Landsc Ecol (2025) 40:101
https://doi.org/10.1007/s10980-025-02111-2

RESEARCH ARTICLE

Post-fire delayed tree mortality in mesic coniferous forests reduces fire refugia and seed sources

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Received: 20 February 2025 / Accepted: 21 April 2025 / Published online: 15 May 2025

Abstract
Context Ecological functions provided by fire refugia are critical for supporting conifer forest resiliency under increased fire activity across the western United States. The spatial distribution and persistence of fire refugia over time are uncertain as fire-injured trees continue to die over subsequent years post-fire.
Objectives We examined how post-fire delayed tree mortality affects the spatial distribution and attributes of fire refugia at patch and landscape scales following high-severity wildfires.
Methods To explore changes in fire refugia patch size, isolation, and fragmentation over time, we used high-resolution satellite imagery (3 m pixel size) following high-severity fires in Oregon's western Cascades to map annual changes in the extent of live tree cover up to 3 years post-fire.
Results Delayed mortality decreased live forest cover across all fire perimeters by 8.5% between 1 month and 3 years post-fire. Though prevalent across all forest types, adult to mature and fire-sensitive conifer species were the most vulnerable to delayed mortality. The number of refugia patches decreased by ca. 20%, and most (ca. 77%) were small, non-core patches (< 60 m from the patch edge). In response to delayed mortality, which increased the extent of high-severity burned areas by 9% (ca. 12,000 ha), the area with little to no seed sources based on refugia distance^2-weighted density increased by 375% (7632 ha).
Conclusions Delayed mortality altered the size and spatial configuration of fire refugia across landscapes. Considering species-specific fire adaptations may help improve post-fire management strategies and a framework of conifer forest resiliency under novel fire regimes.

Keywords Forest resilience · Temperate rainforests · Fire refugia · Tree seed sources · Oregon's western Cascade mountains

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10980-025-02111-2.

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Introduction

Contemporary climate conditions and vegetation structures, including increased fuel aridity

(Abatzoglou et al. 2021; Juang et al. 2022) and fuel availability (Calkin et al. 2015), are altering the typical fire regime that forests in the western United States (US) have historically experienced. Although coniferous forests possess life history and functional traits that enhance their capacity to resist and/or successfully recover (i.e., resilience) from wildfires and promote post-fire persistence (Rodman et al. 2021), rapid shifts in the frequency, extent, and severity of fires away from the historical range in variation coupled with warmer and drier conditions may hinder resistance and recovery and prompt fire-induced transitions to altered or non-forested states (Stevens-Rumann et al. 2018; Busby et al. 2020; Coop et al. 2020; Rodman et al. 2020; Seidl and Turner 2022). Surviving individuals or patches of live trees to first-order fire effects (i.e., post-fire), known as fire refugia, provide critical ecological functions, including habitats for surviving flora/fauna and live seed sources that support forest regeneration following fire (Meddens et al. 2018; Meigs and Krawchuk 2018). The presence of refugia following one (ephemeral) or multiple (persistent) fire events (Meddens et al. 2018) can be critically important for forest resilience, depending on the density, size, and spatial arrangement of refugia patches in terms of size, severity, and distance to unburned boundaries within the fire perimeter (Walker et al. 2019; Busby and Holz 2022). However, recent landscape-scale studies of post-fire refugia decline (Reilly et al. 2023; Busby et al. 2024) have documented a decline in the extent of fire refugia area over time, highlighting the need to further study the effects of post-fire delayed tree mortality on the ecological function of fire refugia and its context for forest resilience.

If the first-order fire effects do not immediately kill a tree, there is potential for second-order (i.e., delayed) fire effects to cause tree mortality in subsequent years following the fire event (Hood et al. 2018; Busby et al. 2024). Post-fire delayed tree mortality (referred to here as delayed mortality) is defined as tree mortality occurring after immediate, first-order fire effects and is a process that takes place over time following a fire (Brown et al. 2013; Jeronimo et al. 2020; Reilly et al. 2023; Busby et al. 2024). Fire-induced tree injuries can cause cambium necrosis in roots, stems, and/or leaves, loss of hydraulic conductivity, and/or cavitation, ultimately leading to mortality (Michaletz et al. 2012; Bär et al. 2019). Delayed mortality can occur due to direct burn injuries as well as a combination of direct and indirect ecophysiological and biophysical effects related to climate (e.g., drought; Cansler et al. 2024), insects, pathogens, competition (Hood et al. 2018), and presumably post-fire heatwaves (Cochard 2021). However, immediate burn severity is the most direct factor leading to delayed mortality, as it is an indicator of first-order tree injuries (Brown et al. 2013; Whittier and Gray 2016). Delayed mortality is expected to be more common in low- and mixed-severity regimes where trees have evolved to resist fire than in high-severity burns where most trees are killed immediately and eventually forests recover (Hood et al. 2018). Certain species exhibit fire-resistant adaptations that act as fire defense mechanisms with traits including increased bark thickness to protect the cambium (Bova and Dickinson 2005), self-pruning of lower branches to limit fire movement into the canopy, rapid growth to escape from a future fire, and maximum crown height to limit crown-scorching (Schwilk and Ackerly 2001; Stevens et al. 2020). These traits allow certain tree species to either resist or tolerate the initial fire effects but may still lead to fire-induced injuries and mortality. Under warmer and drier conditions, both first-order fire effects and combined disturbance effects of delayed mortality are expected to proliferate into the future; therefore, incorporating combined direct and indirect effects at the landscape scale is critical.

