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ARTICLE

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Patterns, drivers, and implications of postfire delayed tree mortality in temperate conifer forests of the western United States

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Abstract

Conifer forest resilience may be threatened by increasing wildfire activity and compound disturbances in western North America. Fire refugia enhance forest resilience, yet may decline over time due to delayed mortality—a process that remains poorly understood at landscape and regional scales. To address this uncertainty, we used high-resolution satellite imagery (5-m pixel) to map and quantify delayed mortality of conifer tree cover between 1 and 5 years postfire, across 30 large wildfires that burned within three montane ecoregions in the western United States. We used statistical models to explore the influence of burn severity, topography, soils, and climate moisture deficit on delayed mortality. We estimate that delayed mortality reduced live conifer tree cover by 5%–25% at the fire perimeter scale and 12%–15% at the ecoregion scale. Remotely sensed burn severity (1-year postfire) was the strongest predictor of delayed mortality, indicating patch-level fire effects are a strong proxy for fire injury severity among surviving trees that eventually perish. Delayed mortality rates were further influenced by long-term average and short-term postfire climate moisture deficits, illustrating the impact of drought on fire-injured tree survival. Our work demonstrates that delayed mortality in conifer forests of the western United States can be remotely quantified at a fine grain and landscape scale, is a spatially extensive phenomenon, is driven by fire–climate–environment interactions, and has important ecological implications.

KEYWORDS
burn severity, delayed mortality, fire effects, fire refugia, forest resilience, remote sensing, temperate conifer forests, western United States

INTRODUCTION

As a warming climate drives greater fire activity across western North American forests (Abatzoglou & Williams, 2016; Juang et al., 2022; Parks & Abatzoglou, 2020), recently observed increases in large, severe, and frequent wildfire events have sparked concerns around forest resilience (Busby et al., 2020; Coop et al., 2020; Keeley et al., 2019; Reilly et al., 2020; Turner et al., 2019; Whitman et al., 2019). The resilience of obligate seeding conifers, which dominate many western North American landscapes, is strongly tied to the spatial distribution and attributes of fire refugia, which provide seed source necessary for tree reestablishment postfire (Blomdahl et al., 2019; Busby & Holz, 2022; Coop et al., 2019; Downing et al., 2019; Meigs & Krawchuk, 2018). Fire refugia also provide critical resources and habitat for wildlife and enhance the biotic and structural diversity of postfire ecosystems (Krawchuk et al., 2020; Meddens et al., 2018). Fire refugia extent may decline over time, however, due to postfire delayed tree mortality.

Postfire delayed tree mortality (hereafter delayed mortality) refers to the phenomenon where trees that initially survive a wildfire subsequently die over an extended temporal period (beyond 1-year postfire) due to direct and/or indirect effects (Hood & Varner, 2019; Appendix S1: Figure S1). Direct effects contributing to delayed mortality include injuries sustained by fire that cause cambium necrosis and reduced hydraulic conductivity of the xylem (e.g., Bär et al., 2019), ultimately disrupting or compromising the physiological functions of trees and their capacity to survive future stress (Hood, 2021; Hood et al., 2018; Michaletz et al., 2012). Indirect effects are much broader by comparison, including pre- and postfire compound disturbance and changes to the biophysical environment that limit resource availability to and/or disrupt key physiological functions in trees (Hood & Varner, 2019). For example, prefire drought (van Mantgem et al., 2013) and competition (van Mantgem et al., 2018, 2020) have been linked to delayed mortality, as have postfire drought (Furniss et al., 2022), competition (Becker & Lutz, 2023; Keyser et al., 2010; Skov et al., 2004), and insect outbreak (Hood et al., 2016; Jeronimo et al., 2020).

Burn severity quantifies and describes patterns of fire-related tree and vegetation mortality at large scales via remote sensing technologies (Keeley, 2009). Early studies in the western United States established that the difference between 1-year pre- and postfire imagery effectively captured fire-related tree mortality patterns, while minimizing the conflicting spectral signal of postfire tree and vegetation recovery (Key, 2006; Key & Benson, 2006). This methodology has served as the basis of the Monitoring Trends in Burn Severity program in the United States (MTBS; Eidenshink et al., 2007), whose data products are widely used by the broader US scientific and management communities (Picotte et al., 2020), and whose methods have become the gold standard for quantifying burn severity globally (e.g., Miller et al., 2009; Miller & Thode, 2007). Refinements to this core methodology have primarily focused on the subjectivity of methods and classifications (e.g., Kolden et al., 2015), the comparative performance of various burn severity indices across vegetation types (e.g., Parks et al., 2014), and the challenge of connecting ecologically meaningful change to remotely sensed burn severity index values (e.g., Harvey et al., 2019; Morgan et al., 2014; Parks, Koontz, et al., 2019). The temporal window of burn severity and tree mortality assessment, however, has received much less attention outside of early theoretical frameworks (e.g., Key, 2006). If tree mortality patterns related to fire effects are substantial beyond 1-year postfire, researchers and managers risk underestimating the impacts of fire on ecological communities, ecological legacies and succession, habitats, and postfire ecosystem trajectories. Field-based studies suggest delayed mortality can have marginal to significant impacts on forest structure and composition up to 10-year postfire and beyond (e.g., Agee, 2003; Brown et al., 2013; Jeronimo et al., 2020; Roccaforte et al., 2018; Whittier & Gray, 2016).

Despite clear empirical evidence of delayed mortality at the tree scale (e.g., Cansler et al., 2020; Hood, 2021; Hood et al., 2018; Hood & Varner, 2019), efforts to track delayed mortality at landscape and regional scales have been limited to date. This gap can be partially attributed to the challenge of detecting delayed mortality in widely used, moderate spatial resolution imagery products like Landsat. Although refined methodologies have been recently developed for detecting delayed mortality via Landsat imagery (e.g., Reilly et al., 2023), linking changes in spectral index values to empirical tree mortality is challenging at this 30-m pixel grain (Parks, Koontz, et al., 2019), given pixels can contain multiple distinct features (i.e., mixed-pixel problem) and the spectral signature of tree mortality and tree or vegetation recovery can become confused (Key, 2006). Multiple higher resolution satellite (e.g., Sentinel [10 m], RapidEye [5 m], and PlanetScope [3 m]) and aerial (e.g., National Agriculture Imagery Program [NAIP; 1 m]) imagery products have become available over the last decade, however, increasing our capacity to classify tree cover and detect change in forest cover at roughly the tree scale (e.g., Chapman et al., 2020; Walker et al., 2019).

Considering the impacts of increasingly large, severe, and frequent wildfires across western North American and specifically western US forests, an improved understanding of how delayed tree mortality patterns alter forest extent, resilience, and persistence can improve the understanding of tree mortality processes at landscape and regional scales, as well as support planning and implementation of land management objectives (e.g., silvicultural treatments, postfire reforestation, landscape restoration, carbon storage and sequestration, habitat for threatened species, among others; Hood & Varner, 2019; Krawchuk et al., 2020). In this study, we quantified landscape-scale patterns of delayed tree mortality at a fine grain (5-m pixel), defined here as the loss of live conifer tree cover occurring between 1- and 5-year postfire (hereafter T1 and T5), across three montane ecoregions of the western United States. Following previous field (Agee, 2003; Brown et al., 2013; Jeronimo et al., 2020) and remote sensing (Reilly et al., 2023) studies, we chose the T1–T5 temporal period in this study as a strategic compromise between capturing a large proportion of cumulative delayed mortality responses and minimizing spectral confusion introduced by postfire tree and vegetation recovery. Specifically, we evaluated the following questions:

1. What is the spatial extent of postfire delayed conifer tree mortality?
2. How is delayed mortality related to burn severity, soils, and topography?
3. To what extent do long-term average and short-term postfire climate moisture deficits (CMDs) alter these relationships?

