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ARTICLE

Vegetation Ecology

A multi-scale assessment of interior Douglas-fir tree mortality for hazard and risk assessments

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Abstract

Land managers use hazard (susceptibility) and risk rating systems to guide the application of forest management treatments that aim to reduce future damages to forests. Rating systems are typically designed for individual damage agents, but tree mortality often results from multiple agents without a clear proximate cause. In interior Douglas-fir (DF, *Pseudotsuga menziesii* var. *glauca*) forests in the Northern Rocky Mountains, USA, multiple damage agents are commonly associated with DF tree mortality, such as insects, disease, weather, and fire. We investigated how recent DF tree mortality from insects and diseases (excluding fire and harvest) shifted stand structure and composition in DF forests and was influenced by susceptibility (e.g., stand structure and composition, topography, and spatial variability in climate) and risk (biotic agent pressure). Our multi-scale analysis used 884 plots remeasured after 10 years from the USDA Forest Inventory and Analysis program with support from spatial datasets. Across a large, forested landscape, 60% of the plots had no new DF mortality, and most plots (80%) experienced mortality <10% of DF basal area. However, severe tree mortality, defined as >25% loss of DF basal area, occurred in 6% of plots. Most of the dead DF trees (68%) were smaller diameter (12.7–29 cm at breast height) and mortality rates of smaller trees were significantly greater than those of larger diameter trees (>29 cm), a finding consistent with natural stand development processes. During the remeasurement period, average DF tree size increased in most plots (80%) and <4% of DF-dominated plots with severe mortality shifted in dominance from DF to another tree species. Greater DF mortality (percentage of initial DF basal area) was associated with lower tree growth rates, larger average tree sizes, greater availability of DF tree hosts for biotic agents, cooler and wetter topo-climatic locations, and higher Douglas-fir beetle population pressure. The relative importance of each variable differed west and east of the Continental Divide. By identifying thresholds in susceptibility and risk variables associated with higher DF tree mortality, our results support adaptive forest management

for multiple damage agents, when the goal is to reduce tree mortality of a widespread and abundant conifer.

KEYWORDS
Dendroctonus pseudotsugae, Douglas-fir, Douglas-fir beetle, hazard and risk models, national forest inventory, *Pseudotsuga menziesii*, root disease

INTRODUCTION

In many temperate forest regions, tree mortality from drought and biotic agents has been widely documented in recent decades (Hammond et al., 2022; Peng et al., 2011; Senf et al., 2018). Mortality is commonly associated with multiple, potentially interacting agents (Agne et al., 2018; Anderegg et al., 2015; Seidl et al., 2015). The "decline-disease spiral" is a useful framework for understanding how agents acting at multiple spatiotemporal scales are associated with tree mortality (Manion, 1991). Marginal site conditions (e.g., low soil water holding capacity) and dense stands with high competition for resources may predispose trees or stands to faster decline (predisposing factors). Unfavorable climate or weather (e.g., drought and/or warm temperatures) or other conditions that impair the physiological functioning of trees (inciting factors) may reduce resistance to biotic agents (e.g., bark beetles and root diseases) and other stressors (contributing factors), individually or collectively causing tree mortality. To help predict when and where trees are vulnerable to mortality and help prioritize stands for management action, land managers need a better understanding of the constraints on tree mortality, with recent hot and dry conditions potentially offering insights into how forests may respond to climate change (Vose et al., 2019).

Among the factors influencing tree mortality (e.g., climate, soil water holding capacity, and insect population size), land managers are limited in what they can directly influence, but they can manipulate stand structure and composition. In the context of drought, insect, and disease-related mortality, the focus of our study, measurements of stand structure and composition are collected to identify stand characteristics that predispose stands to contributing factors (e.g., insects or disease). From field measurements, hazard (susceptibility) rating systems are developed for forest managers to prioritize stands for silvicultural treatments (Bentz et al., 1993; Hicks et al., 1987). Early insect hazard rating systems (c. 1930–1940s) focused on identifying individual trees with high susceptibility to damage agents for selective removal (e.g., large-diameter trees and poor crown condition). However, current approaches to management focus on treating stand conditions by manipulating tree spacing, species, and size, with the goal of meeting multiple management objectives (Hicks et al., 1987; O'Hara et al., 2010). The goals of silvicultural treatments can vary widely, but they are often intended to promote stand structures and compositions that reduce tree mortality (i.e., increase stand resistance) from a specific mortality agent over the long term (DeRose & Long, 2014; Kneeshaw et al., 2021). Importantly, hazard ratings do not predict when or if damage will occur or signify that low hazard stands will not experience damage.

To complement hazard, risk is the short-term (one to multiple years) likelihood that mortality will occur (Shore et al., 2000). The risk of occurrence is determined by the complex and nonlinear relationships among stand susceptibility, climate variability (inciting factors), and agent pressure (contributing factors). For example, the size and proximity of the bark beetle population may be used to assess the risk of bark beetles entering a susceptible stand (Dymond et al., 2006). During periods when bark beetle populations are small, highly susceptible stands may experience minimal risk, whereas during periods when beetle populations are large, even stands with low susceptibility may be at risk for damage. Successful application of silvicultural treatments to reduce insect and disease damage has demonstrated the need to continually refine and evaluate hazard and risk rating systems, particularly in the context of climate-driven shifts in agent–host interactions (Kneeshaw et al., 2021; Morris et al., 2017). To more accurately capture interactions among agents and inform management decisions, improvements to hazard and risk systems are needed at management-relevant scales (i.e., stand to landscape scale) for individual forest types (Kline et al., 2013).

Interior Douglas-fir (*Pseudotsuga menziesii* var. *glauca*, hereafter DF) is the most widespread and commercially valuable tree species in the western United States, including the Northern Rocky Mountains (NRM). In addition to timber production, DF forests are managed for carbon sequestration, old growth character, soil retention, recreation, wildlife habitat, and more (Healey et al., 2016). Changing climate is shifting suitable habitats for DF trees and creating new marginal site conditions across large DF-forested areas, particularly in lower elevation warmer and drier locations (Bell et al., 2014; Bennett et al., 2023;

Kim et al., 2021; Weiskittel et al., 2012). Many DF forests, particularly in the NRM, are considered highly susceptible to damages from multiple agents, including root diseases and insects, from legacies of land and forest management, disturbance, and climate (Krist et al., 2015). During the current multi-decadal warm and dry period (2000 to present; Costanza et al., 2023; Egan et al., 2024; Williams et al., 2022), bark beetles, drought, root diseases, and wildfire have been associated with elevated DF tree mortality (Stanke et al., 2021). For example, nearly 200,000 ha of DF tree mortality were attributed to Douglas-fir beetle (DFB, *Dendroctonus pseudotsugae*) from 1997 to 2023 in the western United States (Andrus, Hicke, & Meddens, 2025). Many of these mortality agents are native and an important part of the natural ecology and functioning of DF forests, such as creating heterogeneity in stand structure (Morris et al., 2017). To understand the scope of recent DF tree mortality and the implications for future forests, forest managers need to know the spatial variability in mortality from multiple agents across large, forested regions and how mortality is reshaping stand structure and composition.

Douglas-fir tree mortality often occurs from multiple, potentially interacting agents (see Appendix S1: Table S1 for the list of agents). Warmer and drier weather (inciting factors) reduces soil moisture, compromises hydraulic systems and tree defenses, and reduces resistance to lethal bark beetle attack (Howe et al., 2024; Huang et al., 2020; Raffa et al., 2008; Restaino et al., 2016). Within areas of suitable host availability, periodic outbreaks of defoliating insects, such as western spruce budworm (*Choristoneura occidentalis* Freeman) and Douglas-fir tussock moth (*Orgyia pseudotsugata*), also reduce tree growth and defenses, making them more susceptible to DFB activity (Cole et al., 2022; Howe et al., 2024; Wright et al., 1984). Similarly, multiple root diseases (RD), such as *Armillaria* spp., compromise the root conductive capacity of DF trees, reducing resistance to bark beetle attack and releasing chemicals that attract bark beetles (Ferrell & Parmeter, 1989; Goheen & Hansen, 1993; Kelsey et al., 2016). Mortality from multiple, co-occurring or interacting agents, particularly following severe mortality, may have important implications for stand structure and composition. For example, endemic populations of DFB may only attack blown down or stressed DF trees, whereas epidemic DFB populations, often produced by abundant host material and drought, may produce low severity (e.g., <5% mortality of forest area per hectare) DF mortality across tens of thousands of hectares with localized areas of much higher severity (e.g., >25% mortality of forest area per hectare; Andrus, Hicke, & Meddens, 2025). Increasingly marginal conditions in some DF habitats and the lack of a single aggressive or proximate agent associated with tree mortality have prompted questions about how to manage for multiple, interacting mortality agents (Bollenbacher et al., 2014).

For DF forests in the NRM, individual hazard rating systems were developed for DFB and RD, but they do not address agent and host interactions under changing stand and climate conditions. Among mortality agents, DFB and RD are considered the primary agents of mortality of larger diameter DF trees, but other agents play a role in the decline spiral, particularly in smaller diameter trees (IDL, 2020). The DFB hazard rating systems are assessed at the stand scale and are based on the preference of DFB for older, large-diameter DF trees, stands with trees stressed from higher competition for resources, and stands with higher densities of DF trees (McMillin & Allen, 2003; Negron et al., 1999). The hazard rating system for DFB includes three stand attributes: (1) the quadratic mean diameter (QMD) of DF > 23 cm dbh as a measure of suitable DF hosts, (2) the living stand basal area (BA) as a measure of competition, and (3) the percent of BA in DF as a measure of host availability (Randall et al., 2019). The RD hazard rating systems incorporate multiple RD agents that affect DF trees in the NRM (see Appendix S1: Table S1 for list of RDs) and were designed to be interpreted at the National Forest to regional scale (Bennett et al., 2022; Holden et al., 2020; Lockman et al., 2016). Root diseases cause greater mortality in stands with higher host availability, such as DF and true fir (*Abies*) species, and are most likely to be present in conducive environments, which are more common west than east of the Continental Divide in the NRM (Byler & Hagle, 1990; Holden et al., 2020; Lockman et al., 2016). In practice, integrating multiple hazard rating systems for individual agents is challenging, so forest managers have proposed the development of hazard models that account for multiple, often co-occurring agents associated with DF mortality.

We investigated how interior DF tree mortality attributed to insects and diseases (excluding fire and harvest), but likely resulting from agent interactions, was affected by susceptibility (tree, stand, and topo-climatic factors) and risk factors in two ecoregions (west and east of the Continental Divide) in the NRM. Our analyses included 884 forest inventory plots remeasured once on a 10-year interval from the USDA Forest Service Forest Inventory and Analysis (FIA) program (Tinkham et al., 2018). Analyses were supplemented with spatial datasets. To characterize regional DF tree mortality, we asked: (1) How did stand structure and composition of DF stands change during the remeasurement period? To understand whether mortality agents affecting DF forests during the study period had preferences for specific tree

size classes, we asked, (2) how did DF mortality rates vary by tree size? To improve hazard rating systems and assess the importance of risk variables, we asked (3) how was DF mortality (percent of DF BA) influenced by susceptibility and risk factors? To inform forest management strategies, we compare our results to existing hazard rating systems, provide decision support for forest managers, and discuss our results in the context of climate-adaptive forest management strategies.

METHODS

Study area

The study area was interior DF forests in the NRM within USDA Forest Service Northern Rocky Mountain Region (Region 1; Figure 1A). Winters in this region are cold and snowy, and summers are warm and dry, but average seasonal temperatures and precipitation regimes vary widely across the study area (Whitlock et al., 2017). West of the Continental Divide climate conditions are wetter and warmer compared to the cooler and drier conditions east of the Divide (Appendix S1: Table S2). From 1950 to 2020, the mean annual temperature increased 1.9–2.1°C (range across climate divisions) in the study area, with the greatest increases in spring temperatures (3.3–3.4°C) compared to other seasons (Burst, 2022). Total annual precipitation was highly variable during the same period, with a slight decreasing trend in annual precipitation west of the Divide (0.7 cm/decade) and a slight increasing trend east of the Divide (0.3 cm/decade) (Burst, 2022). Greater moisture deficits are particularly evident during the warm season (May–September) from 2000 to 2021, especially west compared to east of the Continental Divide in Montana (Egan et al., 2024).

In the NRM, DF occurs across a broad range of biophysical settings from dry to mesic stands with monotypic and mixed-conifer compositions (see Appendix S1: Figure S1 for associated species). The composition and structure of DF stands vary west and east of the Continental Divide due to differences in climate, topographic effects on moisture availability, and disturbance history. West of the Divide, DF occurs with mesic mixed-conifer species, such as grand fir (*Abies grandis*), western larch (*Larix occidentalis*), western hemlock (*Tsuga heterophylla*), and western redcedar (*Thuja plicata*) as well as cold forest (high elevation) species, such as lodgepole pine (*Pinus contorta*), subalpine fir (*Abies lasiocarpa*), and Englemann spruce (*Picea engelmannii*). East of the Divide, DF stands are commonly monotypic or mixed with cold forest conifer species. Ponderosa pine (*Pinus ponderosa*) is a common associate in low elevations and the only co-occurring species that is more drought tolerant than DF (Keane et al., 2018).

Datasets and data processing

Forest inventory and analysis plot data

The FIA program established a systematic grid (~4.7 km) of permanent plots to monitor changes in US forests (FIA, 2024a, 2024b; Smith, 2002). Plots consist of four circular subplots (7.32 m radius), with a central subplot and three subplots spaced ~37 m from the central subplot. Subplots are assigned a "condition" (i.e., forested, non-forested, water) based on collected attributes such as stand structure, composition, and ownership. Because our goal was to aggregate subplot data with a similar structure, composition, and management history to a plot (i.e., sample unit), we only included plots with at least 75% of subplots in the "forested" condition. Prior to aggregating subplot data, we excluded subplots in a different condition. Plots in the western United States are monitored approximately every 10 years, with ~10% of the plot inventory monitored per year. Our study included plots that were remeasured once. In FIA plots, individual trees are tagged to allow more accurate estimates of growth and mortality rates (McNellis et al., 2021). We included plots measured from 2003 to 2009 and remeasured from 2013 to 2019 (see Appendix S1: Table S3 for plot counts). To protect the anonymity of the FIA plot locations, plot coordinates are randomly reassigned new coordinates with the new location generally within 1.6 km of the true location (i.e., fuzzed). For a random set of the plots on private lands, these fuzzed plot locations are switched (i.e., swapped; 177 of 884 plots were on private lands). Topographic variables are collected for each plot and representative of the original plot location (aspect and slope) and the fuzzed location (elevation). To include a finer scale characterization of spatial variability in soil moisture than topographic or climatic variables can provide, the Habitat Type of each plot (collected by FIA) was assigned to one of eight Habitat Type Groups used by USDA Forest Service Region 1 (Milburn et al., 2015). Habitat Type Groups range from CoolMoist to HotDry. Habitat Type Groups are further grouped into four Potential Vegetation Types (WarmDry, WarmMoist, CoolMoist, and Cold).

In addition to plot-level variables, FIA crews collected many tree-level variables (e.g., species, status, dbh) for stems >12.7 cm dbh, and the FIA database included many calculated stand variables (stem density and BA; Burrill et al., 2024). To more accurately estimate mortality, plots with <75 DF stems/ha (~5 trees per plot) were excluded from our analysis. In the field, individual tree mortalities were assigned to a general group of mortality

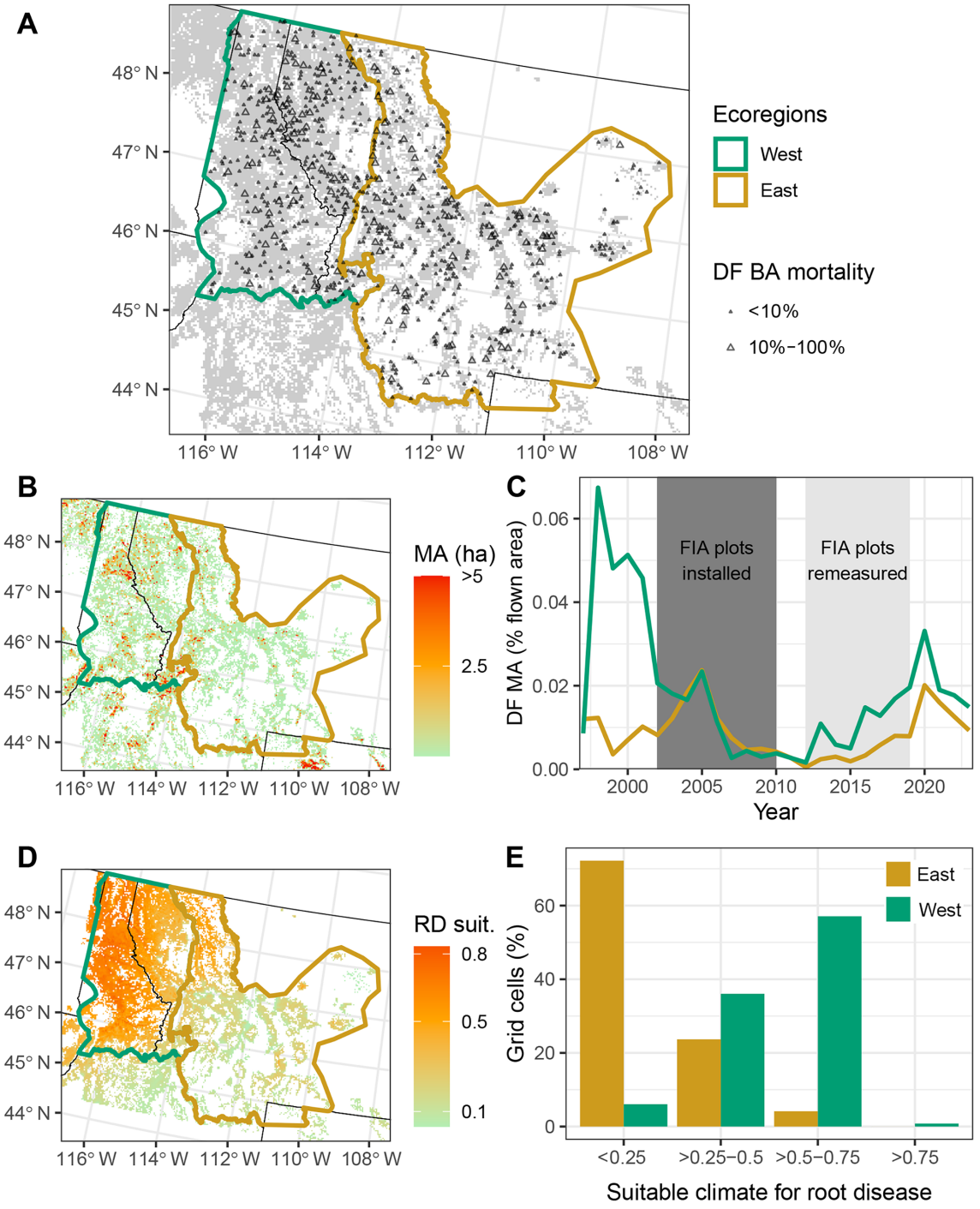

FIGURE 1 (A) Douglas-fir (DF) basal area (BA) mortality of the USDA Forest Inventory and Analysis (FIA) plots (884 plots; fuzzed locations) overlaid on the distribution of interior Douglas-fir (gray) in the Northern Rocky Mountains, USA. DF BA mortality (in percentage) was the percentage of DF BA that died during the remeasurement interval (~10 years) divided by the total live DF BA in the initial plot measurement. The analysis was divided into two ecoregions (EPA Level III modified to US Forest Service Region 1; US EPA, 2010). (B) Cumulative mortality area (MA) of DF attributed to Douglas-fir beetle (DFB) from gridded aerial surveys (1-km grid cells; 1997–2023; Andrus, Hicke, & Meddens, 2025). (C) The annual time series of DF MA from (B) as the percentage of area flown (surveyed), and the FIA plot installation (2002–2009) and remeasurement years (2012–2019) to illustrate the overlap with regional trends in DF mortality. (D) The spatial model and (E) grid cells (percentage by ecoregion) of suitable climate for root disease (RD) (Holden et al., 2020), illustrating the higher suitability in the west ecoregion relative to the east.

agents (rather than individual agents), including insect, disease, wildfire, animal, weather (includes lightning strike and blowdown but not drought), vegetation (competition), and other (agent unknown). More detailed agent assignment is not expected as FIA crews are not professional entomologists or pathologists. To quantify the effects of commonly co-occurring mortality agents in areas not recently affected by fire or harvest, we evaluated plots where the FIA mortality agent group codes included insect and/or disease, representing ~62% of DF tree mortalities in the NRM during the study period (Appendix S1: Table S4). While FIA crews cannot diagnose individual RD agents affecting DF in USFS Region 1, they are trained by pathologists to record indicators of RD presence and estimate impacts of RD using an RD rating system (Hagle, 2011; Lockman et al., 2016).