Patches of fire refugia are critical for maintaining biodiversity by preserving wildlife habitat for both edge and core species (Meddens et al. 2018; Krawchuk et al. 2020) and for providing seeds to neighboring burned areas to repopulate forests following a disturbance (Meddens et al. 2018; Gill et al. 2022). Landscape configurations have been used to characterize the ecological function of forests (e.g., Jules 1998; Didham et al. 2012; Betts et al. 2019) and may also provide fundamental information about how delayed mortality changes the ecological function of fire refugia. Patch-scale metrics such as patch area and core area have been used to assess the viability of fire refugia for wildlife habitats (e.g., Andrus et al. 2021), including core forested areas that provide critical habitats for species reliant on cool and moist conditions within refugia patches (Betts et al. 2019; Phalan et al. 2019) and large patches that preserve diverse forest structures and compositions (Meddens et al. 2018). At the landscape scale, patch isolation, the distance between land cover patches (Cushman et al. 2008), is used to characterize the dispersal distance and availability of seed sources from fire refugia (e.g., Donato et al. 2009; Coop et al. 2019; Busby and Holz 2022; Laughlin et al. 2023) and model habitat connectivity (e.g., Berry et al. 2015). By analyzing how these metrics change over time with the decline of fire refugia, unique insights can be discovered about how delayed mortality changes the ecological function of fire refugia, habitat fragmentation (Valente et al. 2023), and the potential for fire-induced ecosystem conversions (Seidl and Turner 2022). However, few studies have analyzed landscape-scale drivers of post-fire delayed tree mortality (see Reilly et al. 2023; Busby et al. 2024). To the best of our knowledge, no study has quantified changes in refugia spatial patterns across forested landscapes in response to delayed tree mortality.

Landscape- to regional-scale studies via remote sensing offer new insights into landscape-scale patterns and processes of delayed mortality. The use of 30-m (m) resolution Landsat imagery by Reilly et al. (2023) helped acknowledge that the effects of delayed mortality alter burn severity metrics over time and are detectable and useful at this resolution and extent, respectively. The coarse resolution of this imagery comes with limitations, including a loss of information within a minimum mapping unit (i.e., a single pixel) that encompasses a variable spectral signature (Key 2006), which misses the smaller-scale nuances of fire refugia (i.e., overlooking small yet functionally key refugia; <900 m^2). However, forest cover mapping with moderate- to high-resolution imagery, including RapidEye (5-m), PlanetScope (3-m), and the National Agriculture Imagery Program (NAIP; 1-m), can be used to identify smaller-scale individual trees or patches (Rodman et al. 2019; Walker et al. 2019; Busby et al. 2024). Therefore, scaling up to a landscape scale with higher-resolution imagery may reveal novel spatial patterns of delayed mortality that can be linked to the ecological processes of fire refugia.

The 2020 wildfire season in the western US exceeded recent records of annual forest area burned (Higuera and Abatzoglou 2021; Juang et al. 2022), particularly within Oregon's western Cascades via a series of extensive, high-severity fires, known collectively as the 2020 Labor Day Fires (Reilly et al. 2022). While fires of their observed size and severity are characteristic of these temperate forest fire regimes, their relative infrequency makes them seldom studied. Owing to this lack of historical observations (see Laughlin et al. 2023), it is uncertain whether or to what degree large, high-severity wildfires in mesic and productive forests promote ecosystem transitions, especially when combined with post-fire warming and drying conditions and/or short-interval fires (i.e., reburns) that limit conifer regeneration, as reported in drier and colder forests (e.g., Harvey et al. 2016; Whitman et al. 2019; Busby et al. 2020; Stewart et al. 2021; Stevens-Rumann et al. 2022). Therefore, the 2020 Labor Day Fires in Oregon offer a unique opportunity to study the spatiotemporal patterns of delayed mortality in mesic coniferous forests following large, high-severity fires, contributing to a better understanding of the resilience of these forests. Forest progression 3 years post-fire following the 2020 Labor Day Fires was mapped via high-resolution (3-m) satellite imagery and used to quantify patch-scale to landscape-scale patterns of delayed mortality. Considering the predicted increase in large, severe wildfires throughout the western US and their pressing effects on habitat loss, forest regeneration, and forest conversion, further examination of post-fire forest dynamics following high-severity wildfires is warranted to advance our understanding of the spatial patterns of delayed mortality. To address this, the following questions were answered in relation to the 2020 Labor Day Fires in Oregon:

- Q1. How does the extent of delayed mortality vary between each individual fire event and immediate burn severity?
- Q2. How does delayed mortality influence the spatial configuration of fire refugia over time at the patch scale (i.e., patch and core area) and landscape scale (i.e., isolation)?
- Q3. What forest types, species fire traits (i.e., sensitive or tolerant), and forest ages (i.e., young or mature) lead to a higher level of delayed mortality?

Methods

Study area

The western Cascades ecoregion receives on average 800 to 4200 mm of precipitation annually, with temperatures ranging from −3 to 6 ℃ in January and 13 to 22 ℃ in August based on 30-year normals (1991–2020; PRISM Climate Group 2025). Though, the climatic conditions follow latitudinal and altitudinal gradients, where areas at higher elevations and within the northern portion are wetter and cooler than those at low elevations and/or within the southern portion. This region's soil is dominantly well draining, ashy sandy loam andisols (USDA 2025). Forests in the western Cascades are broadly dominated by Douglas-fir (*Pseudotsuga menziesii var. menziesii*), western hemlock (*Tsuga heterophylla*), and western red cedar (*Thuja plicata*) at low to middle elevations, referred to as the Western Cascades Lowlands and Valleys and the Western Cascades Montane Highlands (Fig. 1). At higher elevations in the Cascade Crest Montane Forests, the common coniferous tree species include noble fir (*Abies procera*) and Engelmann spruce (*Picea engelmannii*) at intermediate to high elevations, followed by Pacific silver fir (*Abies amabilis*) and mountain hemlock (*Tsuga mertensiana*) at higher elevations. Species within this forest gradient exhibit variable evolutionary fire adaptations from fire sensitive to fire resistant at low and