METHODS

Study areas

To represent and compare patterns of landscape-scale delayed mortality in the western United States and their potential driving factors within an ecologically relevant framework, our study focused on three major montane ecoregions and two broad conifer forest types that have experienced a large proportion of high-severity wildfire in modern times: upper-montane and subalpine forests in (1) the Cascade Range of Oregon and Washington and (2) the N. Rockies of Idaho, Montana, and Wyoming, and (3) dry conifer forests in the S. Rockies of Colorado and New Mexico. Upper-montane and subalpine forests in the Cascades and N. Rockies are typically dominated by fire-sensitive and/or shade-tolerant conifers (e.g., *Abies grandis*, *Abies lasiocarpa, Abies amabilis, Pinus contorta, Tsuga mertensiana, Tsuga heterophylla, Picea engelmannii*; Agee, 1993; Baker, 2009) and exhibit moderate to high tree densities due to moist and/or cool climate conditions and historically long (50–300+ year) fire-return intervals (Agee, 1998). In contrast, dry conifer forests in the S. Rockies have been historically dominated by fire-resistant and/or shade-intolerant conifers (e.g., *Pinus ponderosa* and *Pseudotsuga menziesii*) and exhibit low to moderate tree densities due to warm and/or dry climates and historically frequent (5–50 year) fire-return intervals (Johnson & Margolis, 2019; Sherriff et al., 2014; Veblen et al., 2000). Of the three study ecoregions, the Cascades experiences the highest maritime effect and greatest annual precipitation, followed by the N. Rockies and S. Rockies. Annual CMD is negatively correlated with elevation, with the strongest effect occurring in the S. Rockies (Figure 1). Soils in the Cascades are primarily composed of well-draining Andisols, in the N. Rockies a mixture of poorly developed Entisols and Iceptisols and well-draining Andisols, and in the S. Rockies well-draining Seitz (USDA, 2022).

We used several sources of spatial data and criteria as initial filters to identify suitable fire perimeters for estimating delayed mortality. First, we used wildfire perimeter delineations and classified burn severity estimates from the MTBS program to select wildfires within each ecoregion that (1) burned between 2008 and 2014 following satellite imagery availability as described in the following paragraph, and (2) experienced relatively large patches of high-severity fire (>10 ha). From a remote sensing perspective, fire severity in this study relates to estimates of percent overstory tree mortality due to fire effects at T1 (e.g., low <25%; moderate 25%–75%; high >75% mortality; Miller et al., 2009). Second, we used the LANDFIRE (Rollins, 2009) Existing Vegetation Type (EVT) layer to identify fire perimeters that were dominated (>75% of forested area) by either (1) upper-montane and subalpine forest types (e.g., spruce, true-fir, hemlock, and lodgepole pine) in the Cascades and N. Rockies or (2) dry conifer forests in the S. Rockies (e.g., ponderosa pine and Douglas-fir). From this subsample, we chose an equal number ($n = 10$) of suitable fire perimeters per ecoregion (Figure 1; Appendix S1: Table S1). If more than 10 fire perimeters per ecoregion were suitable for assessment, we chose the top 10 fire perimeters with the largest extent of high-severity fire.

Imagery classification and accuracy assessment

We paired satellite images taken at T1 (1-year postfire) and T5 (5-year postfire) and used an unsupervised imagery classification scheme to classify the extent of overstory conifer tree cover mortality (loss) within each wildfire perimeter (Figure 2). We chose this temporal period based on results from previous studies, which indicated a large proportion of fire-related tree mortality responses are likely to emerge within the first 5-year postfire (e.g., Agee, 2003; Brown et al., 2013; Jeronimo et al., 2020) and the goal of minimizing conflicting spectral signals associated with tree and vegetation recovery (Walker et al., 2019; Figure 2a). To accurately detect and classify overstory tree cover change over large spatial extents and across a broad range of heterogenous environments, we used Planet RapidEye satellite imagery

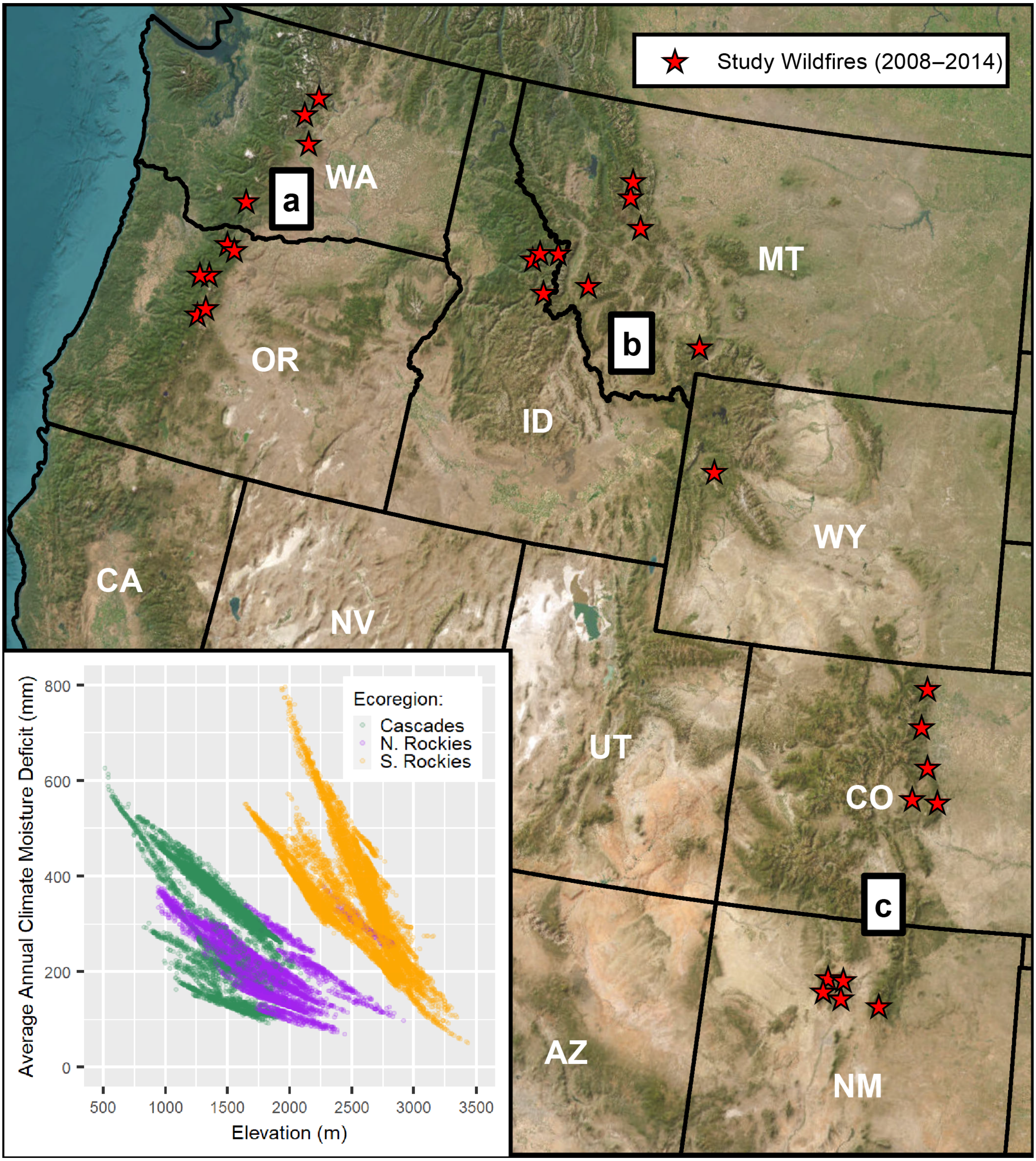

FIGURE 1 Geographic locations of the 30 wildfire perimeters where delayed tree mortality patterns were mapped and quantified. Fires were distributed equally across three mountain ecoregions in the western United States, including (a) the Cascade Range, (b) the Northern Rockies, and (c) the Southern Rockies. Inset scatterplot indicates the distribution of and relationship between elevation and climate moisture deficit to vegetation among areas nested within the study wildfire perimeters, colored by ecoregion (Cascades Range [green], Northern Rockies [purple], Southern Rockies [orange]).