Insect and disease spatial surveys

To characterize broad-scale spatial and temporal variability in DF tree mortality of larger, overstory trees, we used annual, gridded spatial datasets (1 km^2 resolution) of DF mortality area attributed to DFB and areas flown during aerial surveys conducted by the USDA Forest Service National Insect and Disease Aerial Survey program (Andrus, Hicke, & Meddens, 2025; FHP, 2024). Mortality area is the area (in hectares) of killed trees within a 1-km grid cell. Mortality of DF trees was attributed to DFB due to tree size and mortality traits (e.g., crown color), but multiple other agents may have been associated with mortality, such as other bark beetle species, wood borers, defoliators, RD, drought, and competition (but not fire or harvest; see Appendix S1: Table S1 for the list of agents associated with DF mortality). These data provide a longer term context for DF mortality and were used to estimate DFB population pressure on FIA plots.

Spatial model of root disease

To illustrate the broad-scale spatial variability in climatic conditions associated with RD across the study area, we included a map of the suitable climate for RD in USDA Forest Service Region 1 (Holden et al., 2020). The RD spatial dataset was produced using field assessments of RD from FIA data along with biophysical spatial datasets. Estimates of RD suitability were developed for multiple RD agents and host tree species, and not specifically for DF trees (Holden et al., 2020).

Climate data

To understand how the spatial variability in climate influenced DF tree mortality, we extracted average climate from 1962 to 2022 for each FIA plot from TopoTerra (220 m gridded climate; Hoecker et al., 2025). TopoTerra products are downscaled from 4 km gridded spatial climate data using methods that incorporate fine-scale topographic differences in solar radiation rather than estimating climate variables based on elevational lapse rates. The following variables were extracted using bilinear interpolation (to account for uncertainty in plot location): actual evapotranspiration as a measure of site productivity (higher values indicating greater moisture and energy availability), climate water deficit, maximum temperature in July (hottest month), and minimum temperature in January (coldest month). Climate water deficit is the unmet moisture demand from the atmosphere (potential minus actual evapotranspiration), with higher values indicating greater water stress on vegetation.

Ecoregions

Climate, tree species composition, and mortality agents vary east and west of the Continental Divide (see citations in *Study area*). Using the US Environmental Protection Agency (EPA) Level III ecoregions dataset (US EPA, 2010), we aggregated ecoregions west and east of the Continental Divide (two per side) in the NRM into two broader ecoregions (hereafter, West and East; Figure 1A).

Analysis

Effects of DF mortality on stand structure and composition (Research question 1)

Tree mortality from biotic agents that affect specific tree size classes and host species may result in notable shifts in stand structure and composition, altering possible future management options. Following a century (early 1900s to present) of increasing stand density in many (but not all) DF forests in the NRM (Hessburg et al., 2019), Stanke et al. (2021) reported that recent DF mortality resulted in decreases in stand density (all stems ≥2.54 cm at dbh) in areas east but not west of the Continental Divide in the NRM. To understand the frequency of tree mortalities by tree size, we compared trees that survived to trees that died between plot measurements in three size classes relevant to forest management. DFB preferentially attacks trees greater than ~29 cm (Andrus, Egan, et al., 2025). As such, tree size classes were small (12.7–29 cm dbh), intermediate (>29–50 cm), and large (>50 cm). Defoliator-caused mortality is most common in trees smaller than those included in our study (<12.7 cm), though mortality of larger diameter trees does occur (Brookes et al., 1987; Hadley & Veblen, 1993).

We examined how DF tree mortality reshaped stand structure and composition using three common metrics, including DF BA mortality (in percentage), stand dominance (by %BA), and DF QMD (in centimeters). To calculate DF BA mortality (in percentage), we divided DF BA mortality (in square meters per hectare) during the remeasurement interval (~10 years) by the total live DF BA in the initial plot measurement. We assessed whether stands dominated by DF in the initial plot measurement shifted to dominance by another tree species in the remeasurement and the amount of DF mortality associated with shifts in dominance. To understand how average tree sizes changed, we compared DF QMD in the two plot measurements with decreases in QMD likely indicating mortality of many large-diameter DF trees and increases in QMD likely indicating limited mortality and growth of intermediate to larger diameter DF trees.

Comparing DF tree mortality rates by tree size (Research question 2)

Assessing annual mortality rates by tree size helps interpret possible agents of mortality and the impacts of mortality on stand development. We computed annual mortality rates for all DF trees (>12.7 cm) and three tree size classes (same as above). Annual tree mortality rates (in percentage per year) were computed following Sheil et al. (1995) to account for differences in sample sizes among tree size classes and slight differences in the remeasurement interval (mean 10 years, range 9–11 years). For each ecoregion, the distributions of annual mortality rates by tree size classes (right-skewed distributions) were tested for differences using the nonparametric Kruskal–Wallis test (Kruskal & Wallis, 1952). Then, Dunn tests (Dunn, 1964) were used to test for pairwise differences between tree size classes (all p values were "holm" corrected; "rstatix" package in R; Kassambara, 2019).

Effect of susceptibility and risk factors on DF basal area mortality (Research question 3)

We examined how DF tree mortality was influenced by susceptibility and risk predictor variables by ecoregion. For DF tree mortality, we selected DF BA mortality (in percentage) rather than annual tree mortality rates, because it was available for all plots (e.g., large tree mortality was not available for all plots) and used in the National Insect and Disease Forest Risk Assessment (NIDFRA; Krist et al., 2015). Additionally, correlations between DF BA mortality (in percentage) and tree mortality rates (all trees and by size class) were strong, and both were similarly correlated (direction and magnitude) with most susceptibility and risk predictor variables (Appendix S1: Figure S2). In our analysis, we used three analytical approaches: (1) For three levels of DF BA mortality (0%, >0%–10%, >10%), we tested for differences in the distributions of selected predictor variables (selection process described below; Table 1) using Kruskal–Wallis tests followed by pairwise comparisons among levels of each variable with Dunn tests ($p < 0.05$). A 10% level was used based on resource managers' concerns over stand health and timber production when mortality levels exceed 10%. (2) To compare the relative influence and individual effect of a given predictor variable on DF mortality (continuous variable), we used random forest (RF) models (Breiman, 2001). (3) To identify thresholds (splits) in predictor variables that may be used to inform forest management decisions related to DF mortality, we constructed conditional inference trees with DF mortality (continuous response variable) and predictor variables.

We considered many susceptibility predictor variables that described the stand structure and composition, stand growth rates, topography, and spatial variability in climate (Appendix S1: Tables S5and S6). For stand structure and composition, we calculated the following from the initial plot measurement (i.e., pre-mortality): the stand density index (quasi-unitless; the number of 25-cm tree equivalents per hectare), stand density (in stems per hectare), stand BA (in square meters per hectare), BA of DF trees (in square meters per hectare and percentage of total BA), stem density of DF trees (in stems per hectare and percentage of total stems), QMD of DF trees >12.7 and >23 cm, CV of DF tree dbh to characterize tree size heterogeneity, percent of DF trees susceptible to DFB (percent of stems per hectare > 29 cm dbh), and percent of stand BA that was highly susceptible to RD. Root disease host BA was calculated as the percent of BA in DF and true firs (*Abies* spp.), excluding species with lower susceptibility to RD, such as pines (*Pinus* spp.) and western larch. Tree growth rates are the response to soil moisture availability, competition, and damage agents. Stands with faster growing, more vigorous trees may experience lower rates of mortality from biotic agents (Cruickshank et al., 2011; Shore et al., 1999) or higher rates of mortality from more rapid stand development (Larson et al., 2008). We calculated the annual basal area increment (BAI, in square centimeters per year) for co-dominant and dominant DF trees using dbh of individual live trees from plot measurements (Biondi, 1999). Then, we averaged BAI for all trees in a plot to produce a stand average. Because many stand structure and composition variables were highly correlated, we used a hierarchical cluster analysis of variable correlations to select a relatively unique and less correlated subset of variables for analysis (Table 1; Appendix S1: Figure S2), with a

TABLE 1 Predictor variables tested in the random forest model of Douglas-fir (DF) basal area mortality (in percentage), the justification and expected effect for each variable, and effect of each variable by agent from prior studies (see superscript numbers and footnotes).

Predictor variable (units)	Acronym	Justification (expected effect)	Prior findings by agent (effect)[source]
Susceptibility (hazard)			
DF basal area increment (cm^2)	DF BAI	Decreased host vigor and defenses (−)	DFB (−)[a,b] and RD (−)[c,d]
Stand basal area (m^2/ha)	Stand BA	Increased competition for resources (+)	DFB (+)[e,f]
Stand density index (quasi-unitless)	SDI	Increased competition for resources (+)	DFB (no effect)[b,g]
DF basal area (%)	DF BA	Increased competition for resources and greater host availability for biotic agents (+)	DFB (+)[a,b,g,h]
DF quadratic mean diameter (cm)	DF QMD	Greater host availability for DFB (+)	DFB (+)[g,h]
DF tree size heterogeneity (CV, unitless)	CV dbh	Reduced host availability for DFB (−)	DFB (−)
Heat load index (unitless)	HLI	Increased moisture stress (+)	RD (+)[i]
Annual climate water deficit (mm)	CWD	Increased moisture stress (+)	DFB (+)[j]
Risk			
DFB population pressure	DFB pressure	Greater likelihood for DFB attack (+)	DFB (+)[f]
Root disease (presence)	RD PA	Greater likelihood for root disease (+)	RD (+)[d,h]

Note: Many additional variables were considered but excluded due to multicollinearity (see Appendix S1: Table S5 for all variables and Appendix S1: Table S6 for variable summary statistics).
Abbreviations: dbh, diameter at breast height (1.4 m above ground surface); DFB, Douglas-fir beetle.
[a]Shore et al. (1999).
[b]Negron et al. (1999).
[c]Bloomberg et al. (1989).
[d]Cruickshank et al. (2011).
[e]Furniss et al. (1979).
[f]Steele et al. (1996).
[g]McMillin and Allen (2003).
[h]Weatherby and Thier (1993).
[i]Byler and Hagle (1990).
[j]Bennett et al. (2023).

preference for variables easily calculated or commonly used by forest managers (e.g., Randall et al., 2019) and variables used in previous studies of DF mortality (e.g., from DFB; Furniss et al., 1979; Negron et al., 1999).

Drier and warmer topo-climatic locations may increase DF tree stress as well as confer benefits to insect fitness, whereas cooler and wetter topo-climatic locations may be more suitable for some damage agents such as RD. To characterize topography, we included elevation (in meters), folded aspect (180°) (both collected by FIA), and heat load index (calculated from FIA variables). Heat load index measures incident solar radiation based on latitude (fuzzed), slope, and aspect, and ranges from 0 (coolest) to 1 (warmest) (McCune & Keon, 2002). At broader spatial scales than site topography, we characterized the spatial variability in climate with four climate variables as listed in *Climate data*. After preliminary analyses (Appendix S1: Figures S3 and S4), we selected heat load index and climate water deficit for our analysis (Table 1).

Metrics that quantify the biotic agent pressure from RD and DFB are likely associated with the amount of DF mortality in a plot (Dymond et al., 2006). At the scale of our study area, the Insect and Disease Aerial Survey is the only dataset available to estimate insect population pressure for each plot. In the Survey, DF mortality was primarily attributed to DFB during the study period. We use this gridded spatial dataset of DF mortality area to estimate the DFB population pressure by summing the number of hectares of DF mortality within 1, 5, and 20 km of each FIA plot. Only DF mortality that occurred during the FIA plot remeasurement period was included. After preliminary analysis, we selected DFB pressure within 1 km of the FIA for further analysis (Table 1; Appendix S1). For RD, we used an assessment of the proximity of RD to the plot that was collected by FIA crews. Plots with evidence of RD within 15 m of an FIA subplot (i.e., Hagle rating > 0) were assigned "presence" and plots with no evidence of RD within 15 m of an FIA subplot (Hagle rating = 0) were assigned "absence."

To assess the added benefit of including risk and topo-climatic variables in hazard models, we built three RF models for each region: (1) susceptibility and risk variables, (2) stand susceptibility variables only (excluding risk and topo-climatic variables), and (3) the variables in the existing DFB hazard model (Appendix S1: Table S7) for USDA Forest Service Region 1 (Randall et al., 2019). RF models were used to account for nonlinear relationships and complex interactions between DF BA mortality (in percentage) and predictor variables. From our selected subset of predictor variables (Table 1), we used forward feature selection (FFS) with spatially stratified cross-validation to remove variables poorly associated with DF mortality and produce models that could be generalized to unsampled areas (models 1 and 2 only) (Kuhn, 2008; Meyer et al., 2018). Spatial clusters (i.e., folds) were assigned using k-means clustering of the plot location. FFS identified slightly different sets of variables for each ecoregion, and we included all variables from each ecoregion in the final RF models to qualitatively compare the relative influence of predictor variables between ecoregions. The predictor variables identified by FFS were insensitive to the number of spatial folds (10 folds selected with 10, 20, and 30 folds tested). After variable selection, the RF model hyperparameters (e.g., "min.node.size") were tuned using spatial cross-validation and 1000 trees ("caret" package in R; Kuhn, 2008). The final model parameters were identified using the maximally selected rank statistic (Wright et al., 2017). We calculated and compared the relative importance of each variable with a mean decrease in accuracy statistic from permutations ("ranger" and "spatialRF" packages; Benito, 2021; Wright & Ziegler, 2017). To show how individual predictor variables affected DF mortality, we produced accumulated local effects plots, a less biased alternative to partial dependence plots (Molnar, 2018). Models were compared with R^2 values and root mean squared error from spatial cross-validation.

With the top four variables from the RF models (models 1 and 2 only), we used a conditional inference tree to estimate regression relationships and identify binary splits in susceptibility and risk variables associated with higher DF BA mortality ("partykit" package in R; Hothorn & Zeileis, 2011). Conditional inference trees produce a more robust result than traditional inference trees, because they account for the influence of other predictor variables. A split in the conditional inference tree is implemented if the permutation test statistic from one or more bivariate relationships has a p value <0.05. The input variable at each split is selected based on the strength of association, as indicated by p values (Bonferroni-adjusted) from bivariate relationships. All analyses were performed in R v. 4.3.2 (R Core Team, 2024).

RESULTS

Ecoregional trends in DF tree mortality in relation to FIA plot measurement

Annual estimates of DF mortality (percentage of flown area) that were attributed to DFB varied annually from 1998 to 2023 and the 10 years between FIA plot measurements corresponded to a period of relatively low DF mortality from DFB (Figure 1). West of the Continental Divide, DF mortality was highest from 1998 to 2002, a period prior to the initial measurement of FIA plots in our analysis. East of the Continental Divide, DF mortality from DFB peaked in 2005 and was likely recorded on some FIA plots. The period from 2007 to 2012 corresponded to relatively low DF mortality and occurred before plots were remeasured on both sides of the Divide. The increase in DF mortality since 2013 was likely recorded on some FIA plots. The suitability of climate for RD (static spatial layer) was much higher west compared to east of the Continental Divide.

Effects of DF mortality on stand structure and composition

In FIA plots selected for analysis (≥75 DF stems/ha and ≥75% in forest condition), 6.5% of DF stems (≥12.7 cm) died (1012 of 15,514) during the 10-year remeasurement interval (East, 7.1%; West, 5.6%; Figure 2). For both ecoregions combined, most dead DF trees were small (68%, 12.7–29 cm dbh), whereas intermediate and large trees (>29 cm; also, those most susceptible to DFB) represented 32% of dead trees. Comparing percentages of dead trees within tree size classes, a higher percentage of large trees (>50 cm) died, though large trees only represented 7.5% of dead DF trees in both ecoregions. Mortality of small trees only was found in 55% of plots in both ecoregions, whereas mortality of intermediate and large trees was found in 15% (East) or 22% (West) of plots.

Among mortality agent groups (diseases and insects), DF mortality was more commonly associated with disease in the West (85.1%; assumed largely to be RD) and insects in the East (78.7%; assumed to be DFB for intermediate-to-large trees; Figure 2). Mortality from both insects and diseases was recorded on a small percentage of plots in the West (1.8%) and East (3.0%) ecoregions (Appendix S1: Figure S6), suggesting multiple interacting mortality agents (e.g., RD-infected trees attacked by bark beetles).