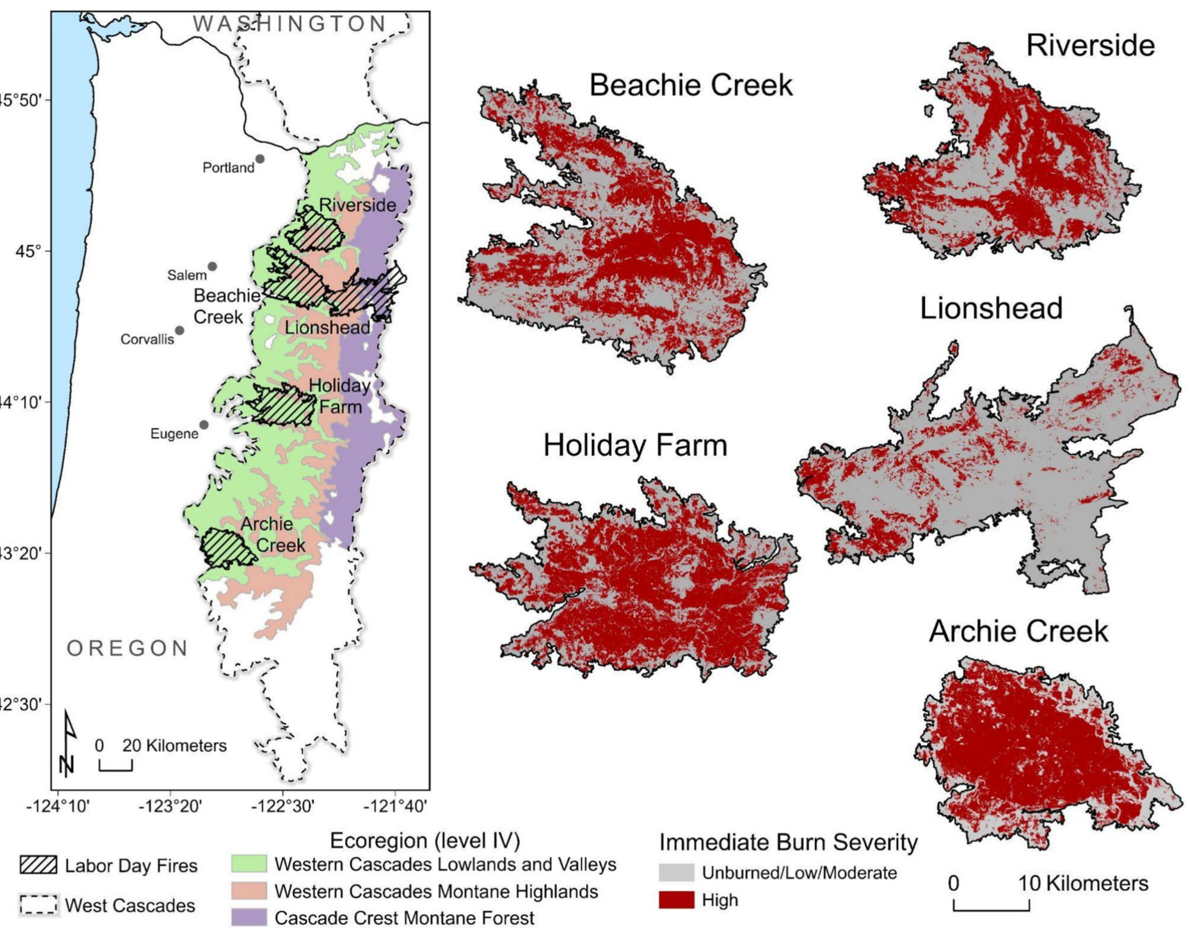

Fig. 1 Study area in the western Cascades ecoregion of Oregon with additional ecoregions (level IV) and the five westside fires from the Monitoring Trends in Burn Severity program (MTBS). Immediate burn severity classes for each fire were created from the relativized difference in normalized burn ratio (RdNBR) and thresholds via postfire Sentinel-II imagery from October 2020. Common vegetation zones within each ecoregion include mixed coniferous and subalpine forests

high elevations (Table 1). The historical wildfire disturbance regime of the western Cascades generally ranges from moderate-frequency, mixed-severity fires to low-frequency, high-severity fires that occur during mid- to late-summer, when conditions are hottest and driest (Reilly et al. 2022). However, what is generally accepted is that the frequency and extent of mixed to high-severity fires are expected to increase across the PNW based on future climate scenarios (e.g., Mote et al. 2014; Abatzoglou et al. 2021; Rupp and Holz 2023).

Approximate coverage across the masked study area is based on the full 90-m sample for the boosted regression tree (BRT) model (see section below). Fire sensitivity of each tree species at different life stages, separated into young (10–60 years) and mature (> 120 years), is reported based on the First Order Fire Effects Model (FOFEM; Lutes 2020).

The five largest Labor Day fires that each burned more than 50,000 hectares (ha) in Oregon's western Cascades during the 2020 wildfire season are Riverside, Beachie Creek, Lionshead, Holiday Farm, and Archie Creek (Fig. 1). The climate within the boundaries of the fires differs from the overall western Cascades ecoregion with 1300 to 3000 mm of precipitation annually and temperatures ranging from 0 to 5 ℃ in January and 15 to 21 ℃ in August based on 30-year normals (1991–2020; PRISM Climate Group 2025). The majority of these fires burned within the western Cascades at mid-to-low elevations, except for the Lionshead Fire, which started burning on the eastern Cascades and then crossed its divide and burned downslope with help from extreme east winds. Given that the hemlock-Douglas-fir forest zone is the most common forest type burned by these fires, *Pseudotsuga menziesii* is used as an example throughout this study.