(Planet Team, 2022) for our assessment. RapidEye imagery was an ideal medium in this study because it (1) can capture fine-grain features such as individual trees or the aggregation of several small trees at a 5-m spatial resolution (i.e., 1- to 5-m crown diameter; Hart & Veblen, 2015), (2) includes the near-infrared (NIR) spectral band

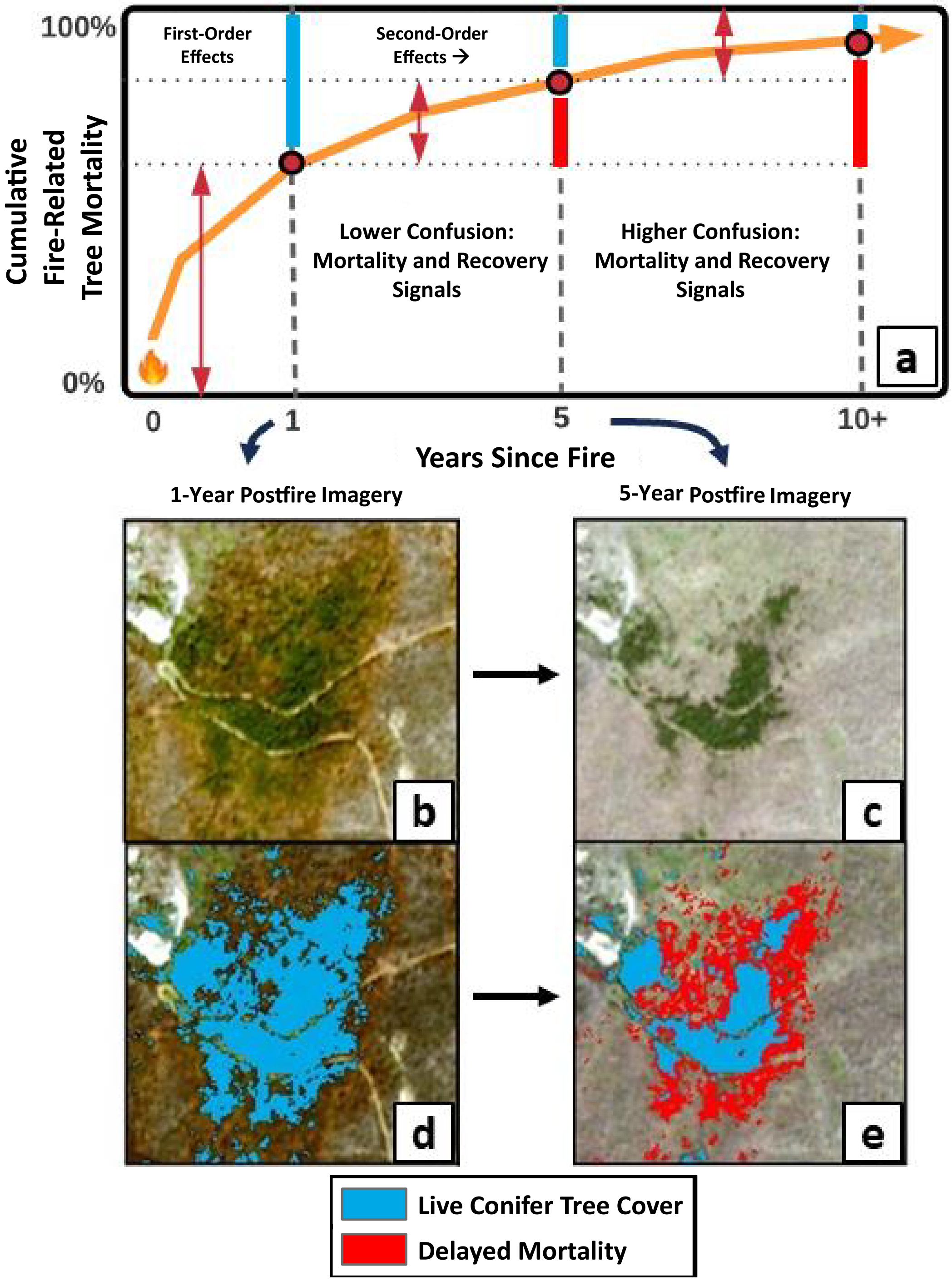

FIGURE 2 Field studies indicate cumulative fire-related tree mortality declines over time since fire (a), with the largest proportion of mortality occurring within 1-year postfire (fire-order effects, the temporal period prior to detectable vegetation recovery). Delayed tree mortality can emerge over longer temporal periods (i.e., 1 to 10+ years postfire; second-order effects, the temporal period following detectable vegetation recovery), yet can become increasingly difficult to detect via remote sensing as tree and vegetation mortality and recovery signals become confused. We quantified delayed tree mortality via remote sensing in this study between 1-year (T1) and 5-year (T5) postfire, to minimize confusion between mortality and recovery signals while capturing a large proportion of delayed mortality that will emerge over time. Panels b–e highlight the satellite imagery classification used to quantify delayed mortality in a single location. True-color satellite image at T1 (b), true-color satellite image at T5 (c), classification of live conifer tree cover at T1 (d), and classification of delayed mortality at T5 (e; difference in live tree cover between T1 and T5).

advantageous for capturing vegetation cover and differentiating between plant functional groups (e.g., conifers vs. angiosperms), (3) minimizes geometric distortions between paired images relative to high-resolution aerial imagery products, and (4) exhibits a high temporal resolution of ~7–14 days. RapidEye imagery was collected between 2009 and 2019, which limited what fire perimeters could be evaluated for postfire delayed mortality (i.e., fires occurring as early as 2008 and as late as 2014, to ensure the availability of both T1 and T5 images).

Preprocessed surface reflectance images at T1 and T5 were clipped to the extent of each MTBS fire perimeter delineation (Figure 2b,c). For each set of paired images, we chose dates that were within one month of each other to minimize geometric and phenological differences between images. We filtered images to <5% cloud and smoke cover to minimize atmospheric distortions and targeted imagery dates near the summer solstice in the northern hemisphere to further minimize potential geometric distortions. In the S. Rockies ecoregion, we selected imagery dates prior to the summer solstice, as available, to minimize the greening effect of angiosperms during the mid-late summer monsoon period (Rodman, Veblen, Chapman, et al., 2019). Areas within each fire perimeter boundary that had reburned were removed from the study. Further, we manually identified (via visual interpretation) areas with obvious signs of postfire salvage logging and removed them from the study; overall, we detected minimal salvage logging extent (<100 ha across fires).

We used an unsupervised classification scheme (Iterative Self-Organizing Data Analysis Technique [ISODATA] clustering) to identify delayed mortality of live conifer tree cover among paired T1 and T5 RapidEye satellite images for each fire perimeter (Figure 2b–e), following procedures outlined by Rodman, Veblen, Chapman, et al. (2019). First, the paired images were visually assessed for correct geospatial alignment using static landscape features (e.g., roads) and realigned when necessary. Second, the normalized differenced vegetation index (NDVI) was calculated for the T1 image and used to separate vegetated areas from nonvegetated via visual interpretation of ISODATA clusters. Third, red and NIR bands were used to separate live conifer tree cover from angiosperm (trees and understory vegetation) cover via visual interpretation of ISODATA clusters. Finally, the T5 image was then cropped to the extent of live conifer tree cover classified in the T1 image, and the steps described above were repeated to classify live conifer tree cover at T5. This classification resulted in three possible categorical values: (1) live conifer tree cover (i.e., alive at both T1 and T5), (2) delayed mortality of conifer tree cover (i.e., alive at T1, dead at T5), and (3) other cover (i.e., bare ground, angiosperm cover, or conifer tree cover dead at T1).

Given that spatially explicit field observations of postfire tree mortality responses over time were not available across our large study area extent, we used high-resolution (1-m pixel) National Agricultural Imagery Program (NAIP; USDA, 2020) imagery as a reference source to assess the classification accuracy of the RapidEye imagery (i.e., a proxy for true live conifer tree cover). Prior studies have indicated that NAIP imagery exhibits a similar accuracy to field data when used as a reference source for classifying conifer tree cover (Coop et al., 2019). Because NAIP imagery was not available at T1 and T5 across every study fire perimeter, we conducted imagery classification accuracy assessments at the ecoregion scale, by aggregating classified fire perimeters that did have NAIP imagery available at both T1 and T5 for the Cascades (6 out of 10 fire perimeters), N. Rockies (7 out of 10 fire perimeters), and S. Rockies (6 out of 10 fire perimeters) ecoregions.

