent with the abovementioned threats to whitebark persistence, yet ~70% of plots met at least one persistence threshold, which presents a positive outlook for whitebark stand recovery following disturbance. Persistence characteristics varied by disturbance type, climate conditions, and forest community association suggesting that these factors may be important when prioritizing resources or considering management options (e.g., Keane et al. 2022; Tomback et al. 2022).

We documented wide variation in disturbance impacts depending on species and size classes that were in line with

Fig. 6. A biplot depicting the first two axes of a redundancy analysis (RDA) regressing species-size abundances (i.e., seedlings, saplings, trees <25 cm DBH, and trees >25 cm DBH) on forest community types, disturbance types, and elevation and climatic moisture deficit ($R^2 = 0.66$). Ellipses represent 1 SD of the mean loading for forest community types, and vectors show the strength and direction of elevation and climatic moisture deficit gradients. MPB: mountain pine beetle.

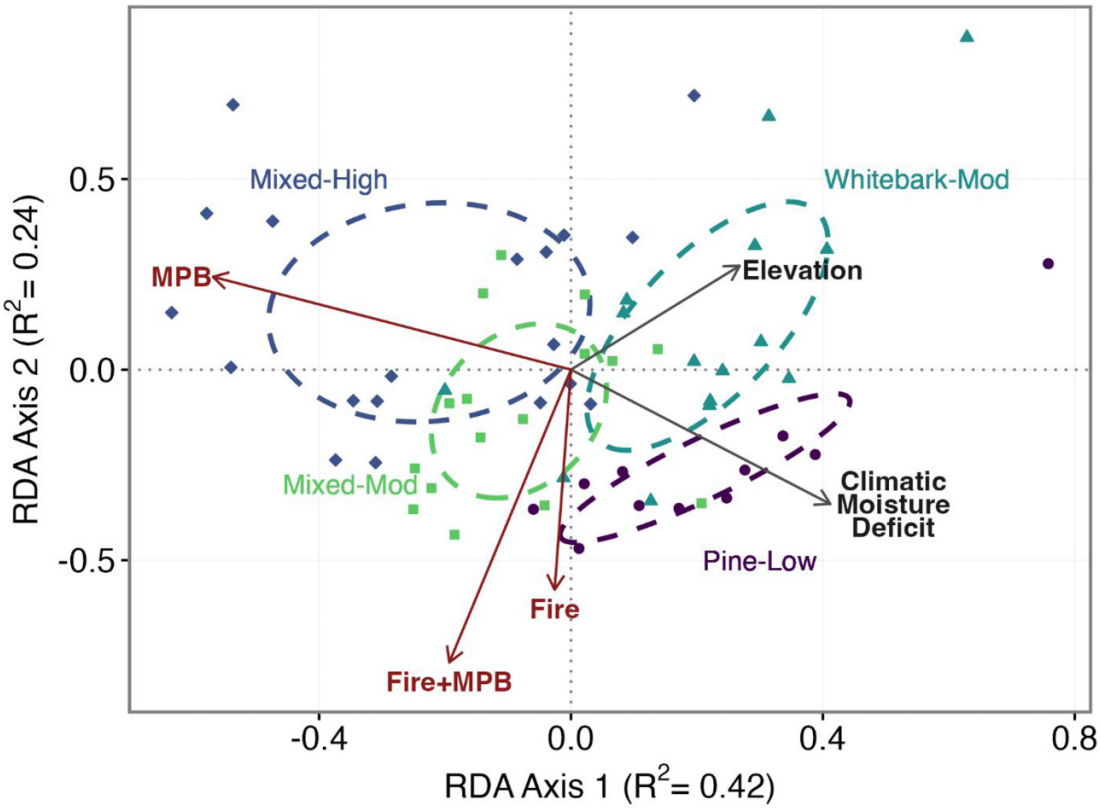


Table 6. Variation among whitebark pine forest communities in elevation (m), climatic moisture deficit (mm), and mortality of whitebark pine (% of density).