Douglas-fir BA mortality (in percentage) was zero in more than half of all plots (West, 61% of 445 plots; East,

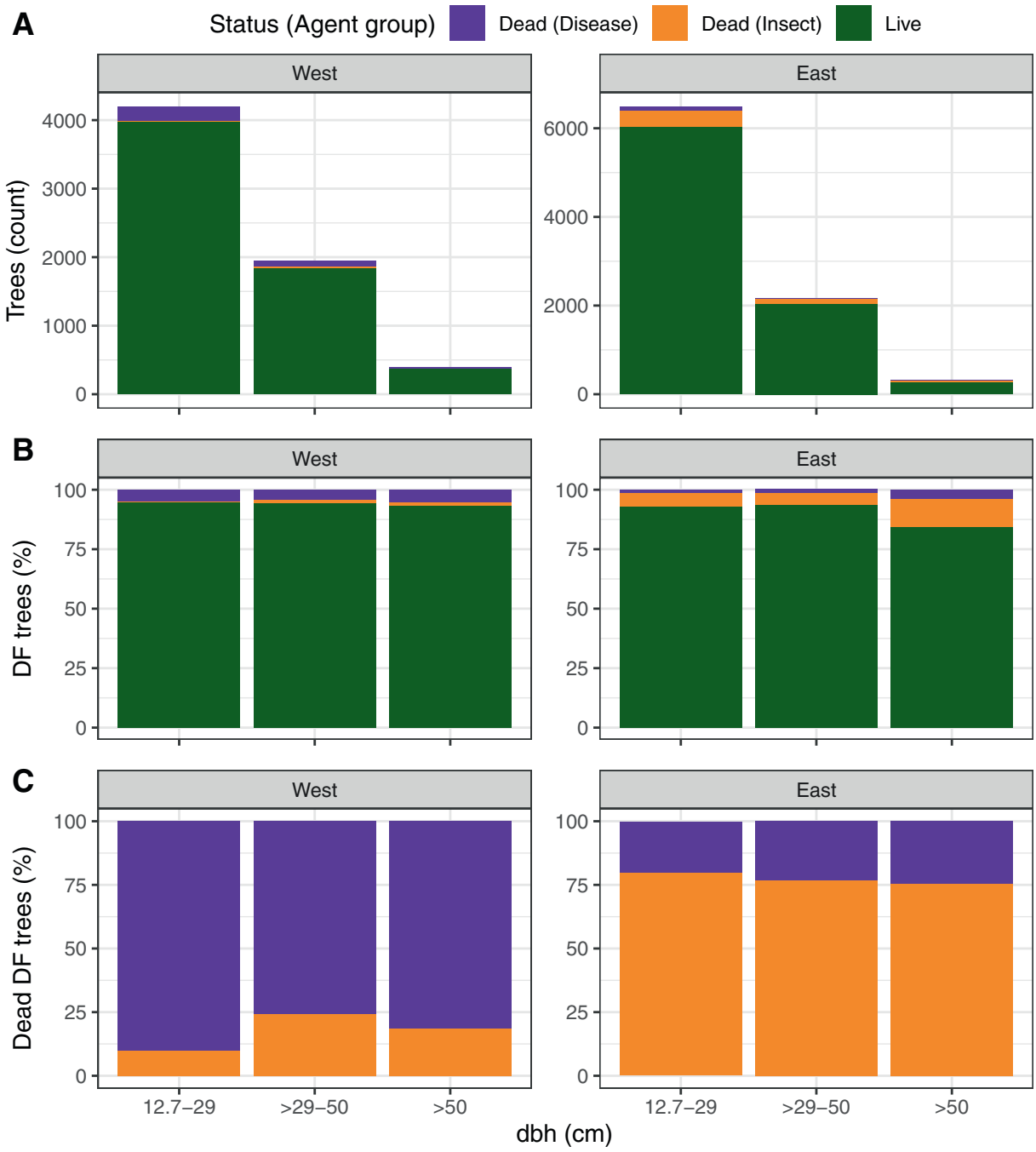

FIGURE 2 (A) Count and (B) percentage of Douglas-fir (DF) trees and (C) percentage of dead DF trees by status and mortality agent group in three dbh categories for two ecoregions (west and east of the Continental Divide) in the Northern Rocky Mountains, USA (see Figure 1 for extents). The analysis used data from the USFS Forest Inventory and Analysis program. Only stems >12.7 cm at breast height and plots with ≥75 DF stems/ha were included. Plot count varies by region (see Appendix S1: Table S2).

64% of 439 plots) during the remeasurement period (Figure 3), with an additional 21% (East) and 24% (West) of plots experiencing >0%–10% DF BA mortality. Few plots experienced >25% BA mortality, including 7.8% in the East and 4.5% in the West. Examining DF BA mortality (in square meters per hectare), >25 m^2/ha of DF BA mortality occurred in 12.3% of plots in the East and 6.8% of plots in the West (Appendix S1: Figure S7).

Across all plots, DF mortality had minimal effects on stand structure and composition. For stand structure, the average DF tree size (DF QMD) increased in >80% of plots, with an average QMD increase of 1.9 cm in the West (range −22.8 to 13.4) and 0.9 cm in the East (range −16.1 to 12.8). The 6% of plots with a reduction in QMD >1 cm experienced DF BA mortality >34% in the West and >40% in the East. For stand composition, nearly all

plots (96.1%) that were dominated by DF (DF BA higher than other species) remained dominated by DF (620 of 645). In the remaining plots (25), dominance shifted to grand fir (0.9%), lodgepole pine (0.9%), ponderosa pine (0.3%), or other species (1.7%).

Annual tree mortality rates by tree size class

For all DF trees >12.7 cm dbh, the median annual mortality rate was 0% of trees per year in both ecoregions (Figure 4; Appendix S1: Table S8). Annual mortality rates were <2.5% (percentage of trees per year) in ~88% of plots in both ecoregions, with only 0.2% of plots experiencing mortality rates >15%.

Comparing mortality rates by dbh class, more plots had higher mortality rates (in number of trees per year) of smaller trees (12.7–29 cm dbh) compared to intermediate (>29–50 cm) and large trees (>50 cm dbh) in both ecoregions (Figure 4; Appendix S1: Table S8). Within ecoregions, dbh classes experienced significantly different annual mortality rates (Kruskal–Wallis test, $\chi^2 > 19.6$, $p < 0.001$). The mortality rate of smaller trees was significantly greater than that of intermediate and large trees in both ecoregions, whereas mortality rates of intermediate trees were only significantly greater than those of large trees in the west ecoregion (Dunn test; $p < 0.01$). However, a higher percentage of plots experienced 100% mortality of large trees (West, 3.1%; East, 6.3%) compared to small and intermediate trees (<1.9%).

Effect of susceptibility and risk on DF basal area mortality

The distribution of DFB population pressure, tree growth, stand structure, and climate and topographic variables differed among the three levels of DF BA mortality in each ecoregion (Kruskal–Wallis, $p < 0.05$; Figure 5), whereas Habitat Type Groups did not (Appendix S1: Figures S8 and S9). Across both ecoregions, pairwise comparisons of DFB pressure among the three levels of DF BA mortality indicated that stands with DF BA mortality >10% had statistically significantly greater DFB pressure compared to stands that had 0% DF BA mortality. Similarly, DF mortality was significantly greater in stands with presence of RD compared to absence of RD (Appendix S1: Figure S10). For both ecoregions, stands with DF BA mortality >10% (compared to 0%) also had lower tree growth rates (BAI; East only), higher average live DF tree sizes (QMD), higher percentages of DF BA (East only), higher stand BA (in square meters per hectare), and similar stand density. Stands in the DF BA mortality >0%–5% category were typically intermediate to the other mortality levels for most variables, except for stand density index, which was significantly greater in the >0%–5% category compared to the other DF BA mortality categories. Many other stand structure variables (excluded due to multicollinearity) were positively related to DF BA mortality (in percentage), such as BA of RD hosts and density of DF trees susceptible to DFB (stems per hectare > 29 cm; Appendix S1: Figures S2 and S5). Among spatial climate and topographic variables, stands with DF BA mortality >10% had significantly lower climate water deficit and heat load index (West only) values than stands with 0% DF BA mortality, indicating that cooler/wetter sites were associated with higher mortality. Results were similar when plots were restricted to >40% DF BA (Appendix S1: Figure S11). Though we detected significant pairwise differences for stand structure and topo-climatic variables, the distribution of values overlapped considerably among the three levels of DF mortality, indicating that stands with and without mortality often had similar characteristics.

In RF models, the relative importance of susceptibility and risk variables varied by ecoregion (Table 2). DFB pressure and the spatial variability in climate water deficit were the top two variables in the West ecoregion but were some of the least important variables in the East ecoregion. Average DF tree growth rate (stand average of BAI) was the most important variable in the East and the third most important in the West. Average tree size (QMD) and DF basal area (in percentage) had a high relative importance in the East but a relatively low importance in the West. The presence of RD was not identified as a useful predictor of DF mortality in either ecoregion. Overall, the RF models explained a low amount of the variation in DF BA mortality as indicated by the out-of-bag (OOB) R^2 from spatial cross-validation of 0.13 in the West and 0.08 in the East. Removing risk and topo-climatic variables from the model slightly improved model accuracy (R^2) in the East but greatly reduced model accuracy in the West. Among the three RF models, the model with the predictor variables from the current DFB hazard model (FS Region 1) had the lowest model accuracy in both ecoregions.

In the RF models with susceptibility and risk variables, a slight increase in DFB pressure (i.e., >1.5 ha of DF mortality area within 1 km of the plot) was associated with a large increase in DF mortality (Figure 6). Greater-than-average DF mortality was observed in stands that had slower growth rates, such as stand average BAI <6.0 cm^2 in the East and <16.0 cm^2 in the West. DF mortality was higher in cooler and wetter areas as indicated by climate water deficit lower than ~300 mm in both ecoregions or heat load index <0.65 in the West. DF

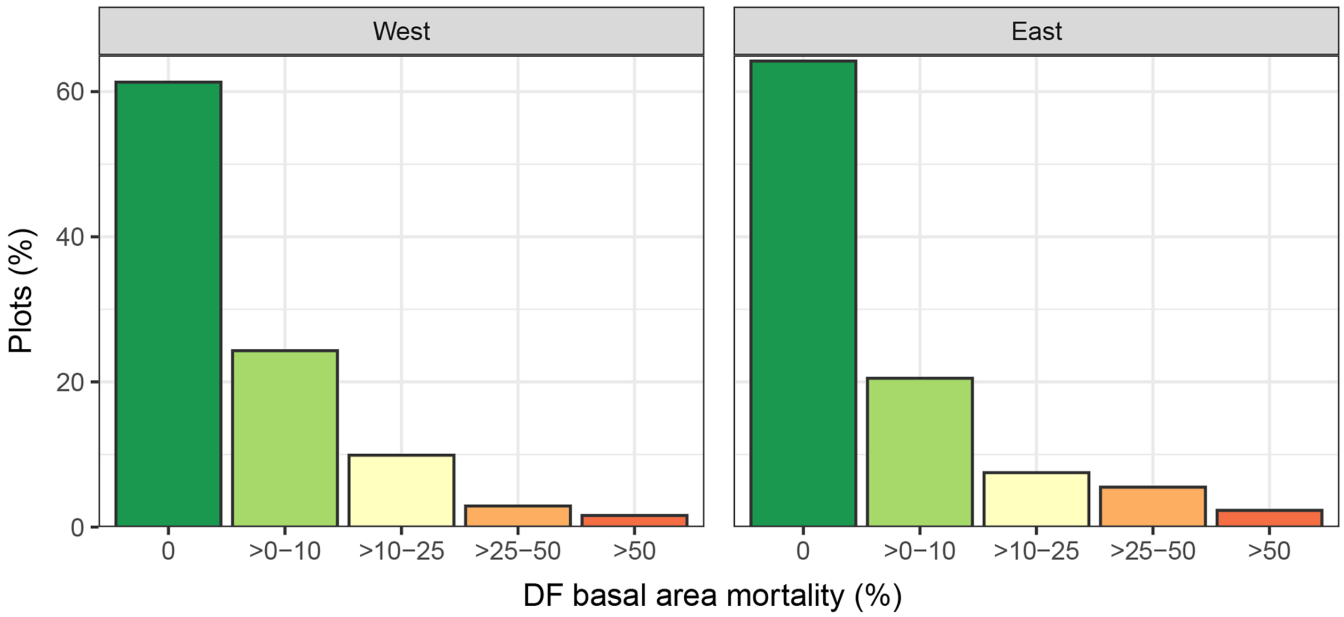

FIGURE 3 Percentage of plots in five bins of Douglas-fir (DF) basal area (BA) mortality (in percentage) in ecoregions west and east of the Continental Divide in the Northern Rocky Mountains, USA. DF BA mortality (in percentage) was the percent of DF BA that died during the remeasurement interval (~10 years) divided by the total live DF BA in the initial plot measurement. Mortality was from disease and insects (excluding wildfire and other mortality agent groups; see *Methods*). The analysis used data from the USFS Forest Inventory and Analysis program. Only stems >12.7 cm at breast height and plots with ≥75 DF stems/ha were included (see Appendix S1: Table S3 for plot counts by ecoregion). Results were similar for DF basal area mortality (in square meters per hectare; Appendix S1: Figure S7).

mortality increased when average DF tree size (DF QMD) exceeded 27 cm in the West and 33 cm in the East. In both ecoregions, DF mortality was greater than average when DF BA exceeded 75% (West) or 80% (East). Greater-than-average DF mortality was also observed in stands with lower stand density (60–150) in the East, such as may occur in stands with many large-diameter DF trees killed by DFB and few smaller trees.

The threshold (splits) in the susceptibility and risk variables associated with higher DF BA mortality (in percentage) was largely consistent between the conditional inference tree models and RF models by ecoregion (Figures 6 and 7). Conditional inference trees with susceptibility and risk variables from the RF model only found significant relationships with DFB pressure in the West and DF BA (in percentage) in the East. In the West, >2.4 ha of DF mortality area within 1 km of the plot (i.e., DFB pressure) were associated with greater DF mortality, particularly on cooler/wetter aspects (heat load index ≤ 0.6). In the East, DF mortality was greater when DF BA exceeded 83%. For conditional inference tree models with only stand susceptibility variables (excluding risk and topo-climatic variables), greater DF mortality was observed in stands with average DF tree sizes (DF QMD) >27.1 cm in the West. In the East, stands with high DF BA (>22 m^2/ha) and low stand density (<140) were associated with higher DF mortality, such as may occur in stands with many large-diameter DF and few small trees. In contrast to RF models, BAI and climate water deficit were not selected in any of the conditional inference tree models (Figures 6 and 7).

DISCUSSION

Only severe mortality altered stand structure and composition

We found that DF mortality from diseases and insects (excluding fire and harvest) was generally characterized by a low-level, diffuse pattern of DF tree mortality interspersed with infrequent patches of severe DF tree mortality (>25% DF BA mortality) during the 10-year FIA plot remeasurement period in the NRM (Figures 2–4). Low DF annual mortality rates (e.g., <2.5%/year) and DF BA mortality (<10%/decade) were the most common and widespread, which is consistent with natural stand development processes (e.g., density-dependent mortality) and endemic DFB population levels. Severe DF mortality was relatively infrequent (5%–8% of plots) and the relative role or interaction of RDs and bark beetles was unclear, but severities were consistent with stands infested by high populations of DFB in the northern and central Rocky Mountains (McMillin & Allen, 2003; Negron et al., 1999). In our study, shifts in stand

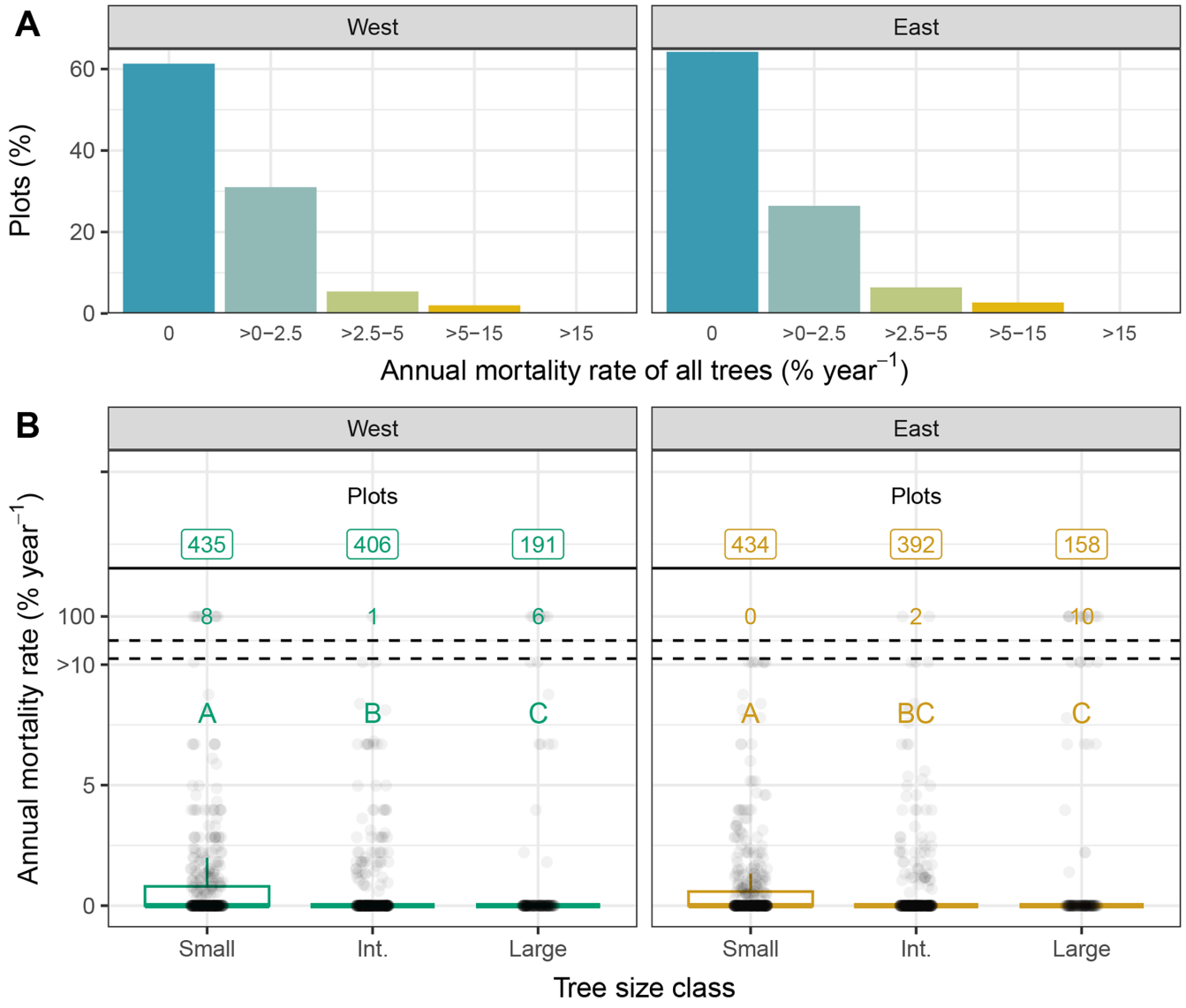

FIGURE 4 (A) Percentage of plots with annual mortality rates (in percentage per year) of Douglas-fir (DF) for all tree sizes (>12.7 cm at breast height) in ecoregions west and east of the Continental Divide in the Northern Rocky Mountains, USA. (B) Boxplots of DF annual mortality rates by tree size class. Tree size classes are small (dbh: 12.7–29 cm), intermediate (>29–50 cm), and large (>50 cm). In the boxplots, the thick horizontal line is the median, the box represents the interquartile range (25th–75th percentiles; interquartile range [IQR]) of the distribution, and the whiskers extend no further than ± 1.5 times the IQR. The two horizontal dashed lines identify the break in the *y*-axis from 11% to 100%, with count of 100% mortality rate values listed at 100%. Points are plot values. Letters indicate the results of pairwise comparisons within ecoregions from a Dunn test ($\alpha = 0.05$, Holm-corrected) following detection of significant differences between groups from a Kruskal–Wallis test. Common letters (e.g., "A") are not significantly different. The analysis used data from the USFS Forest Inventory and Analysis program. Only stems >12.7 cm at breast height and plots with ≥75 DF stems/ha were included (see Appendix S1: Table S3 for plot counts by ecoregion). Results were similar if plots were additionally subset to ≥40% DF basal area (Appendix S1: Table S8).

structure and composition, such as shifts in tree species dominance or considerable reductions in average live DF tree sizes (e.g., >1 cm QMD), were only observed in stands with severe DF mortality. Importantly, our analysis of DF mortality corresponded with a period of relatively low DF mortality (relative to 1997–2023), with considerable mortality in the West ecoregion prior to the initial FIA plot measurement and a rising trend in DF mortality during the remeasurement period (Figure 1). In summary, our analysis provides critical context to land managers about the range in severities of recent DF tree mortality and the implications of severe mortality for stand structure and composition across a large, forested region.