To evaluate the RapidEye-NAIP classification accuracy, we used a stratified random sampling design with equal probability (100 points per possible classified pixel value) to generate 200 accuracy assessment points within each T1 image and 300 points in each T5 image (Congalton, 1991; Rodman, Veblen, Chapman, et al., 2019). This design resulted in a total of six individual image assessments (i.e., two postfire periods in each of the three ecoregions). At each accuracy assessment point location, manual photointerpretation of the pixel intersecting the point was used to assign the reference point a value of either other cover, live conifer tree cover, or delayed mortality of conifer tree cover (in the case of each T5 image). Confusion matrices were generated for each classified image to compare and assess the agreement between RapidEye imagery classifications and conditions observed in the reference NAIP imagery. Imagery classification accuracy varied by postfire temporal period and ecoregion, with overall classification accuracy ranging 0.86–0.94 (Table 1).

Modeling drivers of delayed tree mortality

We used logistic boosted regression tree (BRT) models with a Bernoulli distribution to model the relationships between a suite of predictive variables and postfire delayed conifer tree mortality responses derived from the imagery classification workflow. We explicitly used BRT models in this analysis due to their robustness to issues of multicollinearity and the capacity to account for complex interactions between fitted predictors (Elith et al., 2008). To increase model convergence, reduce

TABLE 1 Confusion matrix of the satellite imagery classification accuracy assessment conducted in 1-year (T1) and 5-year (T5) postfire images.

		Producer's accuracy			User's accuracy			
Ecoregion	**Imagery period**	**Conifer tree cover**	**Other cover**	**Delayed conifer tree mortality**	**Conifer tree cover**	**Other cover**	**Delayed conifer tree mortality**	**Overall accuracy**
Cascades	T1	0.96	0.90	…	0.89	0.96	…	0.93
Cascades	T5	0.85	0.90	0.83	0.80	0.94	0.84	0.86
N. Rockies	T1	0.86	0.91	…	0.92	0.85	…	0.89
N. Rockies	T5	0.86	0.91	0.84	0.81	0.90	0.90	0.87
S. Rockies	T1	0.93	0.95	…	0.95	0.93	…	0.94
S. Rockies	T5	0.87	0.91	0.92	0.92	0.94	0.84	0.90

computation time, and minimize spatial autocorrelation, we used a subsampling scheme of the total raster dataset ($n > 1,000,000$ pixels) spanning all study wildfire perimeters. We first converted the 5-m resolution classified satellite imagery with a binary response (i.e., presence or absence of delayed tree mortality) from raster into a point shapefile. To minimize potential spatial autocorrelation between points, we then applied a 100-m systematic spatial buffer to all data points across all fire perimeters. Next, we drew a 10% stratified random sample from all spatially buffered data points, stratifying by fire perimeter identity to ensure the modeling data were represented proportionally across all study fire perimeters.

Each stratified subsample of data was then fit into one of four ecoregion-based BRT models with the dismo package in R (Hijmans et al., 2021; R Core Team, 2020) using nine predictive variables associated with tree stress (Hood et al., 2018; Hood & Varner, 2019; Appendix S1: Figure S1): (1) burn severity (relativized burn ratio; RBR) at T1, (2) long-term average and short-term postfire CMDs, (3) soil water-holding capacity, and (4) topography and its effects on microclimate. See Table 2 for all predictive variables, including their data sources and methods of calculation. While average annual CMD (Table 2) may capture long-term trends in prefire drought, we did not explicitly evaluate short-term trends in prefire drought (e.g., up to 5-year prefire).

All BRT models were fit with a bag fraction setting of 0.5 to introduce stochasticity, a learning rate of 0.01 to ensure at least 1000 trees were fit in each model, and a tree complexity of 5 to allow for sufficient variable interactions (Elith et al., 2008). Because BRTs are a stochastic modeling technique, we fit 10 iterations of each model and reported results from the best performing model iteration. We assessed BRT model performance by calculating and reporting the area under curve-receiver operator characteristic (AUC-ROC) using 10-fold cross validation (Elith et al., 2008). When generating partial dependence and interaction plots explaining the modeled relationship between predictive variables and delayed mortality, predictor-specific value ranges were clipped at their upper and lower limits where supporting data were sparse (<10% of sample) to limit interpretation of predictions that may be due to model overfitting.

RESULTS

Fire characteristics and delayed mortality

On average, study fires within the Cascades experienced the largest proportion of high-severity fire, followed by the N. Rockies and S. Rockies, respectively (~49%, ~39%, ~33%; Appendix S1: Figure S2). The aggregated percentage of live conifer tree cover across fire perimeters in the year following fire was relatively similar for the Cascades (~13,909 ha; ~35%) and N. Rockies (~13,174 ha; ~45%) but substantially lower for the S. Rockies (~12,533 ha; ~12%), especially among the three largest fires occurring in that ecoregion: Las Conchas (~61,000 ha; ~8%), High Park (~36,000 ha; ~7%), and Waldo Canyon (~8000 ha; ~16%) (Appendix S1: Figure S2, Table S1).

Postfire delayed mortality ranged widely at the fire perimeter scale from 9% to 20% (±1.5% to 3.4%) in the Cascades, 5% to 22% (±0.5% to 2.2%) in the N. Rockies, and 6% to 25% (±0.9% to 4.0%) in the S. Rockies (Figure 3a). At the ecoregion scale, however, mean and median percent delayed mortality were similar between ecoregions, and no statistical differences were detected ($\alpha = 0.05$): approximately 14% and 13% for the Cascades, 12% and 13% for the N. Rockies, and 15% and 16% for the S. Rockies (Figure 3b). While spatial patterns of delayed tree mortality were highly variable, we observed that (1) many conifer-dominated fire refugia patches remained unchanged, (2) some larger patches shrank in

TABLE 2 A description of the spatially explicit predictive variables fit into boosted regression tree (BRT) statistical models and the data sources and methods they were derived by.

Variable	Spatial resolution	Description and methodology	Units	Range
RBR	30 m	The relativized burn ratio (RBR), a measure of burn severity calculated as the difference in vegetation cover between 1-year prefire and postfire using Landsat imagery; Parks et al. (2014). Negative and positive values respectively indicate increases and decreases in vegetation cover relative to prefire imagery.	Unitless	−494 to 800
Average annual CMD	Downscaled to point	30-year (1981–2010) average annual climate moisture deficit (CMD), the difference between reference evaporative demand and precipitation. Derived from the ClimateNA application (Wang et al., 2016) using point elevation to downscale values from 800-m gridded PRISM data.	mm	51 to 917
Postfire deviation from average annual CMD	Downscaled to point	The percent deviation from the average annual CMD observed during the 1- to 5-year postfire period (i.e., deviation from 30-year normal conditions).	%	−20 to 119
Soil available water capacity	30 m	The maximum volume of plant available water in the upper 150 cm of soils. Extracted from the USDA-NRCS SSURGO database.	mm	9 to 273
Elevation	10 m	Elevation above mean sea level; derived from a 10-m digital elevation model (DEM).	m	510 to 3427
Slope	10 m	The angle of the dominant hillslope; derived from a 10-m DEM.	°	0 to 65
HLI	10 m	The heat load index (HLI) (McCune & Keon, 2002), a topographic measure of incident solar radiation; derived from a 10-m DEM.	Unitless	35 to 97
TPI	10 m	The topographic position index (TPI) (Weiss, 2001), a measure of landscape slope position; derived from a 10-m DEM and calculated using 300- and 750-m moving-window radii (i.e., spatial scales). Negative and positives values, respectively, indicate concave and convex topographic positions.	Unitless	−100 to 100

size, particularly along edges, and (3) many small patches disappeared completely (e.g., Figure 4).