	Forest community				
	Pine-low	Mixed-mod	Mixed-high	Whitebark-mod	Overall
Elevation (m)	2576 ± 27[a]	2577 ± 42[a]	2661 ± 32[ab]	2740 ± 54[b]	2658 ± 22
Climatic moisture deficit (mm)	261.5 ± 6.6[a]	251.4 ± 5.9[a]	220.6 ± 9.4[b]	245.3 ± 7.9[a]	242.1 ± 4.4
Tree mortality (% of density)					
Fire	59.8 ± 25.2%	45.2 ± 19.6%	44.8 ± 4%	68.2 ± 31.8%	59.3 ± 10.6%
Mountain pine beetle (MPB)	52.3 ± 19%	24.7 ± 8.6%	19.7 ± 5%	43.5 ± 9.2%	38.8 ± 4.5%
Fire + MPB	73.1 ± 17%	64.9 ± 5.2%	25.8%	31.8%	68.6 ± 7.0%
No fire or MPB	23.3 ± 13.7%	16.6 ± 6.5%	14.1 ± 4.5%	6.9 ± 4%	12.8 ± 2.9%
Overall	52.1 ± 10.2%[a]	34.8 ± 7%[ab]	20.9 ± 4.7%[b]	25.2 ± 6.7%[b]	36.3 ± 3.7%

Note: Estimates represent mean (±1 standard error) and statistical differences among community types are denoted with letters and are omitted in cases of nonsignificance ($\alpha = 0.05$).

our understanding of insect and disease host species preferences and fire dynamics (e.g., Burns et al. 2008; Campbell et al. 2011; Hood et al. 2015). For example, dense stand conditions with large whitebark and lodgepole pines present were heavily impacted by MPB, a finding consistent with expectations that mature trees are more susceptible to bark beetle attack and that denser stands increase the probability of this density-dependent disturbance (Perkins and Roberts 2003; Meyer et al. 2016). In contrast, WPBR was disproportionately found on the smaller tree size classes of whitebark pine, a phenomenon documented in some stands of the Greater Yellowstone region (Shanahan et al. 2016), but others have observed the opposite pattern in seedlings of different height (Shepherd et al. 2018). Infection by WPBR may have been underestimated in our plot network (found on ~48% of plots), as fire also predominantly killed trees in smaller size classes and thus destroyed evidence of prior infection in these whitebark pine size classes. Overall, whitebark pine was not preferentially killed in fire over other species, which is consistent with the lack of fire-resistant traits in subalpine forest species

Table 7. The frequency of plots (ratio of total sampled) per whitebark pine forest community that recorded live whitebark pine basal area ≥5 $m^2 \cdot ha^{-1}$ and healthy whitebark pine seedling densities ≥250 stems·ha^{-1}.

	Forest community				
	Pine-low	Mixed-mod	Mixed-high	Whitebark-mod	Total
Live PIAL basal area (≥5 $m^2 \cdot ha^{-1}$)					
Fire	0:3	0:4	1:2	0:2	1:11
MPB	0:2	0:4	6:10	2:5	8:21
Fire + MPB	0:3	0:3	1:1	0:1	1:8
No fire or MPB	1:3	2:5	3:6	8:10	14:24
Total	1:11	2:16	11:19	10:18	24:64
Healthy PIAL seedlings (≥250 stems·ha^{-1})					
Fire	0:3	1:4	1:2	2:2	4:11
MPB	0:2	2:4	8:10	4:5	14:21
Fire + MPB	0:3	3:3	1:1	1:1	5:8
No fire or MPB	0:3	2:5	6:6	4:10	12:24
Total	0:11	8:16	16:19	11:18	35:64

Note: Healthy seedlings included those lacking WPBR infection. MPB: mountain pine beetle.

of this region (Stevens et al. 2020). Ongoing regeneration in the burned or MPB-attacked stands studied here suggests that seed availability persisted or seeds were cached following disturbance, with variation in regeneration densities likely corresponding to remnant live tree cover, Clark's nutcracker dispersal dynamics, and other microsite factors (Leirfallom et al. 2015; Hankin et al. 2021, 2025).