In late June 2021, the PNW experienced a heatwave event that exceeded century- and millennium-long records of observed and reconstructed temperatures (White et al. 2023). This extreme climate event was found to have landscape-scale crown scorching effects (Still et al. 2023) and melting of mid- to high-elevation snowpack (Kornei 2024), which may lead to growth delays and/or mortality (Breshears et al. 2021) but has yet to be fully elucidated. Primarily, younger trees were shown to be the most affected by this event (Klein et al. 2022), but trees of all ages were affected (Still et al. 2023), possibly including those injured by the 2020 Labor Day Fires. Because of this event, and to separate as much as possible its effect on delayed mortality, October 2020 was chosen as the cutoff date for first-order fire effects, rather than summer 2021, as the burn perimeter and severity of a wildfire are typically quantified the summer after the fire season of interest. Thus, this study assessed delayed mortality in post-fire years one (summer 2021), two (summer 2022), and three (summer 2023).

Post-classification change detection

To create a spatially continuous map of delayed mortality across the fire perimeters, a post-classification change detection methodology was applied with PlanetScope (PS; Planet Team 2023) imagery. PS imagery is collected at a 3-m spatial resolution in

Table 1 Conifer species in the study area from the forest type dataset (LEMMA Team 2020; Bell et al. 2023) with their associated fire adaptivity

Common name	Scientific name	Coverage (%)	Fire sensitivity (young/mature)
Douglas-fir	*Pseudotsuga menziesii var. menziesii*	77.64	Sensitive/resistant
Western hemlock	*Tsuga heterophylla*	9.80	Sensitive/resistant
Pacific silver fir	*Abies amabilis*	2.40	Sensitive/resistant
Western red cedar	*Thuja plicata*	1.87	Sensitive/resistant
Mountain hemlock	*Tsuga mertensiana*	1.82	Sensitive/resistant
Noble fir	*Abies procera*	1.25	Sensitive/resistant
Grand fir/white fir	*Abies grandis/concolor*	0.79	Sensitive/resistant
Lodgepole pine	*Pinus contorta*	0.34	Sensitive/resistant
Engelmann spruce	*Picea engelmannii*	0.08	Sensitive/tolerant
Subalpine fir	*Abies lasiocarpa*	0.01	Sensitive/resistant

red, green, blue, and near-infrared radiometric bands on a near-daily time scale, providing temporally rich, high-resolution imagery that can be used to detect patches of trees across a landscape. The imagery was collected annually from Fall 2020 to Summer 2023 (see Table A1 in Online Resource A) within the fire perimeters as well as within a 1-km (km) buffer around the fire perimeter to account for edge effects. It is acknowledged that performing analysis on off-season imagery presents possible issues with noise from geometric distortion and/or shadows; however, we justified the inclusion of fall imagery to include the effects of the June 2021 heatwave event. For additional information about PS imagery collection and processing, please refer to Online Resource A.

A point sample of 1500 observations was collected for each fire within the fire perimeter (n = 100) and within a 1-km boundary of the perimeter (n = 50) to act as a control and for the training and validation of a forest classification model. A 90-m grid of points was applied to minimize potential spatial autocorrelation between sample points (Congalton 1991), similar to Larson et al. (2013). The point samples were also spatially stratified by ecoregion (level IV; U.S. Environmental Protection Agency 2010) and structural conditions (Landscape Ecology Modeling, Mapping, and Analysis [LEMMA] Team 2020; Bell et al. 2023) to create a dataset that was balanced between conifer species and age. Manual photo-interpretation of forest cover from National Agricultural Imagery Program (NAIP; 1-m spatial resolution) imagery collected in 2022 was performed to create photo-truthed binary forest cover observations at the sampled locations. With the collected sample data, predictors, including the red, green, blue, and near-infrared bands from PS imagery as well as other remote sensing indices relevant to texture, context, and vegetation health (see Table A2 in Online Resource A), were extracted from the sampled points. Given that the NAIP imagery used to validate forest cover was collected in 2022, PS values from the 2022 imagery were extracted from the sample points within the fire perimeters. For the sampled pixels within the 1-km buffer of the fires, PS pixel values from the 2020, 2021, 2022, and 2023 imagery were extracted to each sample point, as these act as pseudo-invariant features (PIFs) that remain relatively stable over time despite seasonal changes in vegetation reflectance. A manual check of each PIF sample was conducted to ensure that no major post-fire changes, such as delayed mortality or salvage logging, occurred.

A supervised binary classification scheme was trained on the sampled points above to create binary forest cover maps from each annual PS image. A boosted regression tree (BRT) from the *gbm* package (Ridgeway et al. 2024) was utilized to classify forest cover annually successfully, with cross-validated overall accuracies ranging from 0.94 to 0.97 (see Table A3 in Online Resource A). Following classification, several filtering methods were applied to exclude shadows, clouds and other atmospheric interference based on the PS UDM2.0 data masks (Planet Team 2023), water features (U.S. Geological Survey 2018), post-fire harvests (Zuspan et al. 2024), locations that were previously burned since 1984 according to the MTBS dataset (Eidenshink et al. 2007), and any areas outside the western Cascades ecoregion. A focal majority filter with a 3×3 moving window was also applied to conform to a minimum mapping unit of 9 m^2. Finally, if a pixel was classified as non-forest it could not be classified as forest the subsequent year(s). Detailed information about the forest classification model and filtering can be found in Online Resource A.