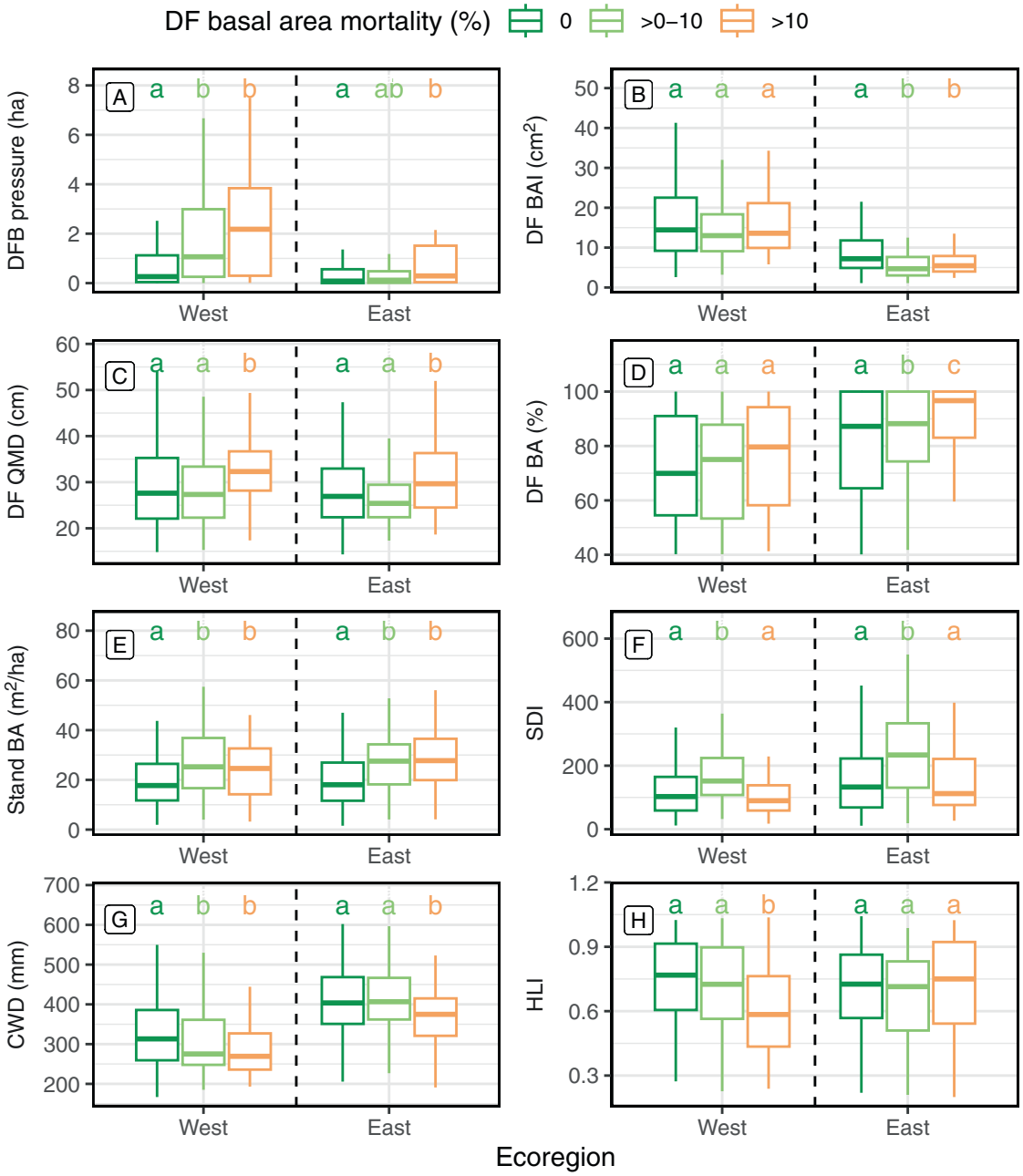

FIGURE 5 Boxplots of (A) Douglas-fir beetle (DFB) population pressure, (B–F) multiple stand structure and composition variables, (G) average annual climate water deficit (CWD; 1962–2022), and (H) heat load index (HLI) for three levels of Douglas-fir (DF) basal area (BA) mortality. Stand structure and composition variables included (B) DF basal area increment (BAI), (C) DF quadratic mean diameter (DF QMD), (D) DF BA (in percentage), (E) stand BA, and (F) stand density index (SDI) for stems >12.7 cm dbh. DFB pressure was the hectares of DF mortality area attributed to DFB within 1 km of the plot from gridded aerial survey data (see *Methods*). In the boxplots, the thick horizontal line is the median, the box represents the interquartile range (25th–75th percentiles; interquartile range [IQR]) of the distribution, and the whiskers extend no further than ± 1.5 times the IQR. Outliers were excluded. Letters indicate the results of pairwise comparisons within ecoregions (Dunn test; $\alpha = 0.05$, Holm-corrected) following detection of significant differences between groups from a Kruskal–Wallis test. Common letters (e.g., "a") are not significantly different. Results were similar if plots with DF BA <40% were excluded. The analysis used data from the USFS Forest Inventory and Analysis program and only plots with ≥75 DF stems/ha were included.

Mortality rates varied by tree size

Our findings that most dead DF trees were smaller diameter (12.7–29 cm dbh) and smaller trees experienced higher mortality rates than larger trees (≥29 cm; Figure 3) may be explained by stand disturbance history, multi-decadal climate variability, and stand development. The NRM experienced widespread fires in the 1800s and

TABLE 2 Summary of relative importance (RI) and performance statistics from three random forest (RF) models testing how Douglas-fir (DF) basal area mortality (in percentage) was influenced by (1) susceptibility and risk predictor variables, (2) stand susceptibility variables, and (3) the variables in the Douglas-fir beetle (DFB) hazard model currently used by USDA Forest Service Region 1.

Model	RI	Predictor variable	R^2	RMSE
1. Susceptibility (hazard) and risk model (all variables, Figure 6)				
West ecoregion	10.7	DFB population pressure	0.13	10.0
	9.3	Annual climate water deficit		
	6.4	Basal area increment (stand average)		
	4.9	Heat load index		
	2.6	DF basal area (%)		
	2.4	DF quadratic mean diameter		
	0.3	Stand density index		
East ecoregion	14.6	Basal area increment (stand average)	0.08	12.8
	10.4	DF quadratic mean diameter		
	7.8	DF basal area (%)		
	5.7	Stand density index		
	4.5	Annual climate water deficit		
	0.9	DFB population pressure		
	0.07	Heat load index		
2. Stand susceptibility model (excludes risk and topo-climatic variables, Figure 7)				
West ecoregion	4.3	Total stand basal area (m^2/ha)	0.02	10.5
	1.8	DF basal area (%)		
	1.2	DF quadratic mean diameter		
East ecoregion	4.7	Basal area increment (stand average)	0.10	12.6
	4.1	DF basal area (m^2/ha)		
	3.7	Stand density index		
	3.5	DF quadratic mean diameter		
3. DFB hazard model				
West ecoregion	2.2	Total stand basal area (m^2/ha)	0.01	11.2
	1.2	DF basal area (%)		
	−0.6	DF quadratic mean diameter		
East ecoregion	4.0	DF basal area (%)	0.05	13.0
	3.1	Total stand basal area (m^2/ha)		
	−0.9	DF quadratic mean diameter		

Note: Performance statistics are from spatial cross-validation. Relatively low or negative values for a predictor variable indicate poor predictive power and nearly identical stand characteristics with a wide range DF basal area (BA) mortality (in percentage). Relative importance may be compared within rather than between models. The analysis used data from the USFS Forest Inventory and Analysis (FIA) program. Only stems >12.7 cm at breast height and plots with ≥75 DF stems/ha were included.

Abbreviation: RMSE, root mean squared error.

early 1900s (Morgan et al., 2008, 2017), extensive high-grade logging (removal of the largest diameter trees) and fire exclusion (Naficy et al., 2010), and the establishment of many new trees during the wetter/cooler period of the 1940–1980s (Bollenbacher et al., 2014). In recent decades, stand structure and composition in some DF forests have shifted toward higher densities of trees and closed-canopy conditions relative to the prior century, with increases in DF density particularly evident in lower elevation dry forests (Hessburg et al., 2019). Smaller DF trees are likely dying from the following factors: (1) predisposing factors, such as intense competition for resources (e.g., light and soil moisture) during the stem-exclusion phase (Oliver, 1980), (2) inciting factors, such as drought events, and (3) contributing factors, such as RD, that kill smaller trees with more easily

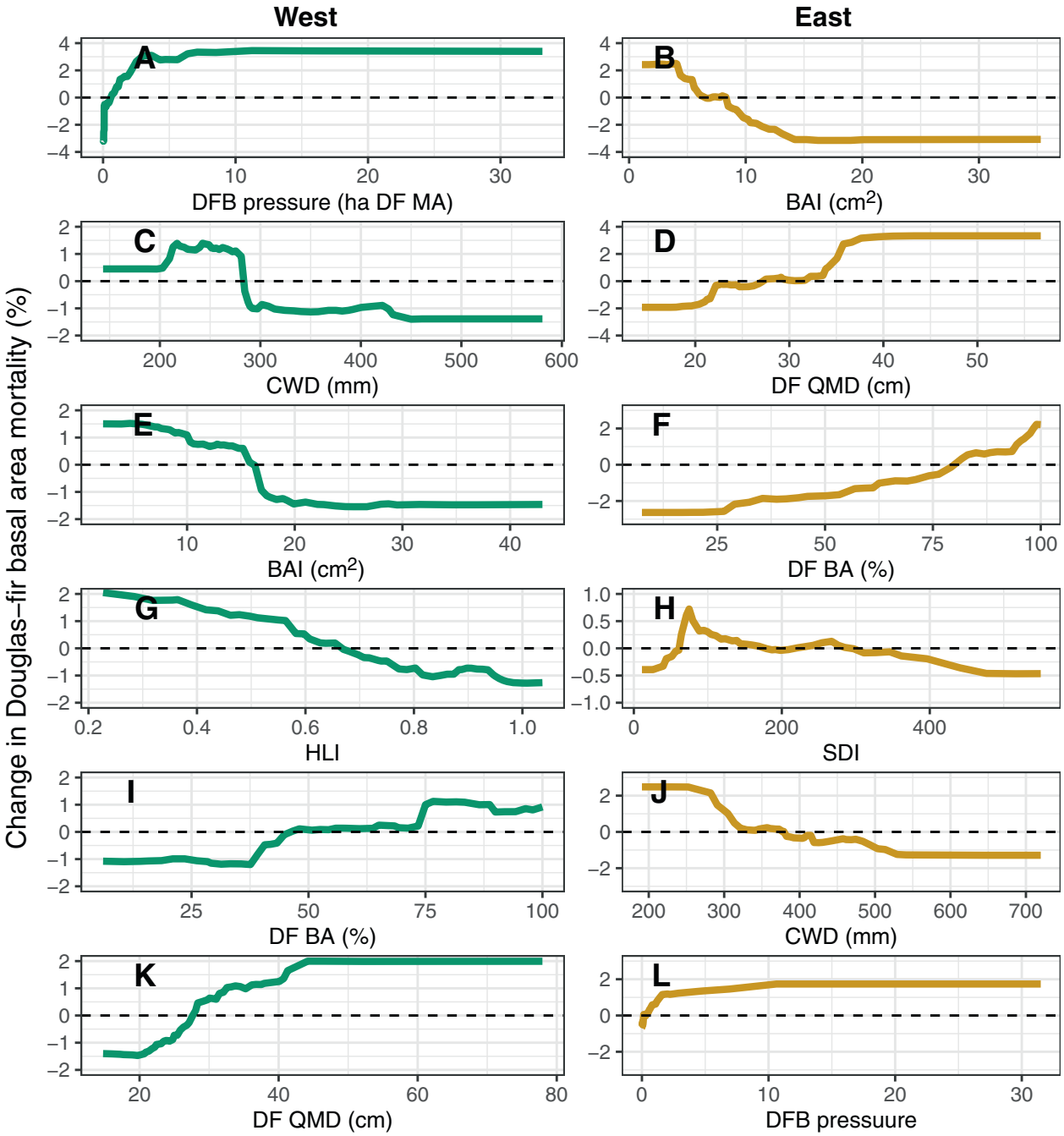

FIGURE 6 Accumulated local effects plots for the top six predictor variables in order of importance for random forest models of Douglas-fir (DF) basal area (BA) mortality in ecoregions west and east of the Continental Divide in the Northern Rocky Mountains, USA. In (A–L), the *y*-axis is the change in DF BA mortality (relative to the mean) for the respective predictor variable (*x*-axis), after accounting for the effects of other covariates. Solid lines above (below) the dashed line indicate higher (lower) than average DF BA mortality for the respective value of the predictor variable. Variable abbreviations are as follows (A, L) Douglas-fir beetle (DFB) population pressure (hectares of mortality attributed to DFB within 1 km of the plot; see *Methods*), (B, E) average basal area increment (BAI) of co-dominant and dominant DF trees, (C, J) average annual climate water deficit (CWD; 1962–2022), (D, K) DF quadratic mean diameter (QMD), (F, I) DF BA (percentage of stand basal area in DF), (G) heat load index (HLI), and (H) stand density index (SDI; all tree species). The analysis used data from the USFS Forest Inventory and Analysis program. Only stems >12.7 cm at breast height and plots with ≥75 DF stems/ha were included.

compromised root structures and bark beetle species that attack smaller, weakened trees (IDL, 2020). Importantly, the mortality of larger diameter trees should not be overlooked. Insect and disease surveys suggest that DF mortality is on an increasing trend (Figure 1), and we found 2% of plots that lost all large-diameter trees (>50 cm) and

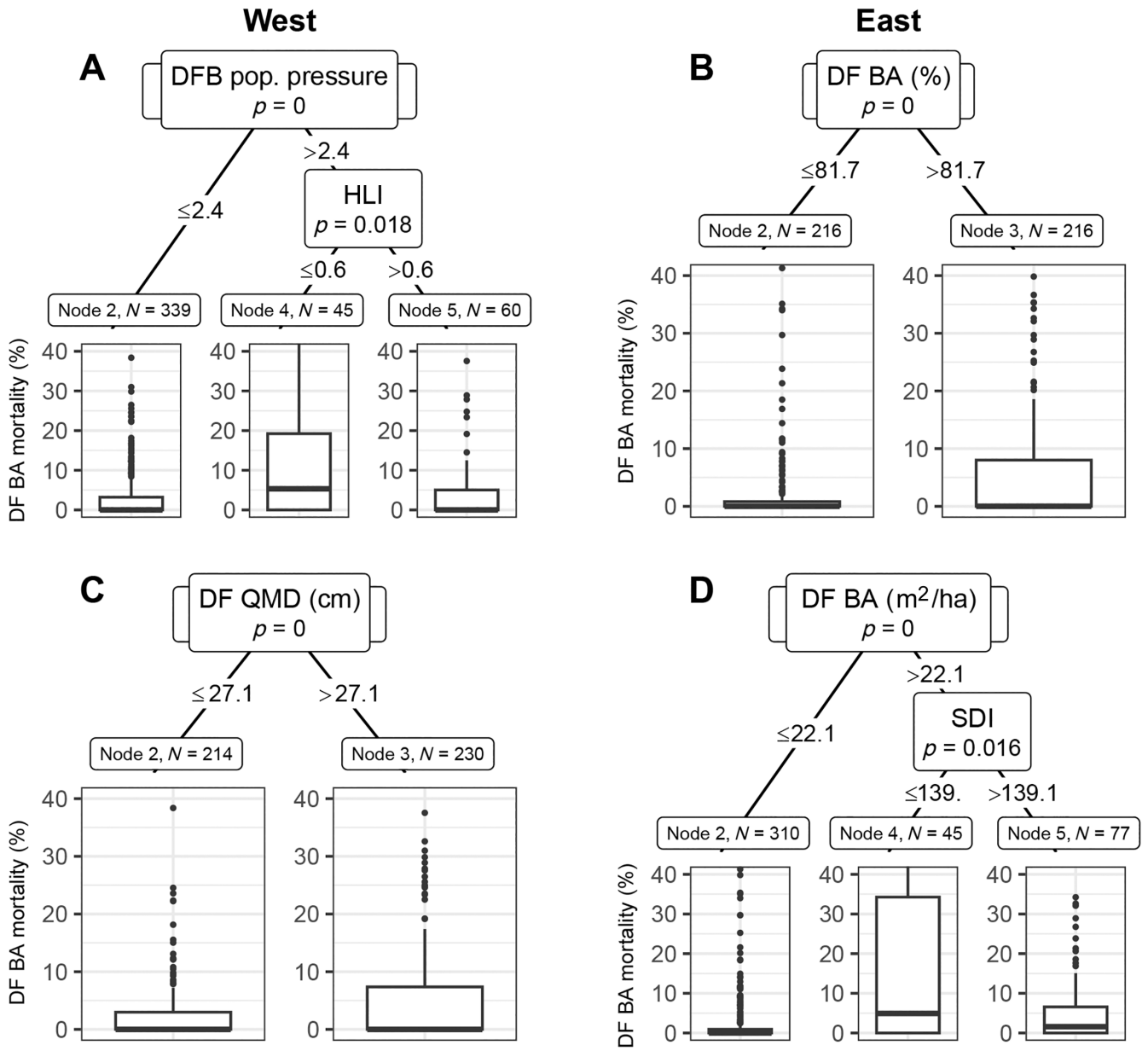

FIGURE 7 Conditional inference trees for Douglas-fir (DF) basal area (BA) mortality for models including (A, B) susceptibility and risk variables or (C, D) stand susceptibility variables only (excluding risk and topo-climatic variables) in ecoregions west and east of the Continental Divide. The *p* values (Bonferroni-adjusted) are displayed for each split. Boxplots of DF BA mortality are displayed for each terminal node. In the boxplot, the thick horizontal line is the median, the box delimits the interquartile range, the whiskers extend to the 10th and 90th percentiles, and points are outliers. Variables from the random forest models were included (Table 2). The analysis used data from the USFS Forest Inventory and Analysis program. Only stems >12.7 cm at breast height and plots with ≥75 DF stems/ha were included. DFB, Douglas-fir beetle; HLI, heat load index; QMD, quadratic mean diameter; SDI, stand density index.

some plots (12%) with annual mortality rates that exceed background tree mortality rates (~2%/year; Das et al., 2016). Additional FIA plot remeasurements are needed to assess whether mortality rates of any size classes are changing over time and how changes in mortality are influenced by climate, stand structure, and disturbance history.