Forest communities aligned with broad elevational and climatic gradients and reflect established types and patterns described by Arno (2001). Disturbance impacts varied by community type across these gradients with mortality rates greater in lower elevation *pine-low* and *mixed-mod* communities than high elevation *mixed-high* and *whitebark-mod* communities. Fire-caused mortality was more prevalent in these lower, drier community types, and fire-impacted stands rarely met persistence thresholds for live basal area and seedling densities. WPBR incidence was also lowest in low elevation communities, particularly *pine-low*, which may reflect low pathogen contagion due to low host and secondary host abundances. MPB outbreak was common in dense, mid- to upper-elevation stands with abundant preferred MPB host species co-dominating with subalpine fir (Raffa et al. 2013; Howe et al. 2021). These stands typically supported abundant regeneration (≥250 stems·ha^{-1}). The *mixed-high* and *whitebark-mod* communities also frequently supported remnant live whitebark basal area sufficient for sustaining cone production and attracting dispersers, but WPBR incidence was highest in these communities. The *mixed-mod* community type was associated with high mortality driven by the co-occurrence of fire and MPB, likely due to the combination of suitable host species with higher fuel loads. Despite high overstory mortality, this community type supported intermediate levels of regeneration and lower incidence of WPBR. Stands that lacked recent fire or MPB ("no fire or MPB") exhibited the highest whitebark basal areas and seedling densities and were found most frequently in the highest elevation whitebark pine dominant community, where cool dry conditions limit the abundance of less drought-tolerant subalpine species (Arno 2001). While not directly observed in this study, mixed-species community types in the Intermountain West region have experienced rising incidence of the non-native mortality agent balsam woolly adelgid (*Adelges picea* Ratzeburg; "BWA") and warrant careful monitoring for compositional and fuel loading implications (Davis et al. 2022; Hicke et al. 2023).

Disturbance type influenced compositional shifts in the overstory and understory, shaping postdisturbance community types and persistence characteristics. In MPB-affected stands, mortality of mature whitebark and lodgepole pines led to greater relative abundance of subalpine fir in the overstory and also conferred a reproductive advantage that led to high subalpine fir seedling abundances. While whitebark pine and subalpine fir seedling densities were higher in terms of absolute density following MPB than fire, the regenerating community had a greater subalpine fir component following both disturbances compared to the surviving overstory community composition. While our study does not directly observe predisturbance conditions, our findings corroborate established succession models (Keane 2001) and empirical studies that also found that MPB outbreaks facilitate mid- to late-seral species shifts to shade-tolerant and nonhost species such as subalpine fir (e.g., Keane and Arno 1993; Airey and Taylor 2024). Substantial infilling of shade-tolerant subalpine fir seedlings was also evident on sites lacking fire or MPB, consistent with other fire-suppressed stands, although to varying degrees (Meyer et al. 2023). The development of high-density conditions may lead to competition-based mortality and (or) heightened susceptibility to drought and subsequent insect attack (Kolb et al. 2016). Increased subalpine fir relative abundance following MPB, or in the absence of fire and MPB, may have implications for future stand and landscape susceptibility to BWA, affecting future fuel conditions and associated fire hazard (Hicke et al. 2023; Campbell et al. 2024).

The role of fire varies widely across whitebark pine ecosystems, depending on continuity of fuels and climatic conditions. Despite fire-impacted stands exhibiting the greatest overstory mortality, especially for mature subalpine fir, fire was positively associated with both whitebark pine and subalpine fir relative abundance in the regenerating community compared to postfire overstory composition. Several studies in Interior and Rocky Mountain whitebark ecosystems have highlighted the fire-dependent nature of whitebark pine forests (Keane et al. 2022) and found that while fire readily kills individual whitebark pine trees, many stands depend on fire for removal of excess fuels, competition reduction, and to improve the availability of Clark's nutcracker seed caching sites (Keane 2018; Retzlaff et al. 2018; Hoffman et al. 2025). Our results indicate some consistency with these beneficial effects; however, low overstory survival and potential for rising competition in some regeneration communities warrants further monitoring to assess long-term implications for whitebark pine.

Management implications

Despite widespread and rapid loss of mature whitebark pine across its range, our study offers a modicum of hope for the functional persistence of whitebark pine stands in central Idaho and northern Nevada. Use of persistence metrics that characterize a stand's ability to support ongoing cone production and successful recruitment of new individuals may help match strategic management interventions to a given community type. In the portions of the range assessed here, postdisturbance trees met the persistence threshold for supporting cone production and disperser populations in roughly one third of plots, and seedling abundances exceeded the persistence density threshold in more than half of plots. These estimates suggest recovery and maintenance of ecological function across many stands following disturbance. Proactive, yet strategic, interventions that promote whitebark pine health, regeneration, and genetic diversity, or otherwise mitigate undesirable disturbance outcomes may still benefit heavily impacted stands (Tomback et al. 2022), and species' viability assessments can help prioritize conservation efforts (US Fish and Wildlife Service 2021).