Predictors of delayed mortality and interactions

Burn severity (RBR; derived from 30-m Landsat imagery at T1) was the most important factor associated with delayed mortality of conifer tree cover, followed by elevation, soil available water capacity, then long-term average and short-term postfire CMD (Figure 5a–d,f). Although the relationships of variables followed similar trends across individual ecoregion models, there were notable differences among models associated with the strength and nonlinearity of responses (Figure 5a,d). For the S. Rockies specifically, burn severity had the strongest effect and relative importance on the probability of delayed mortality relative to other ecoregion models and exhibited a nonlinear, u-shaped response, where a

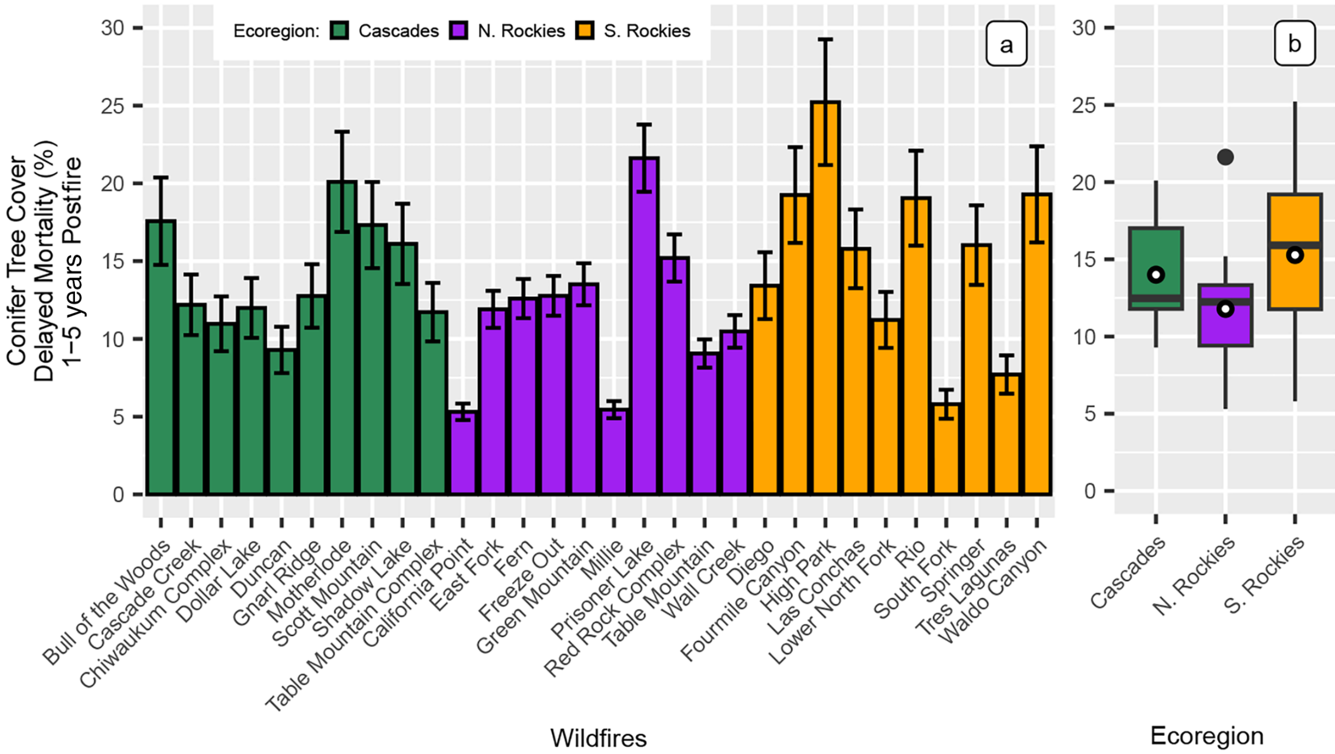

FIGURE 3 Estimated fire (a) and ecoregion-scale (b) percent delayed mortality of conifer tree cover occurring between 1- and 5-year postfire. Error bars (a) indicate potential classification error based on the imagery classification accuracy assessment results (see Table 1). Ecoregion-specific (b) distribution mean, median, and 25th and 75th quantiles are represented by a white dot, a bold black horizontal line, and box's bottom and top horizontal lines, respectively. There were no statistically significant differences (α = 0.05; Wilcoxon rank sum test) detected in delayed mortality rates between ecoregions.

higher probability of mortality was linked to both increasingly negative and positive values of RBR centered at 0 (i.e., increasing deviation from no change in vegetation cover; Figure 5a). We also observed u-shaped responses in all ecoregions associated with CMD (long-term average and short-term postfire deviation from average) and elevation (Figure 5b–d). Less important, convex topography (e.g., ridges) increased probability of delayed mortality (in all ecoregions except the N. Rockies) at the finer computed kernel size of the topographic position index (TPI; 300 m), while for all ecoregions concave topography at the coarser computed kernel size of TPI (750 m, e.g., drainages) increased probability of delayed mortality (Figure 5g,h).

We found a strong interaction between burn severity (RBR) and CMD (Figure 6); these interactions, however, were weak in the Cascades model relative to the other ecoregions. Interaction values and thresholds varied by ecoregion model, but generally, high values of average annual CMD and postfire deviation from average annual CMD increased the probability of delayed mortality beyond 75%, illustrating the existence of thresholds and nonlinear responses to these compound stressors. The predictive accuracy (i.e., cross-validated AUC) among ecoregion BRT models was fair, ranging from 0.72 to 0.76 (Appendix S1: Table S2).

DISCUSSION

Rates of delayed mortality at fire and ecoregion scales

Spatiotemporal patterns of delayed mortality varied with scale, with higher variability in mortality rates observed at finer scales (fire perimeter vs. ecoregion; Agee, 1998; Kane et al., 2017; Turner & Cardille, 2007). At the fire perimeter scale, delayed mortality ranged from 5% to 25%, similar to rates documented by previous field studies focused on monitoring tree mortality patterns over time among plots nested within a single fire perimeter, across a variety of conifer forest types (~0%–46% between one- and two- to seven-year postfire; Agee, 2003; Brown et al., 2013; Jeronimo et al., 2020; Roccaforte et al., 2018; Whittier & Gray, 2016). At the ecoregion scale, mean delayed mortality rates were relatively similar (12%–15%) despite distinct bioclimatic conditions and differences in dominant forest type (upper-montane and subalpine [fir-, spruce-, and