DF mortality influenced by susceptibility and risk

Using multiple analytical approaches, we identified susceptibility (predisposing factors) and risk (contributing factors) variables associated with higher amounts of DF mortality and results varied by ecoregion (Figures 5–7).

Due to the length of the remeasurement interval and plots experiencing similar interannual variability in climate, we could not evaluate inciting factors, such as annual to decadal climate anomalies. Among susceptibility variables, higher DF mortality was associated with greater host availability for biotic agents (DFB and RD), slower growth rates (BAI), larger average tree sizes (QMD), and cooler/wetter sites. Greater host availability, particularly DF BA >75% (Figure 6H,K), likely increases host connectivity for the spread of RD and insect populations, a finding consistent with prior research examining DF mortality from DFB in the Central and Northern Rocky Mountains (Byler & Hagle, 1990; McMillin & Allen, 2003; Negron et al., 1999; Shore et al., 1999). Slower growth rates may indicate stands with root structures compromised by RD for years to decades, hydraulic failure from poor access to soil moisture, higher competition for resources, and other contributing insect and disease effects (Cole et al., 2022; Cruickshank et al., 2011; Klesse et al., 2022; Negron, 1998; Shore et al., 1999). Additionally, slower growth rates and larger average tree sizes (QMD) are known indicators of increased susceptibility to DFB-caused mortality (Negron, 1998; Weatherby & Thier, 1993). As tree growth rates are not included in existing hazard ratings, our finding that tree growth rates were strong predictors of DF mortality may improve managers' ability to forecast DF mortality.

In our study, more mesic DF forests, characterized by cooler and wetter sites and topo-climatic positions, as indicated by lower heat load index and climatic water deficit, were associated with greater DF tree mortality (Figures 5–7), a finding that is consistent with previous studies of the environmental conditions that are conducive to RD (Holden et al., 2020). Our results primarily have implications for the West ecoregion (Figure 6), because few DF stands were sampled (and likely exist) in the East below the climate water deficit threshold (~300 mm) where greater-than-average mortality was observed (Figure 5). Root diseases are more prevalent in cooler and wetter sites where DF often co-occurs with other tree species susceptible to RDs, such as true fir species (Byler & Hagle, 1990; Holden et al., 2020). These cooler and wetter conditions may also indicate higher productivity, higher densities of trees and competition, and more large-diameter trees susceptible to DFB, though prior studies have not identified topo-climatic characteristics that increase susceptibility to DFB (Shore et al., 1999). In contrast to expected climate-driven losses in suitable habitat in drier/warmer locations of the DF distribution in the NRM (Keane et al., 2018), we found that mesic DF forests were more vulnerable to mortality than drier and warmer DF forests during a relatively warm and dry period (compared to prior decades).

Closer proximity of biotic agents, namely DFB and RDs, was associated with greater DF mortality, indicating the value of incorporating risk into hazard model systems. For DFB pressure, a small increase in DFB pressure was associated with large increases in DF mortality, with these effects particularly evident in the West ecoregion (Figures 5A and 6C). Our results indicate that when DFB populations are locally large and causing mortality, DFB activity may have an overwhelming influence on the occurrence of DF tree mortality, a result consistent with other bark beetle-host tree systems in the western United States (Hart et al., 2017; Howe et al., 2024; Preisler et al., 2012). In contrast, DF mortality in areas with smaller DFB populations, such as likely occurred in much of the East ecoregion during the study period, is more strongly influenced by susceptibility variables. For RDs, presence of RD within or immediately adjacent to stands (<15 m) was associated with higher DF mortality, suggesting higher levels of RD inoculum in these areas to infect and compromise root structures. Continued monitoring of biotic agent populations with aerial and field insect and disease surveys, a current activity of the USDA Forest Health Protection program, is helpful for identifying areas at imminent risk to DF mortality.

Implications for adaptive management of DF forests

Forest managers often aim to identify areas susceptible to significant tree mortality from insect and disease and use silvicultural treatments to alter the structure and composition toward stand conditions less susceptible to damage (DeRose & Long, 2014; Kneeshaw et al., 2021). Our study identified stands with greater susceptibility and risk to DF mortality from insects and diseases and assists land managers in developing management prescriptions that may reduce DF tree mortality. Here, we discuss our results within the context of existing adaptive management tactics that address climate change vulnerability and seek to adapt DF forests in the NRM to future conditions (Bollenbacher et al., 2014; Halofsky & Peterson, 2016; Keane et al., 2018). The tactic of reducing resource competition to increase tree vigor is supported by our finding that stands with faster growing trees (BAI) and lower competition (BA) experienced lower DF mortality for all tree size classes (Figure 5; Appendix S1: Figures S2 and S5). For stands in areas where RD is a concern, our result that lower basal area of RD hosts was associated with lower DF mortality (Appendix S1: Figure S2) supports management activities aimed at increasing the abundance of tree species that are less prone to mortality from RD, such as pines or western larch. Common approaches include planting and promoting natural regeneration of species less

susceptible to RD. However, forest management activities in areas with RD may have the negative side effect of increasing RD inoculum and tree mortality in remnants or regenerating trees, because cut stumps are often rapidly colonized by RD that may spread to other trees, primarily through root-to-root transmission (Hagle, 2004). For stands in areas where DF mortality from DFB is a concern, reducing the abundance of large-diameter host trees and the overall proportion of DF BA may confer a reduction in DF mortality (Figure 5). However, silvicultural treatments aimed at reducing the dominance of older and larger diameter DF trees preferentially attacked by DFB may want to consider the trade-offs with ecosystem benefits, such as seed for regeneration, wildlife habitat, fire resilience, and carbon storage (Lutz et al., 2018). Another common management tactic to reduce mortality is to increase structural diversity, but we did not find that structural diversity influenced DF mortality. In DF forests, greater structural diversity may increase the susceptibility to other biotic agents, such as western spruce budworm and dwarf mistletoe (Brookes et al., 1987), and potentially heighten fire hazard under moderate fire weather conditions by increasing fuel continuity from the surface fuel bed to the forest canopy (i.e., ladder fuels). Adaptive management may be achieved through silvicultural prescriptions, prescribed fire, or management of natural disturbances, such as wildfire. Given the high degree of susceptibility of many DF stands in the NRM and unpredictable nature of disturbances, forest management actions that improve the chances for recovery from multiple threats and consider landscape-scale susceptibility may help sustain forest cover (Halofsky et al., 2018; Marini et al., 2022; Seidl et al., 2018).

Our evaluation of DF mortality from insects and disease across all tree size classes suggests additional hazard variables for managers to consider when evaluating stand susceptibility. Many variables identified in our analysis as strongly associated with DF mortality were included in the existing DFB hazard rating system (Randall et al., 2019), but RF models using only the variables in the existing DFB hazard rating produced lower (East) or comparable (West) accuracies to the stand susceptibility model (Table 2). The addition of the average BAI for dominant and co-dominant DF trees in the stand notably improved the RF model with stand susceptibility variables in the East. Though the relative importance of variables in the RF models and the variables selected in the conditional inference trees differed, the thresholds associated with higher mortality were similar in our three analytical approaches. Knowing that managers have varying access to specific forest measurements and many of the predictor variables were highly correlated, our approach was to produce multiple models for DF mortality to allow managers to select a model that is applicable to the stand history, past and future climate, likely mechanisms of tree mortality, and desired future stand conditions.

Limitations

Our analysis identified susceptibility and risk variables associated with DF tree mortality from one or multiple agents that were consistent with expected effects on DF tree mortality (Table 1). However, our models of DF BA mortality (in percentage) had relatively low accuracy (R^2), which is consistent with studies identifying characteristics of stands with and without DFB or bark beetle-caused tree mortality (Hart et al., 2014; Negron, 1998). The FIA plots included many stands with similar stand characteristics that experienced a wide range of DF tree mortality, and it was difficult for the RF model to distinguish susceptible stands with no mortality from non-susceptible stands. The trajectory of tree mortality and the timing of plot remeasurement likely impacted our results as current mortality events may be ongoing within stands, resulting in low estimates of mortality. Overlaid on this are varying rates at which biotic agents result in mortality from relatively slow mortality over decades from RD (Hagle, 2004) to rapid or slow mortality from drought and insects (Cailleret et al., 2017). Additionally, FIA plots were subject to a range of DFB pressure during the remeasurement period, and tree- to stand-scale preferences of bark beetles become less constraining if stands are under greater insect pressure (Negron, 1998; Raffa et al., 2008). We accounted for localized DFB population pressure and RD presence in our analyses and found that more proximate biotic agent pressure was associated with higher mortality, particularly in the West ecoregion for DFB (Figures 1, 5, and 6). However, DFB pressure was estimated from aerial surveys with spatial and attribution errors (agent and host; Coleman et al., 2018). The extraction of spatial data (DFB pressure) and attributes (elevation) from fuzzed plot locations likely had minimal effects on our results due to the spatial scale of plot fuzzing and spatial resolution of DFB pressure (Gibson et al., 2014). Poor model performance may also be explained by opposing tree- to stand-scale preferences of individual mortality agents, complicating the detection of clear relationships with mortality. For example, DFB most commonly kills larger diameter DF trees, whereas defoliation from western spruce budworm typically only kills smaller diameter trees (Hadley & Veblen, 1993). Models of DF tree mortality may be improved by assessing climate effects (inciting factors) on host trees and agents, identifying specific agents associated with mortality (i.e., disease-decline spiral), and tracking how the relative strength of susceptibility factors varies with biotic agent pressure.

CONCLUSION

We demonstrated a multi-scale framework to assess the impacts of tree mortality and investigated how DF tree mortality from multiple agents was influenced by susceptibility and risk across a large, forested landscape. Our analyses using publicly available datasets may be applied to a broader area and to other tree species, with additional benefits as longer time series become available. We found that continued growth of DF trees, relatively low DF tree mortality from insects and diseases, and mortality of primarily smaller diameter trees have led to larger average DF tree sizes and minimal changes in structure and composition during a two-decade period with warmer and drier average climate. As biotic agent activity, especially DFB, is expected to increase under a warmer and drier future, our results inform managers about the implications of severe mortality for structure and composition and management strategies to reduce mortality. To support management of DF mortality associated with insects and disease, we identified thresholds for susceptibility and risk variables that may be directly incorporated into tree mortality prediction tools, such as hazard and risk rating systems. In summary, our results generally support existing strategies for adaptive management in DF forests in the NRM. A key research need is to develop similar methods that incorporate inciting factors (i.e., climate effects) into the assessment of risk as climate change is expected to influence tree stress, biotic agent biology, and their interaction.

AUTHOR CONTRIBUTIONS

Conceptualization: Brytten Steed, James Steed, Jordan Lestina, John Goodburn, and Robert A. Andrus. *Data curation*: Robert A. Andrus, Jordan Lestina, and James Steed. *Methodology*: All authors. *Formal analysis*: Robert A. Andrus. *Writing—original draft preparation*: Robert A. Andrus. *Writing—review and editing*: All authors. *Funding acquisition*: Brytten Steed, John Goodburn, and Joel Egan.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data are available as follows: USDA Forest Inventory and Analysis (FIA, 2024a): https://apps.fs.usda.gov/fia/datamart/CSV/datamart_csv.html; TopoTerra climate data: https://doi.org/10.17605/OSF.IO/W6JVK; gridded biotic agent dataset: https://verso.uidaho.edu/esploro/outputs/dataset/996794512701851; United States Environmental Protection Agency Level III ecoregions (US EPA, 2010): https://www.epa.gov/eco-research/level-iii-and-iv-ecoregions-continental-united-states.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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Appendix S1

Title: *A multi-scale assessment of interior Douglas-fir tree mortality for hazard and risk assessments*

Authors: Robert A. Andrus, Brytten Steed, Joel Egan, Jordan Lestina, James Steed, Patrick Bennett, Arjan J.H. Meddens, John Goodburn

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Table S1: Major root diseases and insect species associated with mortality of interior Douglas-fir trees in the Northern Rocky Mountains.

Root diseases[1]	Common name (*latin name*)
	Armillaria root disease (*Armillaria* spp. (Fr.) Staude)
	Heterobasidion or "annosus" root disease (*H. occidentale* Otrosina & Garbelotto)
	Laminated root disease (*Coniferiporia sulphurascens* (Pilát) L.W. Zhou & Y.C. Dai)
	Schweinitzii root and butt rot (*Phaeolus schweinitzii (Fr.) Pat.)*
	Tomentosus root disease (*Onnia tomentosa* (Fr.) P. Karst.)
	Black stain root disease (*Leptographium pseudotsugae*) [2]
Other diseases	
	Dwarf mistletoes (*Arceuthobium* spp.)
Insects	
	Douglas-fir beetle (*Dendroctonus pseudotsugae*)
	Douglas-fir engraver beetles (*Scolytus unispinosus, Scolytus monticolae*)
	Douglas-fir pole beetle (*Pseudohylesinus nebulosus*)
	Western spruce budworm (*Choristoneura freeman)*
	Douglas-fir Tussock Moth (*Orgyia pseudotsugata*)

[1] (Lockman et al. 2016)
[2] formerly *L. wageneri var. pseudotsugae*

Table S2: Average climate characteristics of Douglas-fir forests East and West of the Continential Divide (Fig. 1) from 1991 to 2020. Climate variables include mean annual precipitation (MAP), summer precipitation (SUMP, June-September), mean maximum temperature of the hottest month (MTHM), and minimum temperature of the coldest month (MTCM). Climate data from PRISM (2019) was extracted to areas with Douglas-fir forest (>1 m^2/ha of basal area per the National Insect and Disease Forest Assessment data (Krist et al. 2014).

Ecoregion	MAP (mm)	SUMP (mm)	MAT (˚C)	MTHM (˚C)	MTCM (˚C)
West	918.3	169.8	5.8	25.9	-7.1
East	700.5	208.7	3.9	24.4	-10.4

Table S3: Number of remeasured USDA Forest Inventory and Analysis (FIA) plots used in the analysis by year of remeasurement (subtract 10 years for initial measurement) in the ecoregions east and west of the continental divide in US Forest Service Region 1 (see Fig. 1 for distribution of plots). The table includes the count of plots with ≥75 Douglas-fir (DF) stems/ha (~ 5 trees per plot) and in parenthesis, the count of plots with ≥75 DF stems/ha and ≥40% DF basal area. Only one plot meeting our criteria was remeasured in 2012 and we excluded it. Plot remeasurements were low in 2020-21 due to COVID restrictions. Plots with incidence of fire or silvicultural treatments were excluded.

Year	R1 (all ecoregions)	West	East
2013	105 (79)	38 (29)	67 (50)
2014	136 (98)	64 (45)	72 (53)
2015	143 (102)	77 (48)	66 (54)
2016	134 (109)	70 (55)	64 (54)
2017	101 (70)	54 (37)	47 (33)
2018	137 (108)	74 (52)	63 (56)
2019	128 (100)	68 (48)	60 (52)
Total	884 (666)	445 (314)	439 (352)

Table S4: Recorded cause of tree mortality by mortality agent group (AGENT CD) for all dead Douglas-fir trees (≥12.7 cm or 5 in at breast height) in 2,267 USDA Forest Inventory and Analysis (FIA) plots with presence of DF trees in the Northern Rocky Mountains. In our analysis, we only included plots with mortality from insect or disease (884 plots), which represented ~62% of tree mortalities in the 2,267 FIA plots. Our criteria thus excluded mortalities from fire, animals, weather, vegetation, unknown, human activity, and no agent (other). Fire-caused mortality and treatments occurred in 147 and 130 FIA plots, respectively (excluded from analysis).

AGENT CD	AGENT	R1 (all ecoregions)	West	East
10	Insect	808	714	94
20	Disease	599	184	415
30	Fire	642	401	241
40	Animal	4	2	2
50	Weather	61	35	26
60	Vegetation	64	31	33
70	Unknown	66	14	52
80	Human Activity	9	4	5
NA	No Agent (Other)	17	9	8

Table S5: All predictor variables considered in the model of Douglas-fir (DF) basal area mortality. The justification and expected effect for each variable are included as well as prior findings for the effect of each variable on DF mortality from Douglas-fir beetle (DFB) and root disease. Groups indicate variables with high correlations from a hierarchical cluster analysis (Fig. S2) and group numbers 1-7 correspond to Fig. S2. One variable per group was considered in the Random Forest model (indicated by a *). Topographic and climate normal variables were excluded from the cluster analysis. Some variables selected for the Random Forest models (i.e., *) were not included in the final models due to their minimal effect on DF basal area mortality. See Table S6 for summary statistics of each variable. DF tree age was for the largest basal area weighted diameter category in the plot, and age was estimated from field counts by FIA crews. Age was only available for approximately half of all plots and removed from further analysis.