Given that many of the West's other forest ecosystems also face critical management challenges and threats to species persistence, conservation efforts in whitebark pine forests should be prioritized where action can have the greatest impact. Silvicultural intervention may improve stand conditions in some cases, and consideration of forest communities, postdisturbance forest dynamics, and persistence metrics based on the availability of healthy mature trees and healthy regeneration will be a valuable gauge for potential success. For example, measures that reduce interspecies competition, enhance whitebark pine vigor, reduce fuels, and (or) improve seed beds may lead to the greatest benefit if applied to mixed species stands such as the *mixed-mod* and *mixed-high* communities identified in this study. In whitebark pine dominant communities such as the *whitebark-mod* community, activities that attract dispersers, improve seed beds, and (or) promote favorable microsite conditions for planting rust resistant seed stock may help whitebark pine maintain its climax role. Prescribed burning and managed wildfire may achieve objectives in some stands (Keane et al. 2022). Use of restoration resources may be less strategic in stands where whitebark pine serves a minor seral role or where mature tree and regeneration abundances both fall below persistence thresholds (e.g., the pine-low community type).

Restoration efforts will be best focused in areas where projected climate conditions will continue to be suitable for establishment (Parks et al. 2025), such as those in the higher subalpine and alpine forest types. Long-term ecological monitoring and evaluation of whitebark pine and associated forest community demographics, stand dynamics, species distributions, restoration treatment effects, and disturbance impacts will be critical to adaptive management decision-making and ensure continued stewardship of this widespread keystone species in an era of unprecedented changes to climate and disturbance regimes.

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Data availability

Data generated or analyzed during this study are available from the corresponding author upon reasonable request.

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Competing interests

The authors declare there are no competing interests. The findings and conclusions in this publication are those of the author(s) and should not be construed to represent any official USDA or U.S. Government determination or policy.

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Appendix A

Fig. A1. Whitebark pine tree size distribution showing the rate of white pine blister rust infection in plots with observed white pine blister rust occurrence (30 of 64 plots). Species abbreviation: PIAL—Whitebark pine (*Pinus albicaulis*).

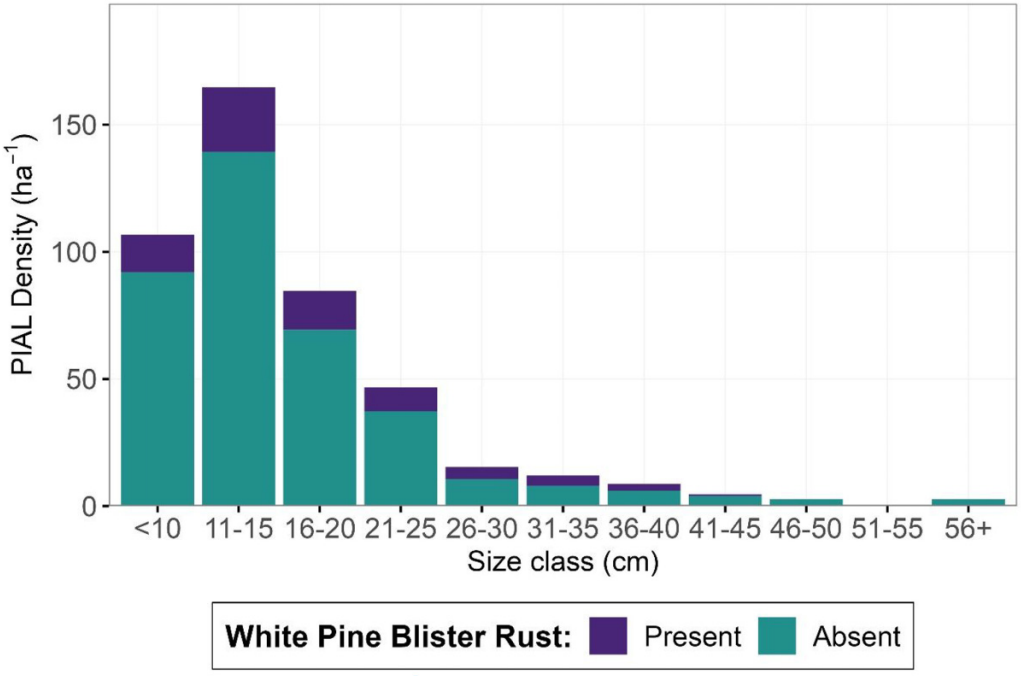

Fig. A2. Stacked bar chart showing the proportion of plots sampled per forest community type that fall within four categories representing contrasting low and high seedling density and tree basal area, respectively. Categories included: <250 seedlings (ha^{-1}) and <5 basal area (m^2·ha^{-1}), >250 seedlings (ha^{-1}) and <5 basal area (m^2·ha^{-1}), <250 seedlings (ha^{-1}) and >5 basal area (m^2·ha^{-1}), and >250 seedlings (ha^{-1}) and >5 basal area (m^2·ha^{-1}).