With the annual filtered forest cover maps, change detection was performed to create forest progression rasters. A pixel was classified as experiencing delayed mortality if a forest pixel became a non-forest pixel in subsequent years. Once a pixel becomes non-forest, it cannot change to a forest pixel to eliminate classification errors. The result was a spatially continuous map of delayed mortality across fire perimeters annually from October 2020 through June 2023, where a pixel can be classified as either non-forest, forest, or delayed mortality (Fig. 2).

Landscape metrics analysis

Annual post-fire forest cover rasters were employed in a landscape metrics analysis aimed at identifying spatial configurations of fire refugia that have been altered by delayed mortality. By employing the *landscapemetrics* package (version 2.0.0) within the R environment, annual forest cover maps were utilized to delineate fire refugia patches with an eight-neighbor rule. Landscape metrics of fire refugia were defined at both the patch scale and

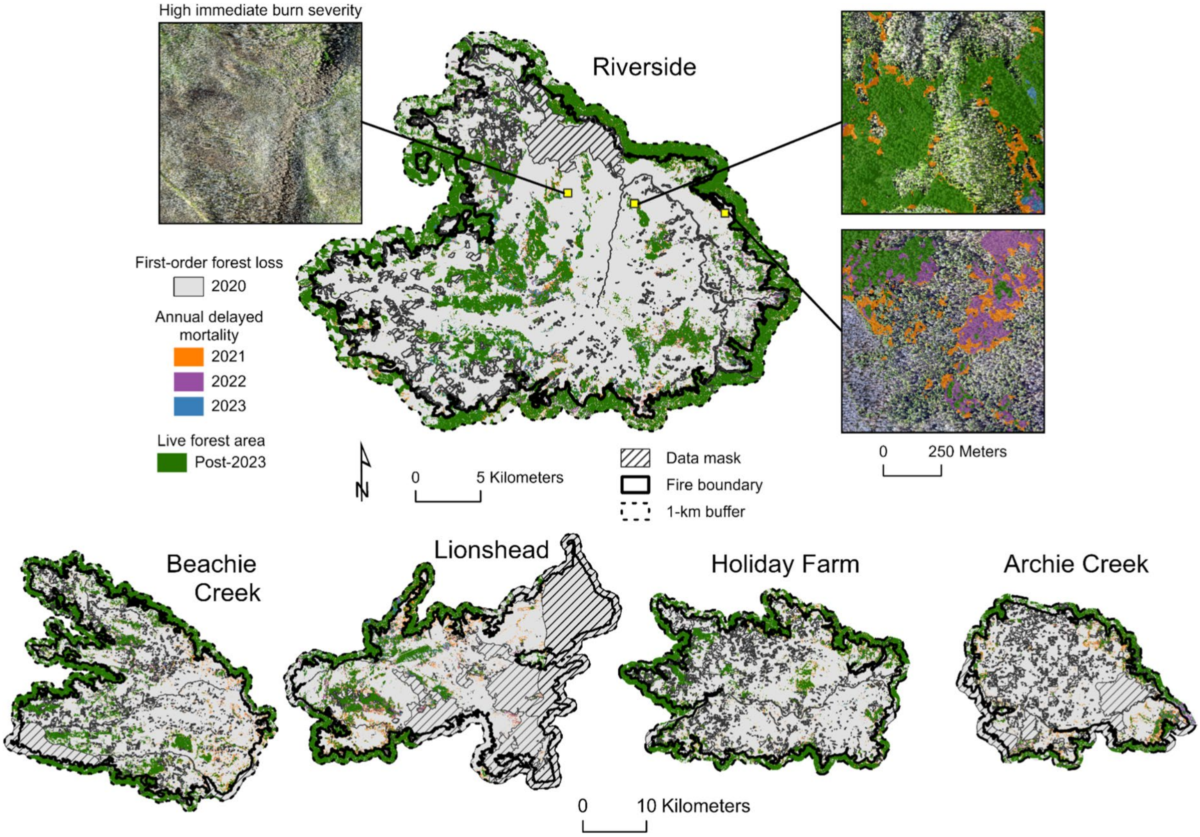

Fig. 2 The extent of first-order forest loss, annual delayed mortality, and live forest area as of June 2023 for the 2020 Labor Day Fires. Maps include boundaries of the fire perimeter, a 1-km buffer, and the data mask. The inset maps display example areas of high burn severity (left) and varying extents of delayed mortality (right), underlying 2022 NAIP imagery for auxiliary detail

landscape scale. Metrics were assessed within a 1-km buffer surrounding the fire perimeters to ensure a comprehensive analysis of post-fire refugia dynamics that may affect species habitat viability and seed dispersal. The following metrics were analyzed individually as well as by immediate burn severity as of October 2020 based on methods by Reilly et al. (2017).

The patch-level metrics included the patch area (ha) and core area (ha). Patch core is defined as a forest extending beyond a 60-m radius from the patch edge, considering the height of the mid-to-tallest trees (i.e., adult to mature *Pseudotsuga menziesii*) in the study area and following the framework established by Harper et al. (2005), who delineated critical habitat areas for species reliant on cool and moist conditions within refugia patches. The landscape-level configuration was characterized via isolation (or proximity) metrics that included the Euclidean distance from a non-forest pixel to the nearest forested pixel (i.e., fire refugia) and refugia distance^2-weighted density (D^2WD; Coop et al. 2019; Busby and Holz 2022). D^2WD was scaled from 0 to 1 to allow for comparison across fire perimeters. Metrics were analyzed in areas burned at high-severity via methods based on Reilly et al. (2017), where a 30-m pixel with greater than 75% forest loss was used. Distance to refugia was categorized into three classes based on thresholds identified by Donato et al. (2009) and Laughlin et al. (2023), which represent the ecological thresholds of seed dispersal for *Pseudotsuga menziesii* including a maximum seed dispersal distance of 400 m. D^2WD was categorized into three classes using Jenks natural breaks since no current thresholds for seed density are known for the species in this forest type.