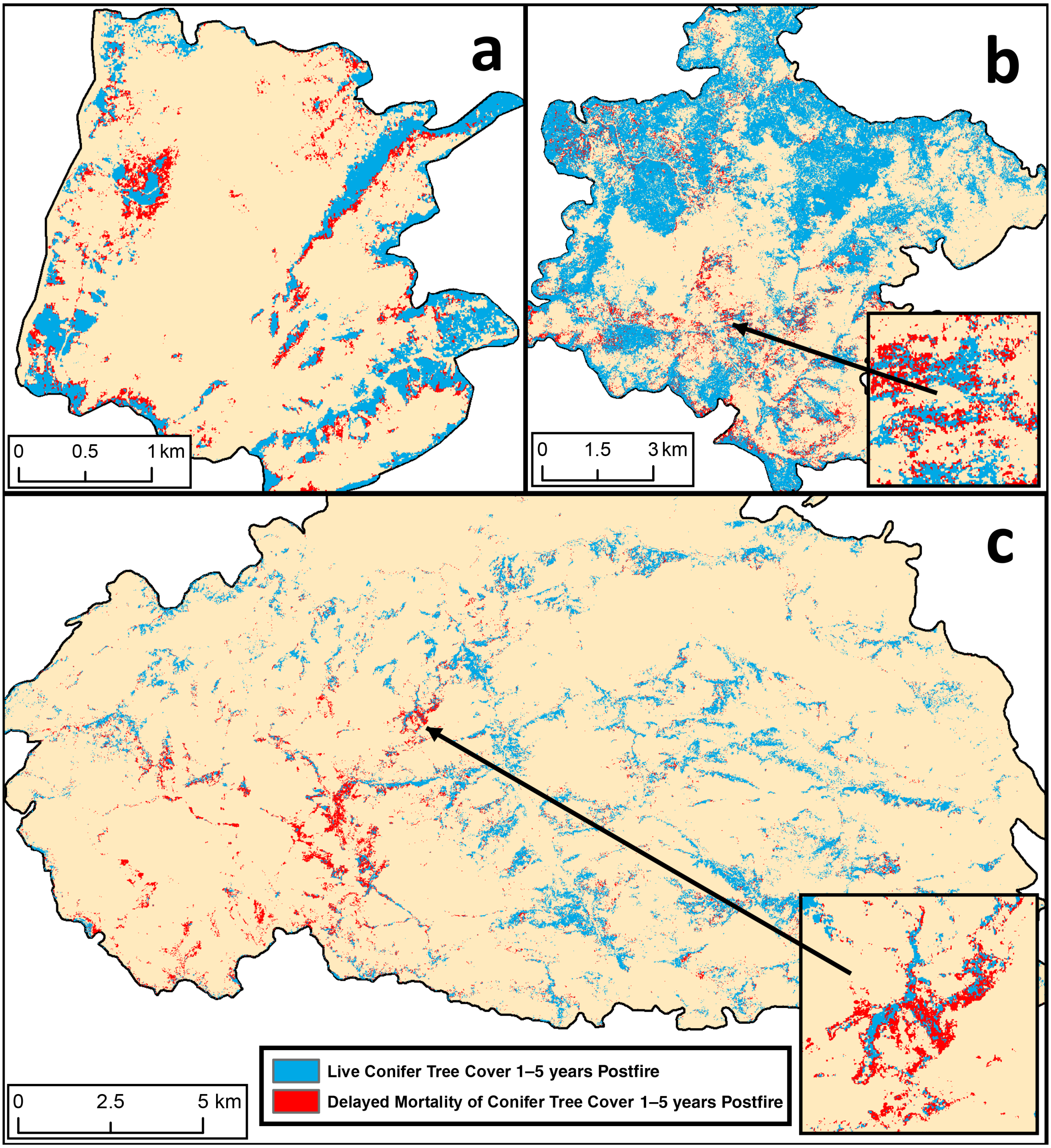

FIGURE 4 Spatial patterns of fine-grain (5 m) persistent live conifer tree cover (blue) and delayed mortality of conifer tree cover (red) between 1- and 5-years postfire at the fire perimeter scale. Tan-colored area represents bare ground cover, angiosperm cover, or conifer tree cover dead at 1-year postfire. (a) The 2008 Gnarl Ridge Fire in the Cascade Range of Oregon, (b) the 2012 Fern Fire in the N. Rockies of Idaho, and (c) the 2012 High Park Fire in the S. Rockies of Colorado. Maps indicate that delayed mortality patterns are highly variable over space, with small and patchy fire refugia sometimes experiencing extirpation and larger contiguous fire refugia shrinking in extent, usually along edges, but generally persisting.

hemlock-dominated] in the Cascades and N. Rockies; dry conifer [pine- and Douglas-fir-dominated] in the S. Rockies). When mapping forested area affected by delayed mortality at a coarser grain (30-m pixel) in California, Washington, and Oregon states, Reilly et al. (2023) also noted high variability at the fire perimeter scale, but greater forest area affected by delayed mortality in cool and moist forest types (Cascades ecoregion) and

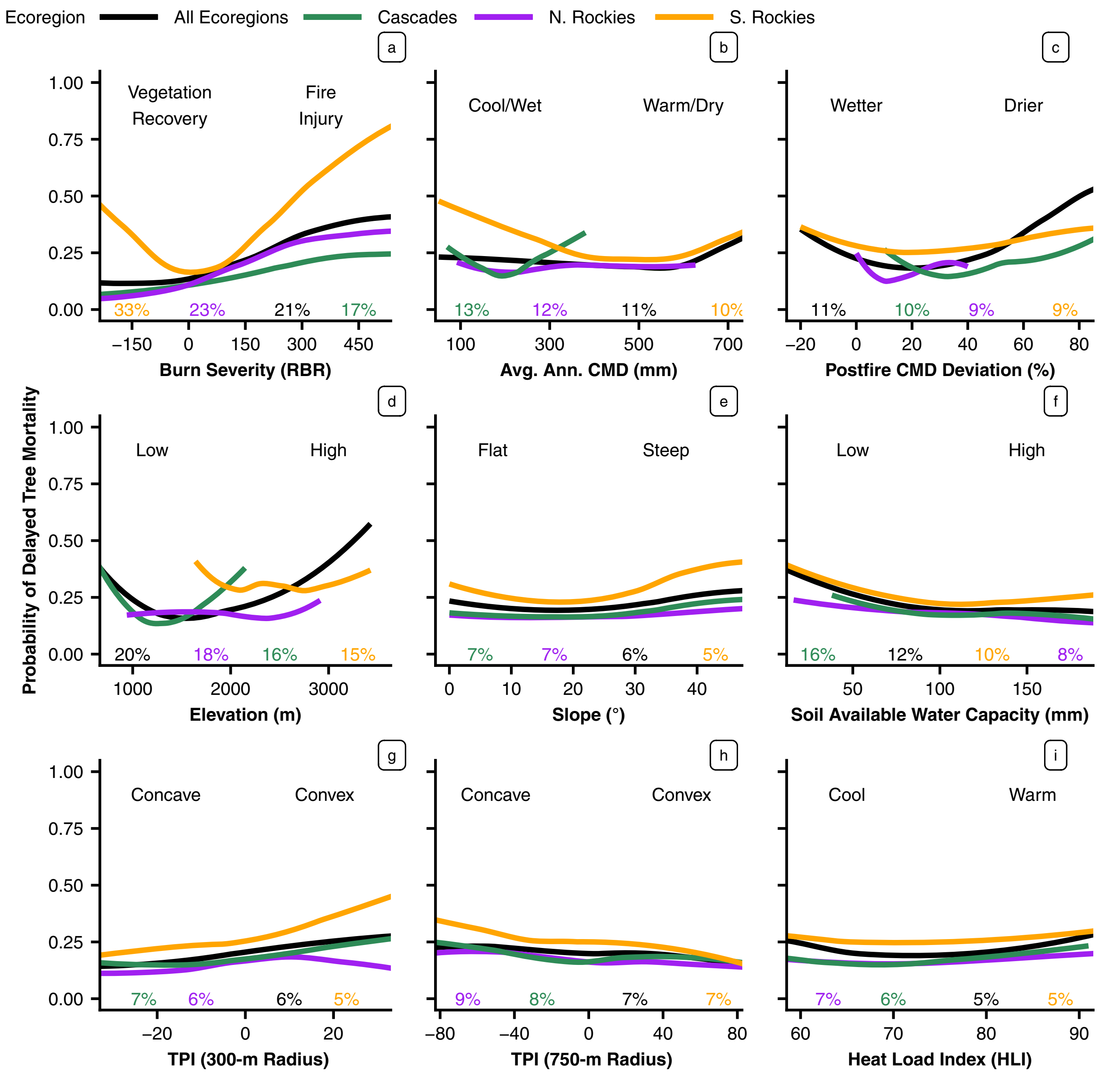

FIGURE 5 Boosted regression tree model partial dependence plots showing the average effect of predictor values (when other predictors are held at their mean value) on the probability of delayed tree mortality, ordered by overall variable importance (listed above *x*-axis). Colored response curves and variable importance percentages in each panel are associated with ecoregion-specific models (All Ecoregions, Cascades, N. Rockies, S. Rockies). (a) Burn severity (relativized burn ratio [RBR]) derived from 30-m Landsat imagery 1-year postfire, (b) 30-year normal (1981–2010) average annual climate moisture deficit (CMD), (c) percent deviation from 30-year normal CMD during the 1- to 5-year postfire assessment period, (d) mean elevation above sea level, (e) angle of the dominant hillslope, (f) maximum soil water capacity available to vegetation, (g, h) the topographic position index (TPI) calculated at fine (300 m) and coarser (750 m) spatial scales, and (i) the heat load index. See Table 2 for a full description of predictive variables; see Appendix S1: Figures S3–S6 for model-specific results including 95% CIs on predictions.

dry forest types affected by compound disturbance (i.e., drought and insect outbreak).