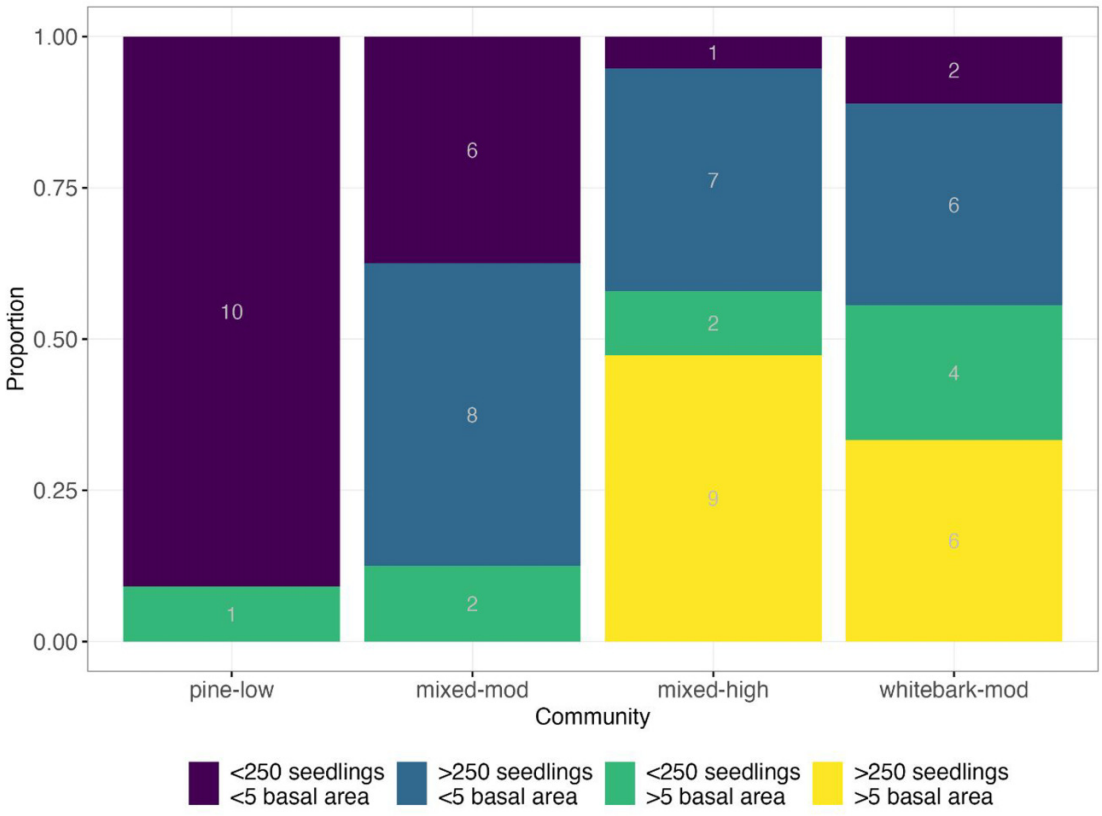

Table A1. Frequency of plots (ratio of total sampled) per USDA National Forest administrative unit that recorded live whitebark pine basal area ≥5 $m^2 \cdot ha^{-1}$, whitebark pine tree mortality ≥50% of basal area, the presence of white pine blister rust (WPBR), and healthy whitebark pine seedling densities ≥250 $stems \cdot ha^{-1}$.