Life stage and fire trait classification

The magnitude of delayed mortality based on life stage and fire adaptation was assessed to understand what forest types may be more vulnerable to secondary fire effects. Forest locations were categorized into young (10–60 years), adult (60–120 years), and mature (> 120 years) based on Powell (2012) via the basal area weighted stand age layer from the 2019 GNN dataset (LEMMA Team 2020; Bell et al. 2023). Forest locations were also categorized into fire adaptivity classes including sensitive, tolerant, and resistant based on dominant species and tree diameter according to the First Order Fire Effects Model (FOFEM; Lutes 2020; see Online Resource C).

Results

Forest classification and mapping of delayed mortality

The spatial extent and structure of fire refugia exhibited a heterogeneous spatial distribution over time, varying both spatially and temporally within the fire perimeters (Fig. 2). Certain areas experienced significantly higher rates of delayed tree mortality compared to others, and tree mortality generally occurred at the edges of refugia patches. Moreover, the extent of delayed mortality varied annually, with most tree mortality occurring within the first year post-fire from October 2020 to June 2021 and gradually tapering off over subsequent years (Fig. 2). This was true for all fires except for the Riverside Fire, which had nearly even relative proportions of forest loss annually for 3 years post-fire. Furthermore, the Lionshead Fire had the largest proportion of fire refugia lost within its fire perimeter compared to the other four fires (Fig. 3), with 7370 ha (32.1%) of forested area lost after the first-order fire effects occurred within the 3 years post-fire. The proportion of live forest area post-2023 (Fig. 3) was much greater than that in previous analyses (e.g., Evers et al. 2022; Reilly et al. 2022) because of the inclusion of the additional forested area within a 1-km buffer of each fire perimeter.

An analysis of the area of forest loss due to delayed mortality by immediate burn severity as of October 2020 revealed that mortality occurred in low-, moderate-, and high-severity areas across all five fires. Over 50% of the mortality occurred in areas that burned at low-severity, leaving 10% or lower proportional forested area lost in low-severity areas (see Table B5 in Online Resource B). The proportional area loss within each immediate burn severity category by fire varied. Notably, the Lionshead Fire, which burned at a higher elevation than the other four fires, had the highest proportion of forested area lost in the low-severity category and the lowest proportion in the high-severity category.

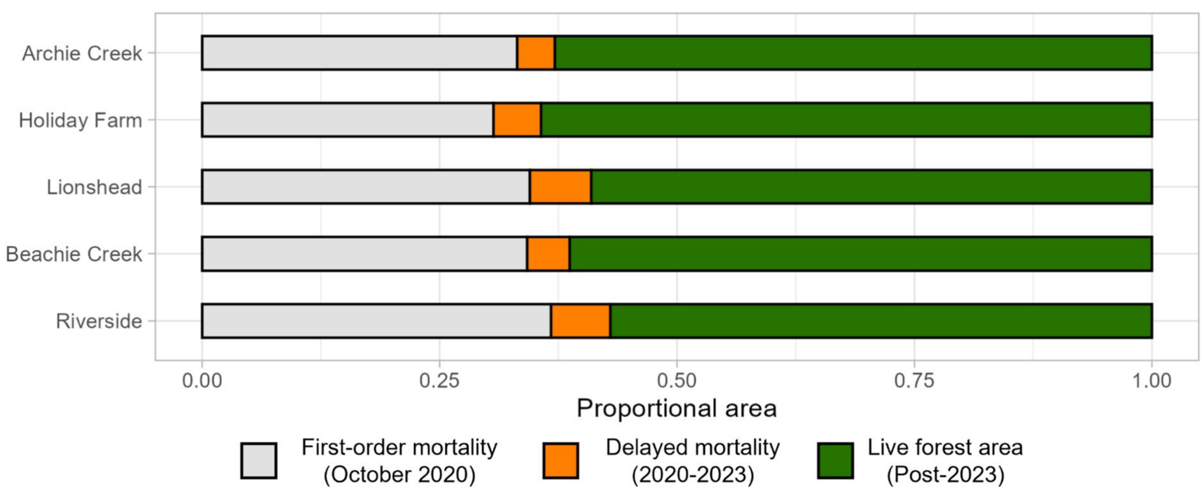

Fig. 3 Proportional areas of first-order mortality, delayed mortality, and live forest annually across all fires. The additional area within a 1-km buffer of each fire perimeter is included

Comparably, fires that burned at lower elevations, including Beachie Creek and Archie Creek, had a greater proportion of forested area lost due to delayed mortality in high-severity areas.