Group	Predictor variable (units)	Acronym	Justification (expected effect)	Prior findings and source
	Stand Susceptibility (Hazard)			
1*	Stand basal area (m^2/ha)	Stand BA	Increased competition for resources (+)	Positive effect on DFB[5,6]
1	Root disease host basal area (m^2/ha)	RD BA	Greater host availability for root diseases (+).	Positive effect on RD[9]
1	DF basal area (m^2/ha)	DF BA	Increased competition for resources and greater host availability for biotic agents (+)	Positive effect on DFB[1,2,7,8]
1	DF trees susceptible to DFB (stems/ha)	DF sus. DFB	Greater host availability for DFB (+)	Positive effect on DFB[7]
2	DF tree age	Age		Positive effect on DFB and RD[8]
2*	DF quadratic mean diameter (>12.7 DBH)	DF QMD	Greater host availability for DFB (+)	Positive effect[7,8]
2	DF quadratic mean diameter (>23 cm DBH)	DF QMD	Greater host availability for DFB (+)	Positive effect[7,8]
3*	DF tree size heterogeneity (Coefficient of variation of DBH, unitless)	CV DBH	Greater diversity in stand structure (-)	Negative effect on DFB
4	Canopy cover of all trees (%)	CC	Increased competition for resources (+)	Positive effect on DFB[6]
4*	Stand density index (unitless)	SDI	Increased competition for resources (+)	No effect on DFB[2,7]
4	Stand density (stems/ha)	None	Increased competition for resources (+)	Positive effect on DFB[5,6]
5*	Average basal area increment (cm^2)	BAI	Decreased host vigor and greater susceptibility to biotic agents (-)	Negative effect on DFB and RD[1,2,3,4]
7*	DF basal area (%)	DF BA (%)	Increased competition for resources and greater host availability for biotic agents (+)	Positive effect on DFB[1,2,7,8]
7	Basal area of DF > 23 cm DBH	None	Increased competition for resources and greater host availability for biotic agents (+)	Positive effect on DFB[1,2,7,8]
9	Aspect (Folded 180)	None	Increased moisture stress (+)	Positive effect on RD[5]
9*	Heat Load index (unitless)	HLI	Increased moisture stress (+)	Positive effect on RD[5]
9	Elevation (m) above sea-level	Elev.	Variable (+/-)	
10*	Annual climate water deficit	CWD	Increased moisture stress (+)	Positive effect on DFB[10]
10	Actual evapotranspiration	AET		
10	Total annual precipitation (mm)	MAP	Decreases tree stress (-)	Negative effect on DFB
10	Maximum monthly temperature in warmest month (˚C)	MTWM	Increases tree stress (+)	Positive effect on DFB
10	Minimum monthly temperature in coldest month (˚C)	MTCM	Increases DFB survival (+)	Negative effect on DFB
11	Habitat Type Group	HTG	Variable (+/-)	
	Risk			
6	DFB population pressure	DFB pressurue	Greater likelihood for DFB attack (+)	Positive effect on DFB[6]
8	Root disease (presence/absence)	RD PA	Greater likelihood for root disease (+)	Positive effect on RD[4,8]

[1]Shore et al. 1999, [2]Negron et al. 1999, [3]Bloomberg et al. 1989, [4]Cruickshank et al. 2011, [5]Furniss et al. 1979, [6]Steele et al. 1996, [7]McMillin et al. 2003, [8]Weatherby and Their 1993, [9]Byler & Hagle 1990, [10]Bennett et al. 2023

Table S6: Summary statistics for predictor variables in model of DF mortality. Data from FIA plots with ≥ 75 Douglas-fir (DF) stems/ha (~ 5 trees per plot). Root disease pressure was excluded because it was a presence (1)/absence(0) variable.

		West		East	
Group	**Variable**	**Median (IQR)**	**Range (Min.-Max.)**	**Median (IQR)**	**Range (Min.-Max.)**
	Susceptibility (hazard)				
1	Stand basal area (m^2/ha)	23 (18.4)	1.9 - 144.2	22.9 (16.7)	1.6 - 73.8
1	Root disease host basal area (m^2/ha)	19 (15)	2 - 77	16 (16)	2 - 75
1	DF basal area (m^2/ha)	11.8 (11.6)	1.3 - 46.7	13.8 (16.5)	1.5 - 73.8
1	DF trees susceptible to DFB (stems/ha)	59 (59)	0 - 342	74 (89)	0 - 416
2	DF tree age (years)	81.5 (45.4)	23.3 - 287	111.5 (84)	5 - 552
2	DF quadratic mean diameter (>12.7 cm DBH)	27.6 (11.8)	14.8 - 77.9	26.2 (10.1)	14.3 - 56.7
2	DF quadratic mean diameter (>23 cm DBH)	35 (10.4)	22.9 - 79.4	33.4 (9)	23.1 - 81.3
3	DF tree size heterogeneity (unitless)	2.9 (1.2)	1.2 - 12.6	2.9 (1.3)	1 - 11.4
4	Canopy cover (%)	63 (25)	14 - 99	50 (26)	10 - 90
4	SDI (unitless)	133.5 (147.3)	11.6 - 550	170.1 (203.9)	10.9 - 550
4	Stand density (stems/ha)	377 (297)	74 - 1502	416 (372)	74 - 1547
5	Average basal area increment (cm)	14.3 (11.8)	2.2 - 43	6.7 (6.4)	1.1 - 35.3
7	DF basal area (%)	57.4 (45.6)	6.1 - 100	81.6 (51)	7.5 - 100
7	Basal area of DF > 23 cm DBH (%)	58.8 (49.3)	0 - 100	86.9 (41.5)	0 - 100
9	Aspect (Folded 180)	94 (92)	0 - 180	88 (90)	0 - 180
9	Elevation (m)	1244 (472)	567 - 2253	1824 (412)	832 - 2600
9	Heat load index	0.7 (0.3)	0.2 - 1	0.7 (0.3)	0.2 - 1
10	Climatic Water Deficit (mm)	284.5 (120)	143.5 - 580.7	395.5 (103.2)	191 - 719.6
10	Actual evapotranspiration (mm)	478.5 (85.1)	306.7 - 605.3	375.4 (82.4)	250.9 - 540.9
10	Average water-year precipitation (mm)	844.6 (387.1)	345.8 - 1964.1	603.8 (246.3)	337 - 1767.3
10	Max. monthly temp. in warmest month (˚C)	26 (2.3)	21.3 - 30.6	24.6 (2)	20.4 - 30.5
10	Min. monthly temp. in coldest month (˚C)	-7.9 (2.4)	-13.2 - -2.9	-11.1 (1.2)	-15.7 - -7.4
	Risk				
6	DFB pressure	0.5 (2.1)	0 - 33.2	0.1 (0.6)	0 - 31.5

Table S7: Criteria for evaluating stand hazard (susceptibility) to Douglas-fir beetle (DFB) in US Forest Service Region 1 (Randall et al. 2019). DFBs primary host is the Douglas-fir (DF) tree. The numbers associated with the low to high hazard are multiplied to produce a single stand hazard rating value, including very low (0), low (>0-2), moderate (>2-17), and high (>17).

Hazard criteria			
Criteria	Low (0.5)	Moderate (2)	High (3)
Quadratic mean diameter (cm) of DF >23 cm	<25.4	>25.4 - <35.5	≥35.5
Stand basal area (m^2/ha) (all species, >12.7 cm DBH)	<23.0	>23.0 - <57.4	≥57.4
DF basal area (%) (DF ≥23 cm only)	<50%		≥50

Table S8: Summary statistics for annual mortality rates (%/year) for USDA Forest Inventory and Analysis plots with (1) ≥75 Douglas-fir (DF) stems/ha (~ 5 trees per plot) and (2; in parenthesis) ≥75 stems/ha and ≥ 40% DF basal area. The primary agents of mortality were recorded as insects and/or disease. Data are summarized by plots East and West of the Continental Divide (Fig 1) and for four tree size classes. Size classes include stems > 12.7 cm DBH (all), >12.7 cm to 29 cm DBH (small), >29 cm to 50 cm DBH (intermediate), and > 50 cm DBH (large). Summary statistics include median, mean, interquartile range (IQR), and range (minimum to maximum value).

Ecoregion	Tree size class	Plots	Median	Mean	IQR	Range (Min.-Max.)
East	All	439 (352)	0 (0)	0.8 (0.9)	0.69 (0.835)	0-22 (0-22)
East	Small	434 (349)	0 (0)	0.9 (1)	0.585 (0.76)	0-19.73 (0-19.73)
East	Int.	392 (325)	0 (0)	1.1 (1.2)	0 (0)	0-100 (0-100)
East	Large	158 (143)	0 (0)	7 (7.8)	0 (0)	0-100 (0-100)
West	All	445 (314)	0 (0)	0.7 (0.7)	0.89 (0.885)	0-16.4 (0-16.4)
West	Small	435 (305)	0 (0)	2.5 (1.7)	0.8 (0.8)	0-100 (0-100)
West	Int.	406 (293)	0 (0)	0.8 (0.6)	0 (0)	0-100 (0-10.4)
West	Large	191 (154)	0 (0)	3.5 (4.3)	0 (0)	0-100 (0-100)

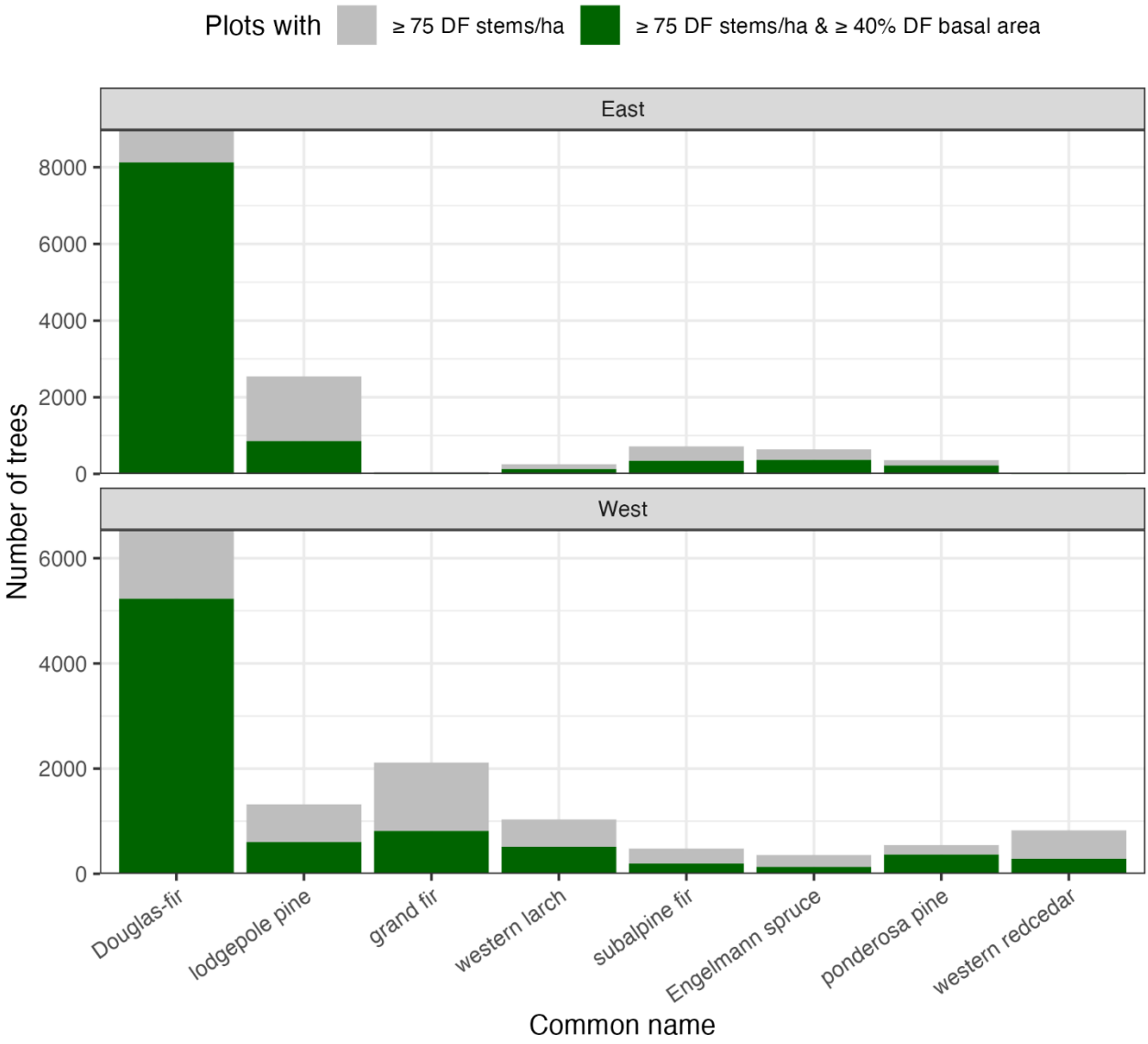

Fig. S1: Common cohabitating tree species of Douglas-fir (DF) East and West of the Continental Divide in USDA Forest Service Region 1 as illustrated by the number of trees by species in Forest Inventory and Analysis (FIA) plots with ≥ 75 DF stems/ha (full length of bar; 884 plots) and ≥ 75 DF stems/ha and ≥ 40 % DF basal area (green only; 666 plots) in USFS Region 1 (Fig. 1). DF trees were the most common tree species overall, but associated tree species differ between East and West. In East, DF associates with high elevation, cold forest species, such as lodgepole pine, subalpine fir, and Englemann spruce. In West, DF associates with mesic mixed conifer species, such as grand fir, western larch, and western redcedar as well as the same cold forest species found in East. Ponderosa pine is a common associate in both East and West at low elevations.

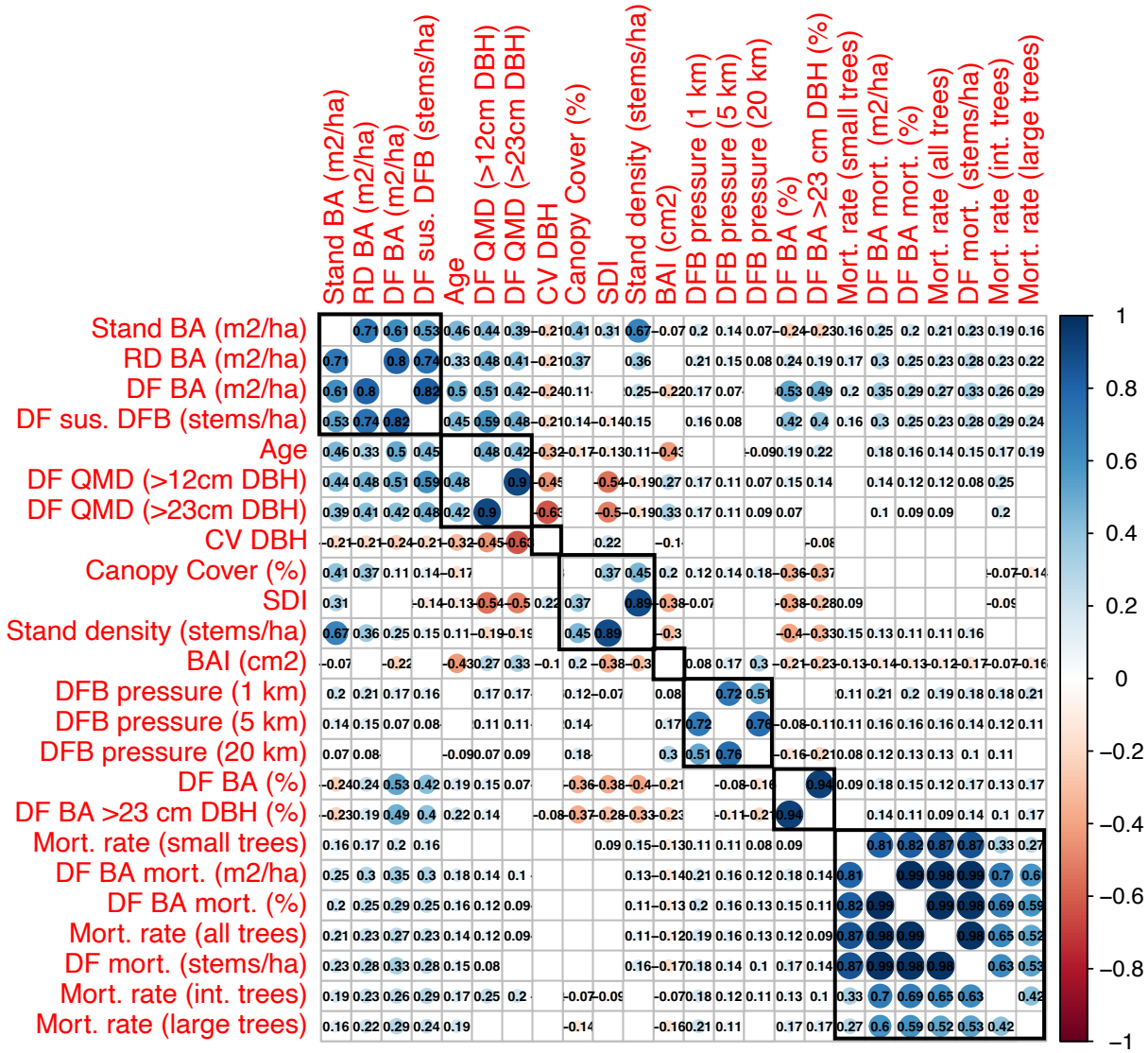

Fig. S2 (Stand variable correlation table): Spearman's correlation table of seven tree mortality metrics (bottom right) and 18 susceptibility and risk variables. Variables that are highly correlated are indicated by greater absolute numbers, larger dots, and darker color, with blue indicating positive correlation and red indicating negative correlation. Only statistically significant ($p < 0.05$) relationships are shown. Variables are ordered based on their similarity (hierarchical clustering). Boxes delineate eight variable groupings and one variable per box was selected for the Random Forest (RF) model (see bolded variables below). Stand structure or composition variables were computed for the initial measurement (i.e., pre-mortality). From the top by box (bolded variables included in Random Forest model), **(box 1)** Stand basal area (BA) (m^2/ha), root disease (RD) BA (m^2/ha), **DF BA (m^2/ha)**, DF susceptible (sus.) to Douglas-fir beetle (DFB; stems/ha); **(2)** tree age (see below), **DF quadratic mean diameter (QMD) of trees > 12.7 cm (5 in) DBH** and > 23 cm (9 in) DBH; **(3) coefficient of variation (CV) of diameter at breast height (DBH)**; **(4)** canopy cover (%) of live trees, **stand density index (SDI)**, stand density (stems/ha); **(5) average basal area increment (BAI)** of co-dominant and dominant trees; **(6)** Measures of insect population pressure include the sum of DF mortality area (MA, ha) from gridded aerial survey data within **1 km,** 5 km, and 20 km of the FIA plot; **(7) DF BA (%)**, DF BA of trees > 23 cm DBH (%); Tree mortality metrics included mortality rate of all Douglas-fir (DF) trees (> 12.7 cm DBH), small (> 12.7-29 cm), intermediate (>29-50 cm) and DF large trees (>50 cm DBH) and **DF basal area mortality** (m^2/ha and **% of DF basal area**) during the remeasurement period (~10 years). Tree age was for the largest basal area weighted diameter category in the plot, and age was estimated from field counts by FIA crews. Age was only available for approximately half of all plots and removed from further analysis. FIA plots with ≥ 75 stems/ha in USFS Region 1 were included. See Table 1 for further explanation of variables and expectations.