	National Forest administrative unit						
	Boise National Forest	Salmon-Challis National Forest	Payette National Forest	Sawtooth National Forest	Frank Church River of No Return Wilderness	Humboldt-Toiyabe National Forest	Total
PIAL mortality (≥50% basal area)							
Fire	0:4	–	2:5	–	2:2	–	4:11
MPB	3:4	3:10	0:4	2:3	–	–	8:21
Fire + MPB	–	1:1	0:1	1:1	3:5	–	5:8
No fire or MPB	0:4	0:7	0:1	0:8	0:1	0:3	0:24
Total	3:12	4:18	2:11	3:12	5:8	0:3	17:64
Live PIAL basal area (≥5 $m^2 \cdot ha^{-1}$)							
Fire	0:4	–	1:5	–	0:2	–	1:11
MPB	1:4	4:10	1:4	2:3	–	–	8:21
Fire + MPB	–	0:1	1:1	0:1	0:5	–	1:8
No fire or MPB	1:4	4:7	1:1	5:8	0:1	3:3	14:24
Total	2:12	8:18	4:11	7:12	0:8	3:3	24:64
WPBR present							
Fire	2:4	–	1:5	–	0:2	–	3:11
MPB	3:4	7:10	4:4	1:3	–	–	15:21
Fire + MPB	–	0:1	1:1	0:1	0:5	–	1:8
No fire or MPB	2:4	4:7	1:1	3:8	0:1	2:3	12:24
Total	7:12	11:18	7:11	4:12	0:8	2:3	31:64
Healthy PIAL seedlings (≥250 $stems \cdot ha^{-1}$)							
Fire	1:4	–	3:5	–	0:2	–	4:11
MPB	1:4	6:10	4:4	3:3	–	–	14:21
Fire + MPB	–	1:1	1:1	1:1	2:5	–	5:8
No fire or MPB	1:4	3:7	1:1	6:8	1:1	0:3	12:24
Total	3:12	10:18	9:11	10:12	3:8	0:3	35:64

Note: Healthy seedlings included those lacking WPBR infection. MPB: mountain pine beetle.

Table A2. The number of plots in each forest community type grouped by disturbance and administrative unit.

	Pine-low	Mixed-mod	Mixed-high	Whitebark-mod
Frequency of plots per disturbance type				
Fire	3	4	2	2
MPB	2	4	10	5
Fire + MPB	3	3	1	1
No fire or MPB	3	5	6	10
Total	11	16	19	18
Frequency of plots per National Forest administrative unit				
Boise National Forest	2	6	2	2
Frank Church River of No Return Wilderness	5	2	1	0
Humboldt Toiyabe National Forest	1	0	0	2
Payette National Forest	0	4	6	1
Salmon-Challis National Forest	3	1	6	8
Sawtooth National Forest	0	3	4	5
Total	11	16	19	18

Note: MPB: mountain pine beetle.

Table A3. Tree species abundances by size class in whitebark pine forest community types defined using hierarchical cluster analysis.

		Whitebark pine forest community			
Size class	Species	Pine-low	Mixed-mod	Mixed-high	Whitebark-mod
Seedlings	PIAL	71 ± 29	284 ± 50	1012 ± 274	437 ± 95
Seedlings	ABLA	40 ± 18	668 ± 75	3944 ± 1264	91 ± 24
Seedlings	PICO	69 ± 39	351 ± 113	295 ± 85	72 ± 32
Seedlings	Other	4 ± 2	16 ± 6	52 ± 22	64 ± 27
Saplings	PIAL	78 ± 27	185 ± 43	386 ± 96	267 ± 42
Saplings	ABLA	76 ± 28	206 ± 64	424 ± 87	38 ± 17
Saplings	PICO	55 ± 32	58 ± 18	76 ± 21	50 ± 27
Saplings	Other	0 ± 0	0 ± 0	13 ± 12	32 ± 19
<25 cm DBH	PIAL	15 ± 6	89 ± 20	291 ± 63	422 ± 106
<25 cm DBH	ABLA	16 ± 10	111 ± 32	199 ± 39	20 ± 7
<25 cm DBH	PICO	67 ± 26	62 ± 22	117 ± 32	57 ± 32
<25 cm DBH	Other	47 ± 45	5 ± 5	8 ± 4	18 ± 7
>25 cm DBH	PIAL	22 ± 14	18 ± 8	48 ± 16	59 ± 21
>25 cm DBH	ABLA	0 ± 0	18 ± 4	21 ± 9	6 ± 3
>25 cm DBH	PICO	20 ± 16	18 ± 6	28 ± 13	2 ± 2
>25 cm DBH	Other	22 ± 12	1 ± 1	9 ± 5	19 ± 7

Note: Means ± 1 standard error. Size classes include live seedling (less than 1.37 m height), sapling (1.37 m height to 7.6 cm DBH), small tree (7.6–24.9 cm DBH), and large tree (25 cm or greater DBH). Species abbreviations include ABLA—Subalpine fir (*Abies lasiocarpa*), PIAL—Whitebark pine (*Pinus albicaulis*), PICO—Lodgepole pine (*Pinus contorta*), and other—species of low abundance.