Patch-level and landscape-level metrics

Post-fire in October 2020, there were 185,662 fire refugia patches within all five fire perimeters. Overall, the majority of patches present following the first-order fire effects were very small (<0.01 ha; n=124,226; 66.9%), indicating a highly fragmented and fine-scale, patchy mosaic of fire refugia. The post-fire effects of delayed mortality decreased the extent of these patches over time. In some cases, individual patches fragmented into multiple smaller patches, which was reflected by the increase in the total number of refugia patches across the landscape between June 2021 and June 2022 (Table 2). Among the individual patches of fire refugia that existed post-fire in October 2020, 76.9% (n=142,725) of the patches were fully lost due to delayed mortality by 2023. The total extent of the refugia patches decreased over time, with 24,147 ha (19.2% of the total fire refugia area in October 2020) of first-order fire refugia lost within 3 years post-fire (October 2020–June 2023). The rate of delayed mortality decreased over time, and the greatest loss of fire refugia occurred between October 2020 and June 2021, with lower, but still important, losses occurring in subsequent years (Table 2). This loss equated to an extra 8.5% loss of forested area that existed pre-fire based on the first-order fire effects as of October 2020. Even though most delayed mortality occurred in the low and moderate immediate burn severity areas (see Table B5 in Online Resource B), the percent change in patch area had a disproportionate influence in the high-severity areas where <25% of the forested area remained after the first-order fire effects (see Table B6 in Online Resource B).

Among the existing patches of fire refugia post-fire in October 2020, only 0.004% (n=748) of the patches were large enough to encompass a core area, as defined here (>60 m from the patch edge). All the patches with core were found in areas with low burn severity. Core forest area totaled 36,348 ha after the fires in October 2020, comprising 28.6% of the total refugia within the entire burn perimeter and 1-km boundary. Compared with smaller refugia patches, the core refugia area remained relatively stable over time, losing only 9958 ha (27.4%) of the core area by June 2023. The same number of patches with core areas still existed 3 years post-fire in June 2023, except for only three that were fully lost. Over time, the number of patches with core increased to 811 by 3 years post-fire due to the fragmentation of larger patches. Comparatively, only 22.8% (n=42,192) of the patches without core areas still existed 3 years post-fire.

When delayed mortality within the first 3 years post-fire was considered, the isolation metrics revealed that fire refugia patches became more isolated where delayed mortality occurred along the edge of forest patches. This effect was most pronounced in the Holiday Farm Fire (Figs. 4, 5), although it also occurred in the other four fires. As the Euclidean distance between forested patches increased across all fires between October 2020 and June 2023, the total non-forested area over 400 m away from refugia increased by 129.3% (Fig. 4; Table B7 in Online Resource B). Non-forested areas within 200 m of refugia showed a decrease in area by 3 years post-fire, an indication of patch fragmentation into smaller patches with reduced proximity. The use of the D^2WD metric helped identify locations with little to no seed source availability. The refugia density in these areas

Table 2 Summary statistics of fire refugia patch size and temporal loss due to delayed mortality

Year	# of patches	Forested area (ha)	Delayed mortality (%)	Forest area loss (ha)	Cumulative percentage of forested area lost due to fires based on pre-fire forest cover (%)*
2020	183,662	127,005	–	–	55.6
2021	134,867	115,006	9.5	11,999	59.8
2022	136,189	106,957	7.0	8049	62.6
2023	125,776	102,585	4.1	4372	64.1

*Percentages of forest cover loss are lower than what has previously been reported (e.g., Evers et al. 2022; Reilly et al. 2022) because the forest area within a 1-km buffer of the fire perimeters was included to remove possible edge effects

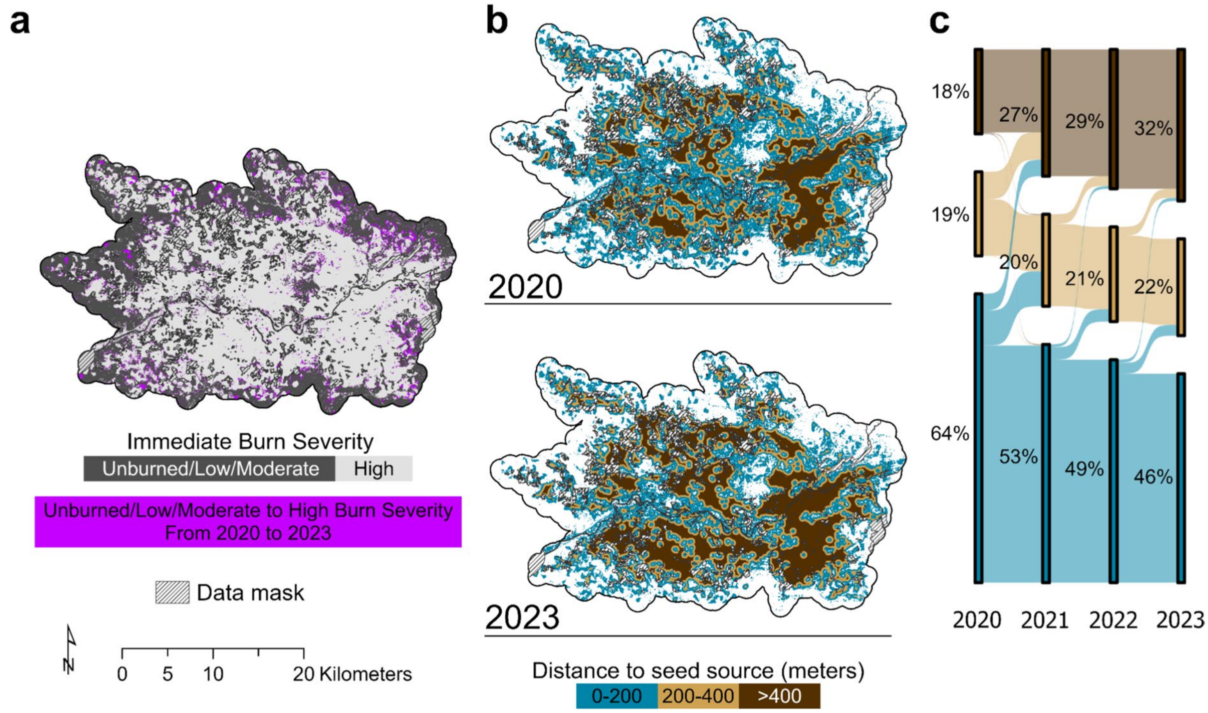

Fig. 4 **a** Areas of the Holiday Farm Fire changing from unburned/low/moderate immediate burn severity (0–75% mortality) post-fire in October 2020 to high burn severity (> 75% mortality) in June 2023. Remote sensing-based burn severity was based on thresholds by Reilly et al. (2017). **b** The Euclidean distance to fire refugia immediately post-fire in October 2020 and 3 years post-fire in June 2023. Distance to seed source was classified based on thresholds identified by Donato et al. (2009) and Laughlin et al. (2023). **c** Sankey diagram showing the proportionate non-forested area extent for each distance class across all fires annually from October 2020 to June 2023