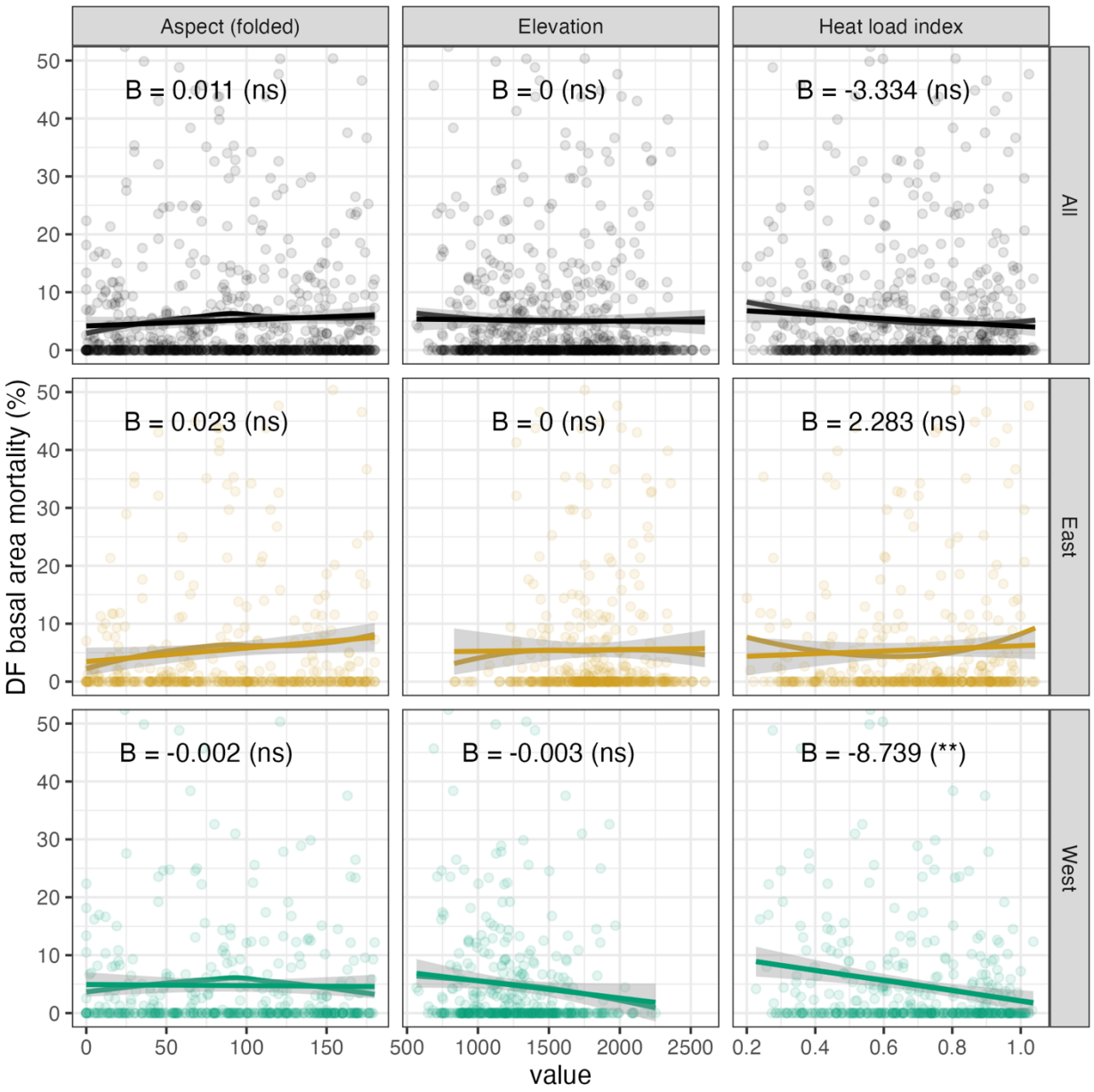

Fig. S3 (Topographic variables): X-Y scatterplots for candidate topographic predictor variables and Douglas-fir basal area loss (%) for all plots and plots in two ecoregions (west and east of the Continental Divide). FIA plots with ≥75 stems/ha in USFS Region 1 were included (See Table S2 for plot counts). The straight line is a linear model with standard error to show the overall trend in the data, and B is the coefficient with statistical significance. The curved line is a loess smoother (non-parametric locally weighted regression) to highlight potentially non-linear relationships. See Table 1 for variable expectations. All plots were zoomed into the range of basal area loss 0 to 50% for visualization purposes only. P-values for linear model are 'ns' for not significant ($p > 0.05$), '*' for $p < 0.05$, and '**' for $p < 0.01$. Results were similar if 0 values for basal area loss were removed.

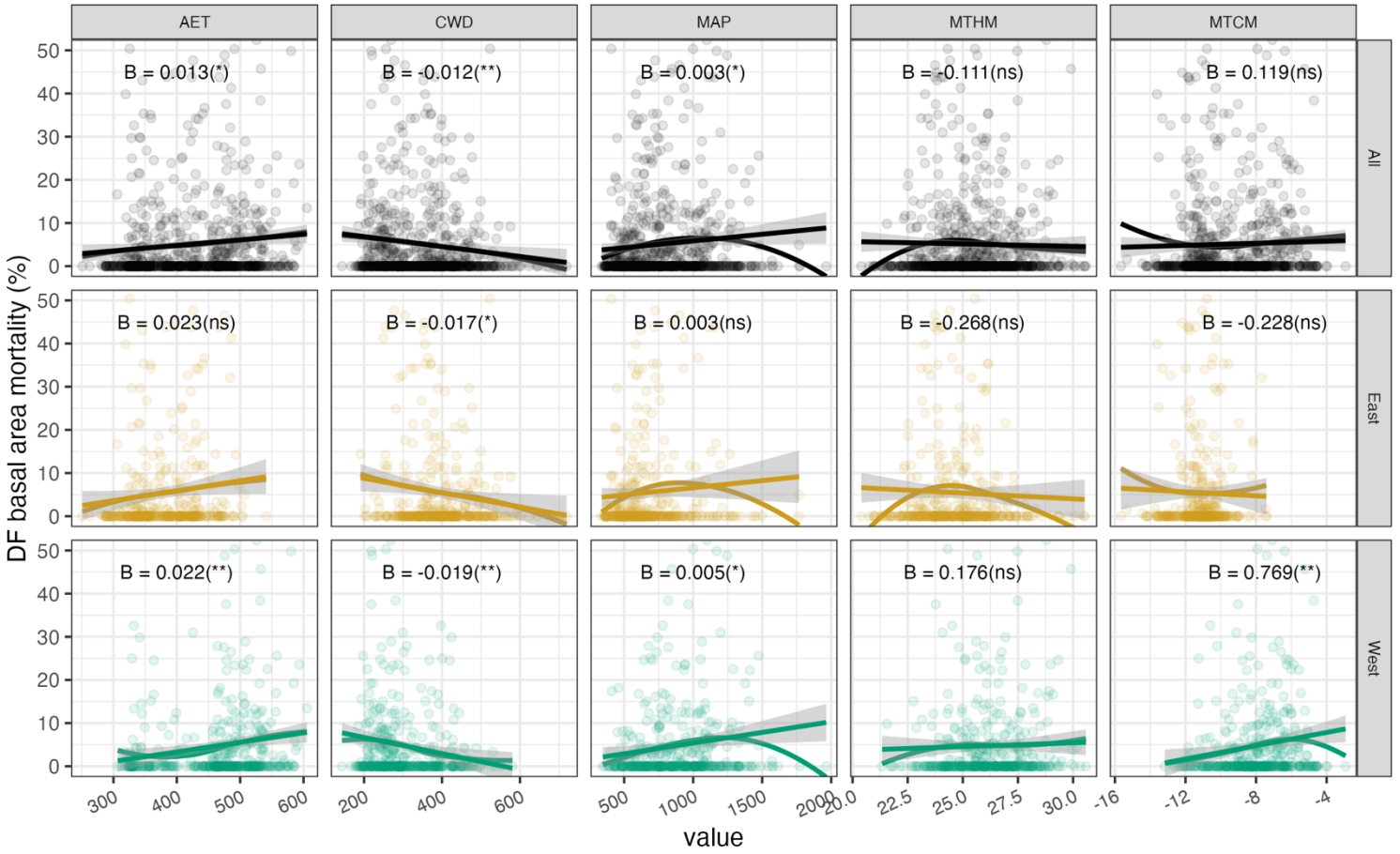

Fig. S4 (spatial variability in climate variables): X-Y scatterplots for five candidate predictor variables describing the spatial variability in climate and Douglas-fir (DF) basal area mortality (%) for all plots and by plots in two ecoregions (west and east of the Continental Divide). FIA plots with ≥75 stems/ha in USFS Region 1 were included (See Table S2 for plot counts). Climate predictor variables describe average climate (i.e., normals) from 1962 to 2022. The straight line is a linear model with standard error to show the overall trend in the data, and B is the linear model coefficient with statistical significance indicated in parenthesis. The curved line is a loess smoother (non-parametric locally weighted regression) to highlight potentially non-linear relationships. AET (mm) is the actual evapotranspiration, CWD (mm) is the climate water deficit, MAP (mm) is mean annual precipitation, MTHM (˚C) is the maximum temperature in the hottest month (July), and MTCM (˚C) is the minimum temperature of the coldest month (Jan). All plots were zoomed into the range of basal area mortality 0 to 50% for visualization purposes only. P-values are 'ns' for not significant ($p > 0.05$), '*' for $p < 0.05$, and '**' for $p < 0.01$. Results were similar if 0 values for basal area mortality were removed.

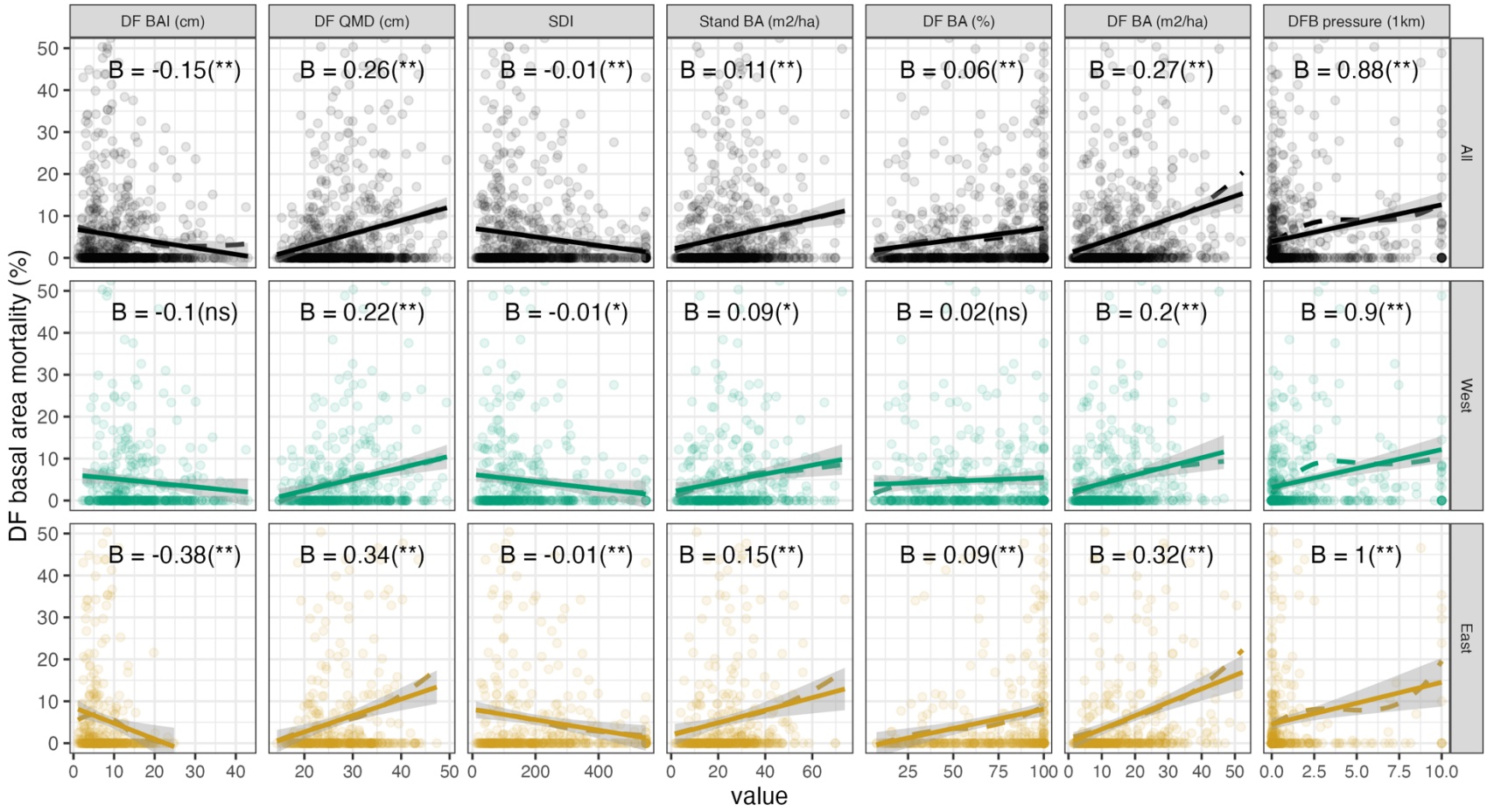

Fig. S5 (Tree growth, DFB pressure, and selected stand structure variables): X-Y scatterplots for Douglas-fir (DF) basal area (BA) mortality (%) and candidate tree growth and stand predictor variables for all plots (top row) and plots in two ecoregions (west and east of the Continental Divide). All stand variables were computed from the initial plot measurement (i.e., pre-mortality). FIA plots with ≥75 stems/ha in USFS Region 1 were included. The straight line is a linear model with standard error to show the overall trend in the data, and B is the coefficient with statistical significance. The curved line is a loess smoother (non-parametric locally weighted regression) to highlight potentially non-linear relationships. DF BAI is the average plot basal area increment of co-dominant and dominant DF trees (cm^2), DF QMD is DF quadratic mean diameter of trees >12.7 cm (5 in), SDI is the stand density index (unitless), DF BA (%) is the DF basal area (% of total basal) of trees >12.7 cm (5 in), and DF MA (1 km) is an indicator of insect pressure. DF MA is the mortality area (ha) of DF trees within 1km of the FIA plot from gridded aerial survey data. See Table 1 for variable expectations. All plots were zoomed into the range of basal area loss 0 to 50% for visualization purposes only (i.e., models not affected). P-values are 'ns' for not significant ($p > 0.05$), '*' for $p < 0.05$, and '**' for $p < 0.01$

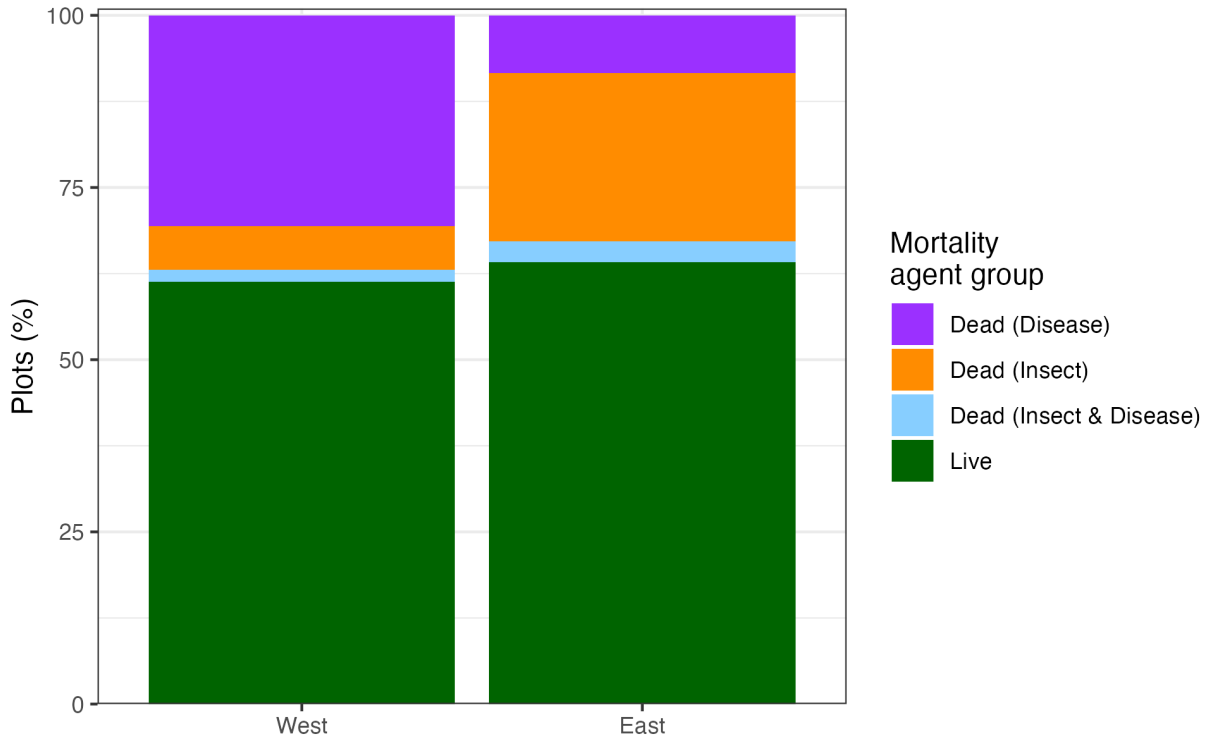

Fig. S6: Percent of plots where disease, insect, or insect/disease were recorded on Douglas-fir tree mortalities west and east of the Continental Divide. USFS Forest Inventory and Analysis (FIA) plots with ≥75 stems/ha in Northern Rocky Mountains were included.

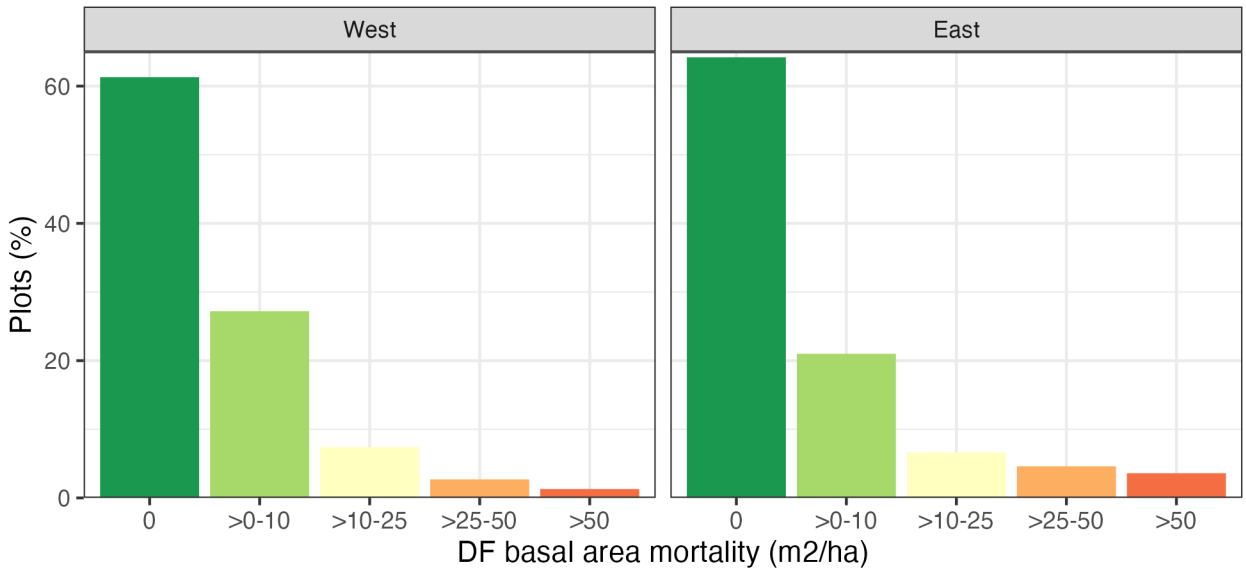

Fig. S7: Percent of plots in five bins of Douglas-fir (DF) basal area mortality (m^2/ha) in two ecoregions west and east of the Continental Divide in the Northern Rocky Mountains. Mortality was from multiple agents, including disease and insects (excluding wildfire; see methods).