When interpreting these and the following results, it is important to reiterate that our methods may primarily capture delayed mortality of overstory tree cover (i.e., 5-m pixel size may not detect mortality of understory young and/or suppressed older trees with small crowns and wide stem spacing). Although unlikely within areas burned at moderate to high severity, delayed mortality rates observed in this study may in part encompass

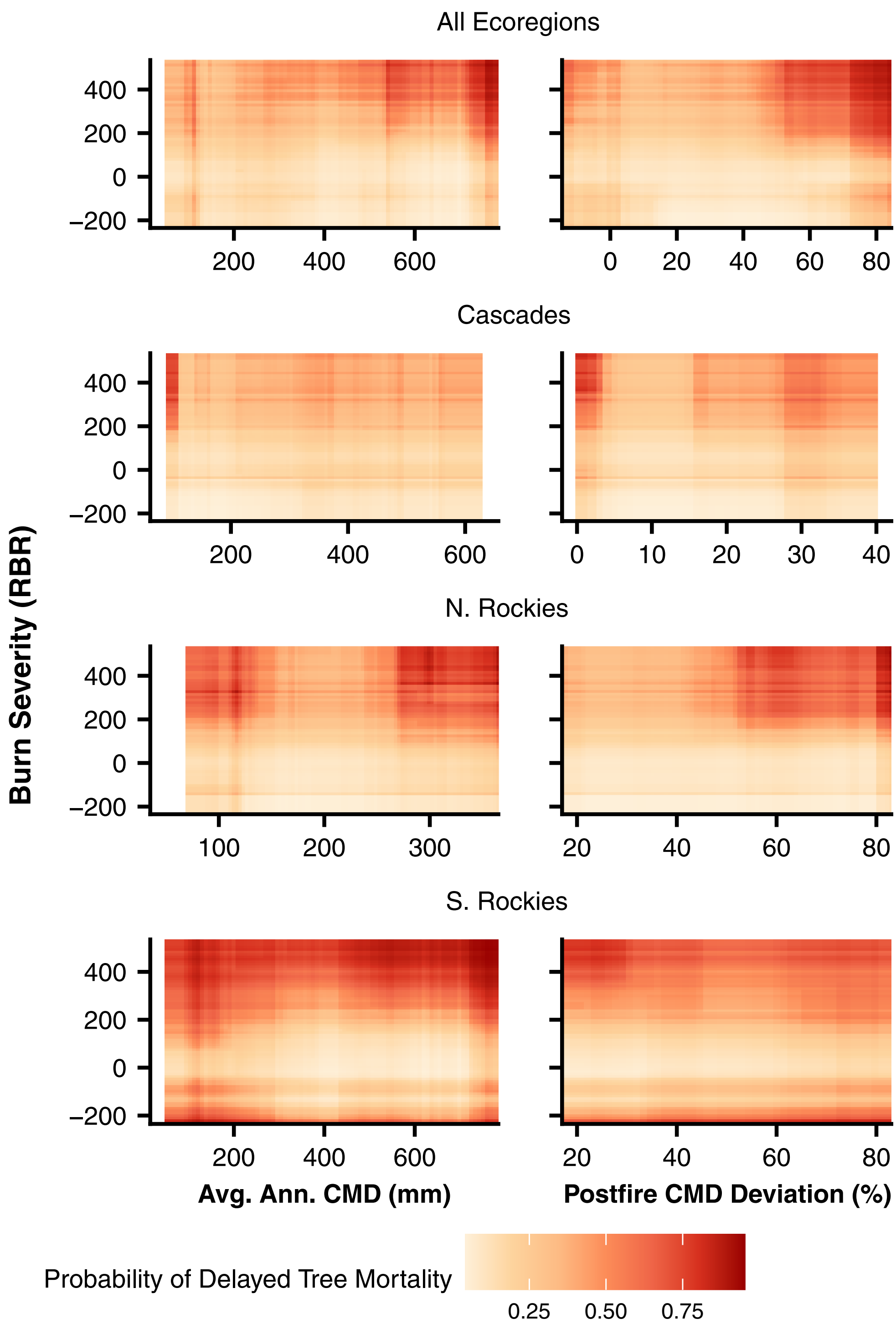

FIGURE 6 Changes in the probability of delayed tree mortality at the ecoregion scale due to interactions between 1-year postfire burn severity (relativized burn ratio [RBR]) and two measures of climate moisture deficit (CMD), 30-year (1981–2010) average annual CMD and percent deviation from average annual CMD during the 1- to 5-year postfire assessment period. Darker red shading indicates increased probability of delayed tree mortality due to variable interactions.

background mortality rates, which appear to vary geographically in the western United States, but are increasing over time due to climate warming (e.g., 0.5%–1.5% per year in the Pacific Northwest and Inland West; van Mantgem et al., 2009).

Delayed mortality, fire size, and postfire tree extent

Multiple factors and their respective variability within each ecoregion may be important when considering the larger and long-term impacts of delayed tree mortality. Spatial variation and heterogeneity in fire perimeter size, proportion of high-severity fire, size of high-severity patches, and prefire extent of tree cover within fire perimeters may cause starkly different impacts on ecosystem functions among and within ecoregions and forest types—even when the mean rates of delayed mortality are similar. Considering the wildfires analyzed in this study, the S. Rockies exhibited substantially greater mean fire perimeter size compared with the Cascades and N. Rockies, primarily due to the comparatively large Las Conchas (~61,000 ha) and High Park (~37,000 ha) fires. Prefire tree density is typically much lower in dry conifer forests of the S. Rockies than upper-montane/subalpine forests in the Cascades and N. Rockies, and we observed that the ratio of live conifer tree cover to other cover types at T1 was also much lower in S. Rockies fire perimeters relative to the Cascades and N. Rockies (~12%, relative to ~35% and ~45%, respectively). Thus, a mean delayed mortality rate of 15% may compound already critically low postfire conifer tree cover within dry conifer forests of the S. Rockies (e.g., Las Conchas fire, ~61,000-ha perimeter with an estimated ~5000 ha of live conifer tree cover remaining at T1), significantly affecting the abiotic template (e.g., microclimate) and the species that rely on, and ecological processes that are connected to, conifer tree density and extent (e.g., habitat, corridors; biomass sequestered, seed dispersal; Andrus et al., 2021; Driscoll et al., 2021; Falk et al., 2022; Nimmo et al., 2019).

In the western United States, critically limited seed source availability is a key driver of fire-induced forest state transitions (Coop et al., 2020; Stevens-Rumann & Morgan, 2019), which may be further compounded by delayed mortality (Busby, 2021; Busby & Holz, 2022; Reilly et al., 2023), particularly within arid environments where climatic opportunities for successful tree establishment are increasingly rare and/or temporally sporadic (Davis et al., 2020, 2023). Substantial increases in large high-severity fires (Abatzoglou & Williams, 2016; Juang et al., 2022; Parks & Abatzoglou, 2020) have already initiated large-scale losses of dry conifer forest cover within the southwestern United States (Coop et al., 2020; Guiterman et al., 2022; Stevens et al., 2021) and losses are anticipated to continue increasing, especially in lower elevation trailing-edge forests under a warming climate (Donato et al., 2016; Kemp et al., 2019; Parks, Dobrowski, et al., 2019). Within arid and trailing-edge forests, delayed mortality of fire refugia (i.e., reduced seed source availability over time) may increase long-term forest loss when early postfire climate conditions do not favor seedling establishment (e.g., Rodman et al., 2023). More work is needed to assess the impact of delayed tree mortality on postfire seed source availability (i.e., density and configuration over space) and associated tree establishment patterns, over time, across a range of forest types (i.e., expression of functional traits) and site conditions (i.e., cool and wet to warm and dry).

Drivers of delayed tree mortality and interactions

Burn severity (observed at T1) was the most important predictor of delayed mortality across ecoregions, exhibited a nonlinear relationship, and had the largest magnitude of effect on delayed mortality probability in dry conifer forests of the S. Rockies. These results suggest that remotely sensed estimates of patch-scale burn severity are a strong proxy for fire effects, and thus the severity of fire injuries sustained by surviving trees within a patch (Key & Benson, 2006). Across several fire perimeters in western Oregon, Brown et al. (2013) and Whittier and Gray (2016) both observed a similar positive relationship between plot-scale burn severity at T1 and the delayed mortality rate of remaining live trees over time. Fire-caused injuries lower the physiological capacity of affected trees to survive baseline environmental stressors (e.g., high temperature and low precipitation) as well as postfire disturbances like insect infestation, pathogens, reburns, and drought (Hood, 2021; Hood et al., 2018).