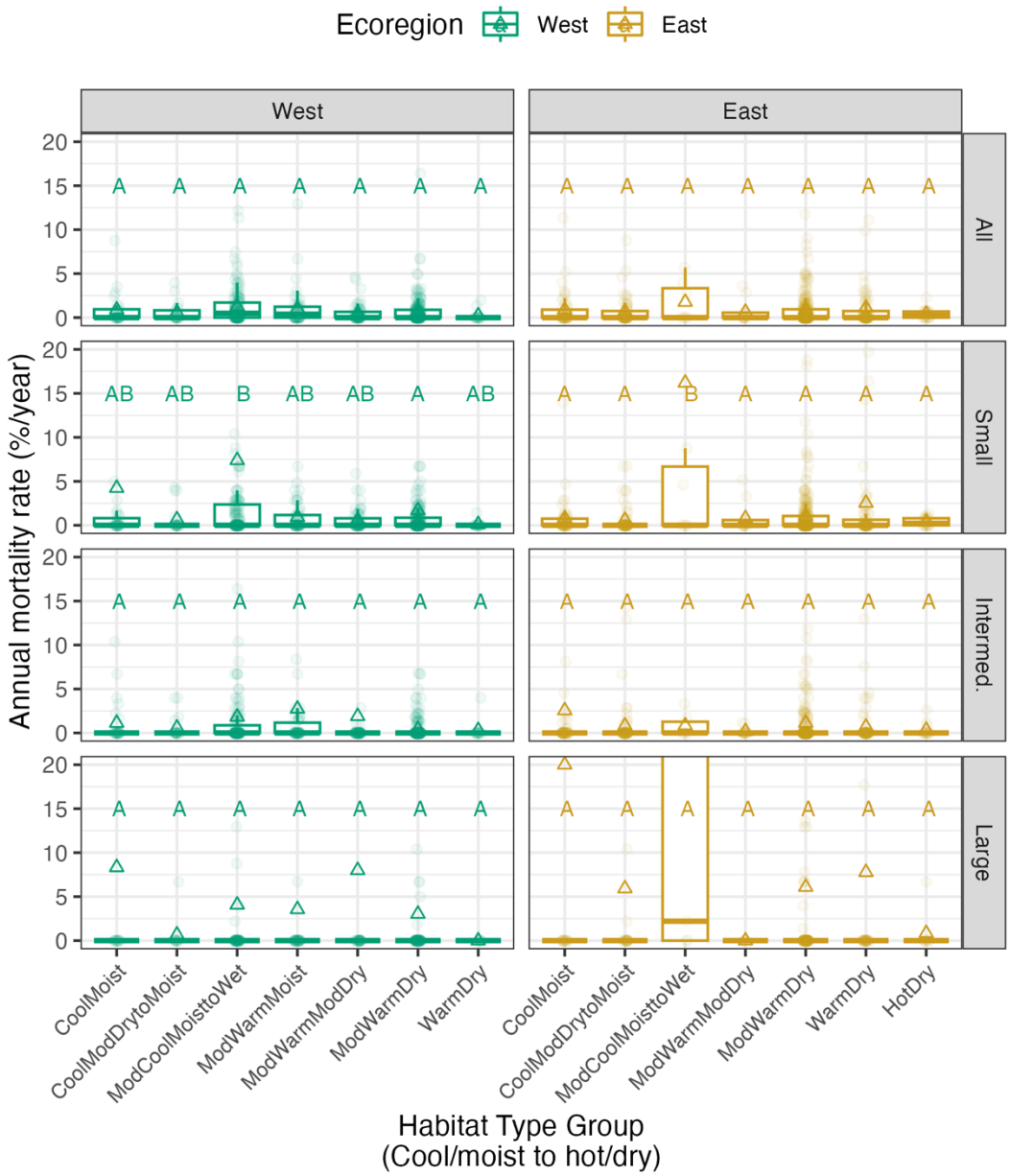

Fig. S8: Annual mortality rates (% year^{-1}) by Habitat Type Groups (HTG) for four size classes of trees (rows) and two ecoregions (columns). HTGs were organized from cool/moist (left) to HotDry (right) and were collected by USFS Forest Inventory and Analysis (FIA) crews in the field. HTGs are commonly used by forest managers to group areas with similar biophysical characteristics (e.g., topography, climate, soils, disturbance regimes) that result in similar vegetation composition, structure, and function. The tree size classes were all trees (>12.7 cm diameter at breast height), small trees (12.7-29 cm), intermediate trees (>29-50 cm), and large trees (>50 cm). Letters across the top of each panel display the results of pairwise comparisons of the marginal mean values between size classes (α = 0.05) within ecoregions. Common letters (e.g., 'A') are not significantly different (i.e., $p > 0.05$). The following HTGs were excluded due to insufficiently representation: cold, cool/wet, sparse, and none. FIA plots with ≥ 75 stems/ha in USFS Region 1 were included. Root disease was expected to be more common in moist (grand fir) to wet (western hemlock) and less common in cool (subalpine fir) or dry (ponderosa pine) habitat type series (Byler et al. 2011). Few statistically significant differences were found in this analysis and HTG was excluded from further analysis. Similarly non-significant results were found in exploratory analyses for sub-ecoregions (two for west and east) and all ecoregions combine as well as for aggregations of HTGs into higher level Potential Vegetation Types.

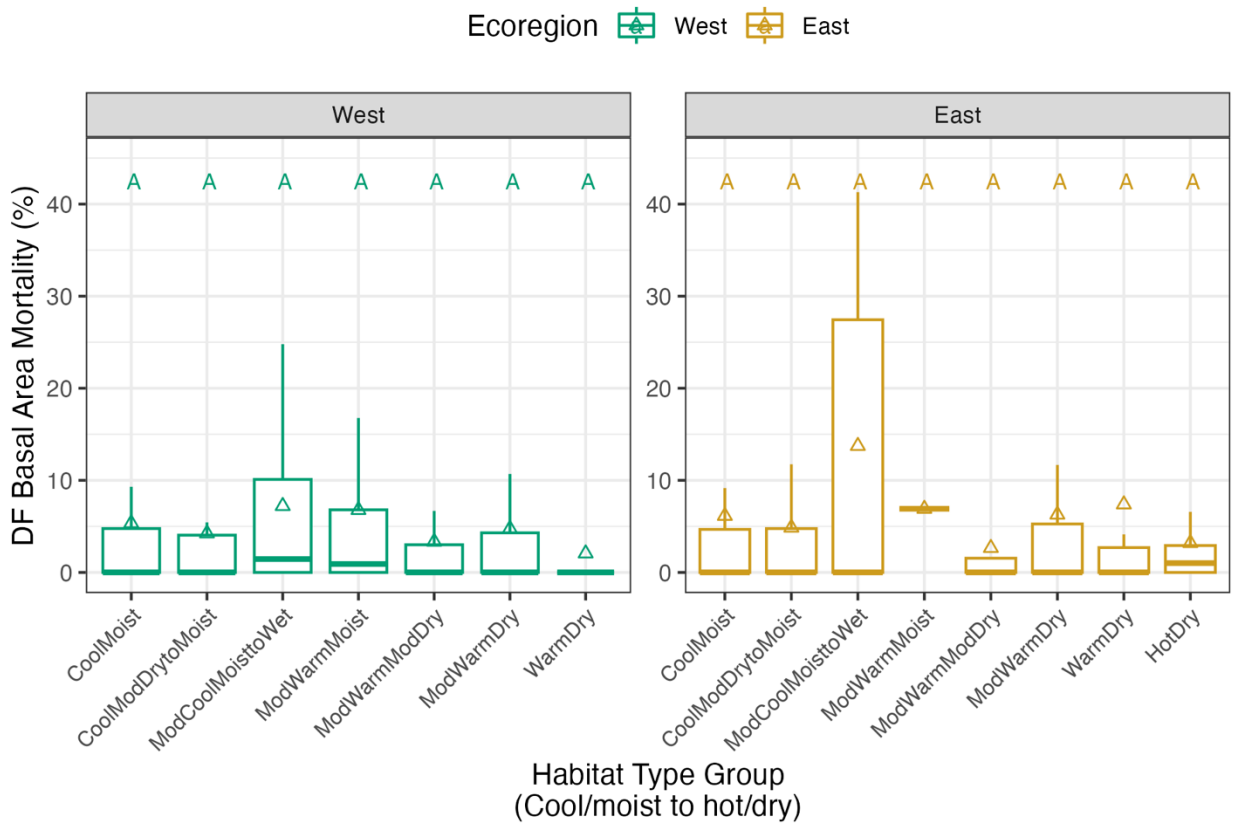

Fig. S9: Douglas-fir **(**DF) basal area mortality (%) by Habitat Type Groups (HTG) in two ecoregions. HTGs were organized from cool/moist (left) to HotDry (right). Letters across the top of each panel display the results of pairwise comparisons of the marginal mean values between size classes ($\alpha = 0.05$) within ecoregions. Common letters (e.g., 'A') are not significantly different (i.e., $p > 0.05$). The following HTGs were excluded due to insufficiently representation: cold, cool/wet, sparse, and none. Root disease was expected to be more common in moist (grand fir) to wet (western hemlock) and less common in cool (subalpine fir) or dry (ponderosa pine) habitat type series (Byler et al. 2011). FIA plots with ≥75 stems/ha in USFS Region 1 were included. Few statistically significant differences were found in this analysis and HTG was excluded from further analysis. Similarly non-significant results were found in exploratory analyses for sub-ecoregions (two for west and east) and all ecoregions combine as well as for aggregations of HTGs into higher level Potential Vegetation Types.

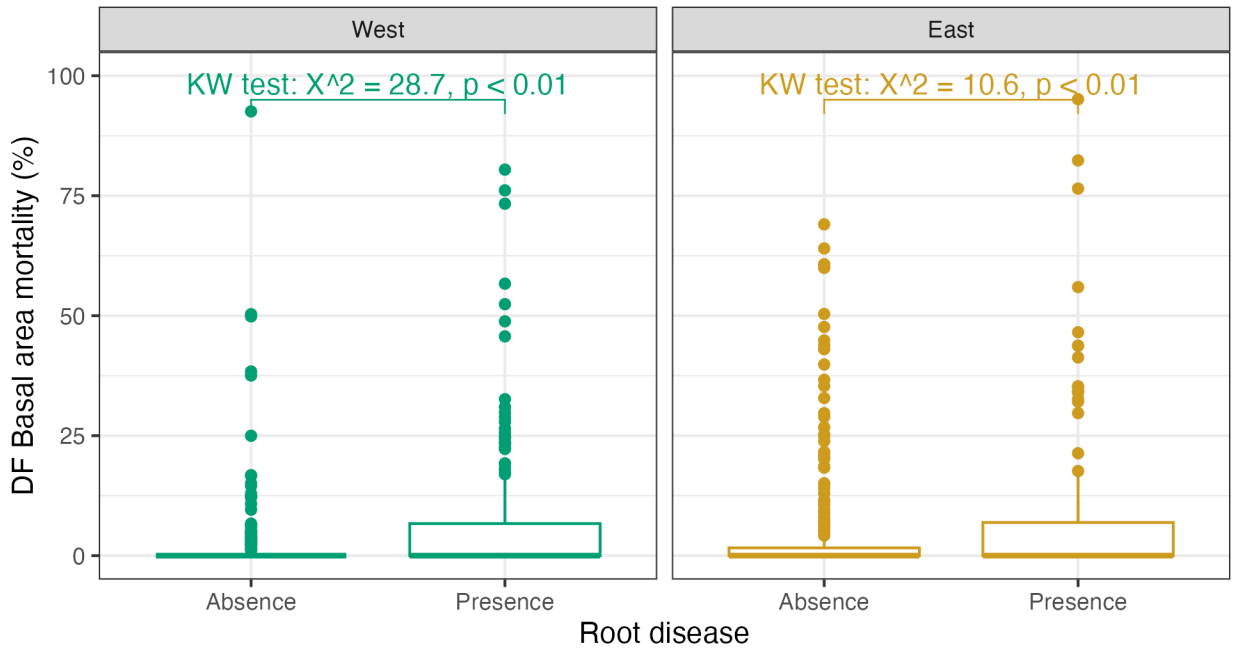

Fig. S10: Douglas-fir (DF) basal area mortality (%) in plots with presence or absence of root disease in areas west and east of the Continential Divide in the Northern Rocky Mountains. DF mortality for sites with presence or absence was compared with a Kruskal-Wallis test (see figure for test results). Plots were from the USDA Forest Inventory and Analysis (FIA) Program, and root disease presence was defined as evidence of root disease within 15 m of the plot, a metric collected by FIA crews.

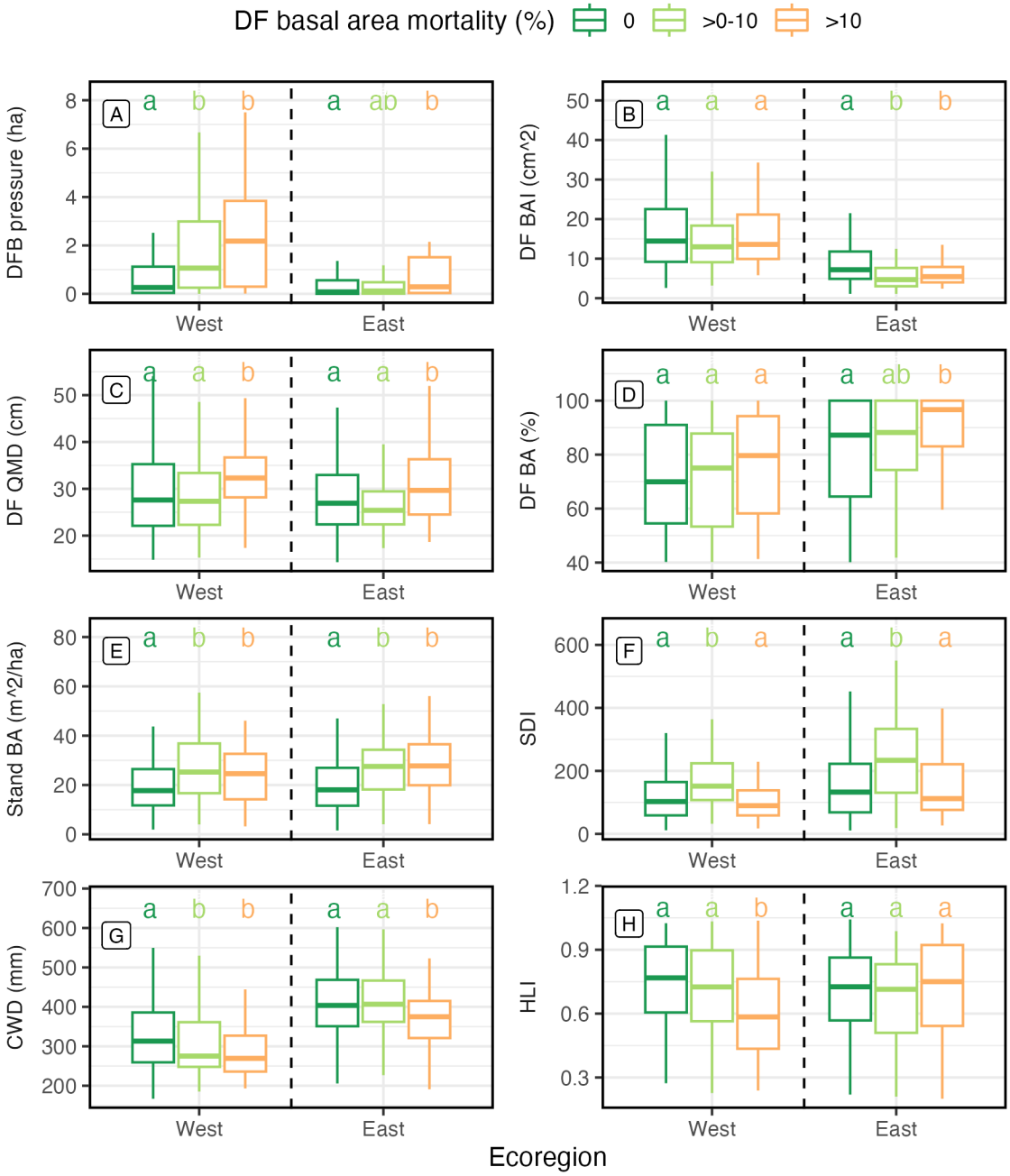

Fig. S11: Boxplots of (A) Douglas-fir beetle (DFB) population pressure, (B-F) multiple stand structure and composition variables, (G) annual climate water deficit (CWD; 1962-2022), and (H) heat load index (HLI) for three levels of Douglas fir (DF) basal area (BA) mortality (%). Stand structure and composition variables included (B) DF basal area increment (BAI), (C) DF quadratic mean diameter (QMD), (D) DF BA (%), (E) Stand BA (m^2/ha), and (F) stand density index for stems > 12.7 cm diameter at breast height. DFB pressure was the hectares of DF mortality area (MA) attributed to DFB within 1 km of the plot and DF MA estimates were from gridded aerial survey data (see methods). In the boxplots, the thick horizontal line is the median, the box represents the interquartile range (25th–75th percentiles; IQR) of the distribution, and the whiskers extend no further than +/-1.5 times the IQR. Outliers were excluded. Letters indicate the results of pairwise comparisons within ecoregions (Dunn test; $\alpha = 0.05$, Holm-corrected) following detection of significant differences between groups from a Kruskal-Wallis test. Common letters (e.g., 'a') are not significantly different. Results are for plots with >75 DF stems/ha and ≥40 DF BA, and very similar to the same figure produced for plots with > 75 DF stems/ha only (see Fig. 4).

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