In contrast to the other ecoregions, rapid recovery of vegetation at T1 (i.e., RBR < 0; Figure 5a) in the S. Rockies was observed and associated with increased probability of delayed mortality across fire perimeters. While we lack sufficient data to parse out and confidently unveil these trends mechanistically, it is plausible that more than one process was at play (e.g., cambium necrosis; carbon starvation due to the depletion of nonstructural carbon or phloem deformation; xylem dysfunction; soil infertility). One possible factor influencing this relationship could be competition for soil moisture between surviving fire-injured trees and recovering vegetation (including resprouting trees). Delayed mortality has been linked to pre- (e.g., van Mantgem et al., 2018, 2020) and postfire (e.g., Becker & Lutz, 2023; Keyser et al., 2010; Skov et al., 2004) competition among trees and competition with understory vegetation has been shown to decrease growth and increase mortality among conifer juveniles of certain species (e.g., Tubbesing et al., 2020). The effects of understory vegetation recovery on delayed tree mortality are poorly established to date, however. Notably, the S. Rockies experiences greater summer (monsoonal) precipitation compared with the Cascades and N. Rockies, meaning the relationship between rapid postfire regreening by angiosperms and delayed tree mortality could be coincidental (i.e., decoupled) and not necessarily causal.

Climatic moisture deficit and soil characteristics also play important roles in influencing environmental conditions that enhance or constrain postfire tree mortality (Agee, 1993; Hood et al., 2018). Moisture deficit has been reported to be a key predictor of postfire tree regeneration across the western United States (Stevens-Rumann & Morgan, 2019) and more recently as a predictor of delayed mortality (e.g., Furniss et al., 2022). We generally observed that factors related to moisture stress increased delayed mortality. Of these factors, long-term average and short-term postfire CMD exhibited the strongest interactions with burn severity, illustrating a compound stress effect. These interactions were weak in the Cascades, which is also the least moisture-limited and continental ecoregion (i.e., lower average drought stress to vegetation).

Elevation and CMD (which is highly and inversely correlated with elevation; Figure 1) exhibited nonlinear u-shaped responses, which may speak to local climate and respective differences in the distribution of conifer tree species, their functional traits in high- and low-elevation environments, and related ecological thresholds. Tree species in low-elevation environments generally exhibit greater fire resistance and drought tolerance (e.g., ponderosa pine and Douglas-fir), yet experience greater average and acute moisture stress, while tree species populations in high-elevation environments generally exhibit lower fire resistance and are more drought sensitive (e.g., true firs; Agee, 1993; Stevens et al., 2020). While moisture stress may be relatively limited in high-elevation environments, local adaption to those conditions may in turn make tree populations more vulnerable to a world with more extreme climate and/or weather events (i.e., droughts, heatwaves; Andrus et al., 2023; Harvey et al., 2021). Alternatively, tree populations at intermediate elevations may be buffered from high moisture stress common at low elevations, while exhibiting better adaption to droughty conditions than tree populations at high elevations (Mutke, 2011). Similarly, but at landscape and regional scales, tree populations that have adapted to environments with more moderate climate conditions (e.g., Cascades), regardless of elevation, where historically extreme weather events have been less common, may be particularly sensitive to relatively minor increases in climate- and weather-related moisture stress (i.e., CMD; Andrus et al., 2023; Bonebrake & Mastrandrea, 2010).

Compared with elevation and CMD, topographic attributes such as slope and the TPI were less important predictors of delayed tree mortality, yet the strength and direction of their relationships may still be informative. Hillslopes greater than 30° were associated with greater delayed mortality, potentially due to increased precipitation runoff observed in early postfire hydrophobic soils, and thus lower soil moisture availability to trees (e.g., Boisramé et al., 2018). TPI calculated at finer (300-m radius) and coarser (750-m radius) scales exhibited opposite relationships, where convex or concave topographic positions were associated with increased delayed mortality, respectively. Finer scale calculations of TPI capture fine-scale landscape features (e.g., relatively steep drainages, ridgelines, and cliffs), whereas coarser scale calculations of TPI capture broad landscape features (e.g., valleys, lower slopes, ridge slopes) by smoothing surfaces (Weiss, 2001). While concave landscape positions (negative TPI) have been associated with an increased probability of fire refugia presence and/or persistence under benign to moderate fire weather conditions (Krawchuk et al., 2016), such positions also support higher tree densities and surface fuel loadings (i.e., greater soil moisture availability and site productivity; Agee, 1993, 1996), and thus may facilitate more severe fire effects and fire injuries on surviving trees when fire weather is more extreme (i.e., high fuel aridity, winds, or both). Fine- and broadscale species distributions may further explain these differences, given topographic position and hillslope aspect can strongly influence species' pre and postfire composition over space (Agee, 1993). Fire- and drought-sensitive species may be biased to both fine-scale convex and broadscale concave topographic positions, given their respectively cool (e.g., high-elevation ridgeline) and/or wet (e.g., drainage basin) site conditions. These species may be especially vulnerable to delayed mortality, given their susceptibility to fire injuries and poor tolerance of exposed postfire site conditions.

Future work

Future studies focused on quantifying, estimating, and exploring landscape- and regional-scale patterns of delayed mortality would benefit from modeling relationships with other conceptually influential factors we did not account for, such as pre and/or postfire compound disturbance effects like prefire drought (e.g., van Mantgem et al., 2013), insect or pathogen outbreak, tree and understory vegetation composition, reburns, and postfire competition dynamics between trees (e.g., van Mantgem et al., 2018, 2020) and other functional vegetation groups. Further, analyzing patterns using continuous time-series data (i.e., utilizing more than two postfire images) may better capture (1) temporal patterns (e.g., dating) of delayed mortality responses, (2) impacts of compound disturbance and vegetation competition dynamics (e.g., Bright et al., 2020; Vanderhoof et al., 2018), and (3) help minimize misclassification errors (e.g., Holsinger et al., 2022; Reis et al., 2020). Comparison of delayed tree mortality patterns across multiple imagery products (including aerial and space-based LIDAR) at different spatial resolutions could provide the means for multiscalar analyses of drivers and patterns (Warner et al., 2009; Wulder et al., 2009), while the utilization of field data as a reference source could improve classification accuracy and confidence in imagery classifications, and allow for the linkage between spectral signature changes and forest structure and composition. Finally, the development of automated postfire delayed mortality classification approaches using publicly available satellite imagery products (e.g., Landsat and Sentinel; Howe et al., 2022; Reilly et al., 2023) may significantly increase the consideration of tree mortality patterns over longer temporal periods among scientists and managers.

While there is a great opportunity to explore large-scale delayed tree mortality patterns globally and across alternative forest types, caution is needed. The relatively slow-growing, obligate seeding conifer forests highlighted in this study are an ideal ecosystem subject, given postfire tree and vegetation recovery is slow enough to minimize its confusion with delayed mortality signals via remote sensing. Ecosystems whose prefire- and postfire-dominant species exhibit alternative functional traits, such as fast-growing and/or resprouting angiosperms, may be less suited to delayed mortality assessments (i.e., without exhaustive fieldwork; Morgan et al., 2014). Thus, intimate knowledge of dominant species' life history traits should first guide the development and feasibility of any remote sensing-based delayed mortality study.

CONCLUSIONS

Fire refugia enhance conifer forest resilience, landscape-scale biodiversity, and provide habitat after large and severe wildfires, yet their persistence over time may be limited. Our results support evidence from prior field studies and indicate that delayed tree mortality between 1 (T1) and 5 (T5) years postfire occurs across a range of conifer forest types in the western United States, at a landscape scale, and at magnitudes that are ecologically important. Among the fires assessed, as much as a quarter of live conifer tree cover observed at T1 succumbed to injuries, competition, drought, or other compound disturbances by T5. Delayed mortality was especially prevalent in areas that burned at higher severity and were compounded by long-term (annual averages) and short-term (immediately postfire) climate moisture deficits. This work highlights the importance of assessing tree mortality responses beyond 1-year postfire where and when possible, especially considering observed and forecasted increases in high-severity fire, drought, and compound disturbances under a warming climate.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Supporting data and code associated with this research (Busby et al., 2024) are made available at: https://doi.org/10.6084/m9.figshare.21498627.v1.

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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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