was less than 0.08, which was extensive across all fire perimeters due to the high immediate burn severity of the fires (Fig. 5; Table B8 in Online Resource B). Area with zero seed sources where the D^2WD metric was equal to zero increased by 375% from 2036 to 9668 ha between October 2020 and June 2023. These results indicate that as the isolation of refugia patches increases, the total area with little to no seed supply is expected to increase based on the seed dispersal capability of the conifers.

Variation in delayed mortality by life stage and fire trait

Considering forest structure and individual species' fire adaptations, a lower percentage of fire-resistant and fire-tolerant species experienced delayed mortality than their fire-sensitive counterparts when they were not killed immediately by first-order fire effects (Fig. 6). The coniferous populations most vulnerable to delayed mortality were adult to mature and fire-sensitive (Fig. 6). We attributed the survival of first-order fire effects to their life stage and exposure to moderate-to-low burn severity. Delayed mortality was attributed to their fire-sensitive traits (i.e., thin bark and low branches), which promote heat-induced injuries into the stem, root tissues, and upper canopy (Hood et al. 2018).

Discussion

This study presents a novel quantification of spatiotemporal patterns of delayed mortality following high-severity fires to gain a better understanding of how essential ecological functions of fire refugia can change over time. Our analysis revealed a trend of increasing isolation among fire refugia patches over time, potentially hindering seed dispersal and hampering and/or delaying tree species

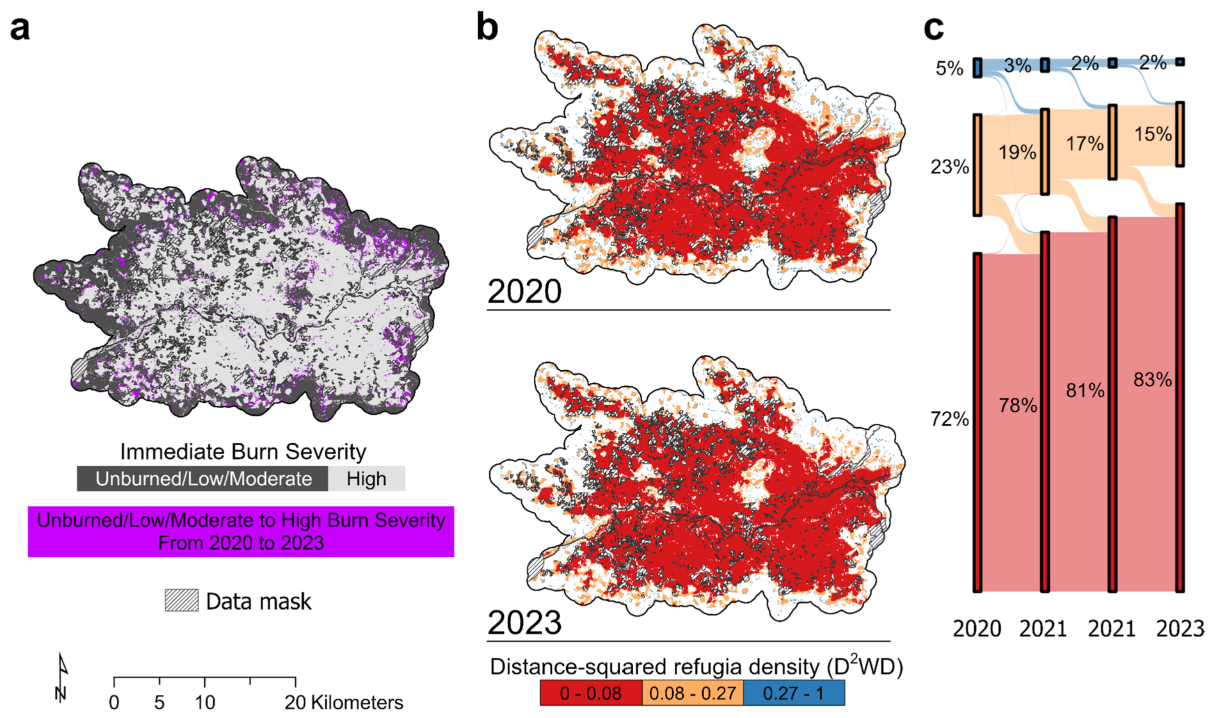

Fig. 5 **a** Areas of the Holiday Farm Fire changing from unburned/low/moderate immediate burn severity (0–75% mortality) post-fire in October 2020 to high burn severity (> 75% mortality) in June 2023. Remote sensing-based burn severity was based on thresholds by Reilly et al. (2017). **b** D^2WD of fire refugia immediately post-fire in October 2020 and 3 years post-fire in June 2023. D^2WD was classified using Jenks natural breaks. **c** Sankey diagram showing the proportionate area covered by each D^2WD class across all fires annually from October 2020 to June 2023

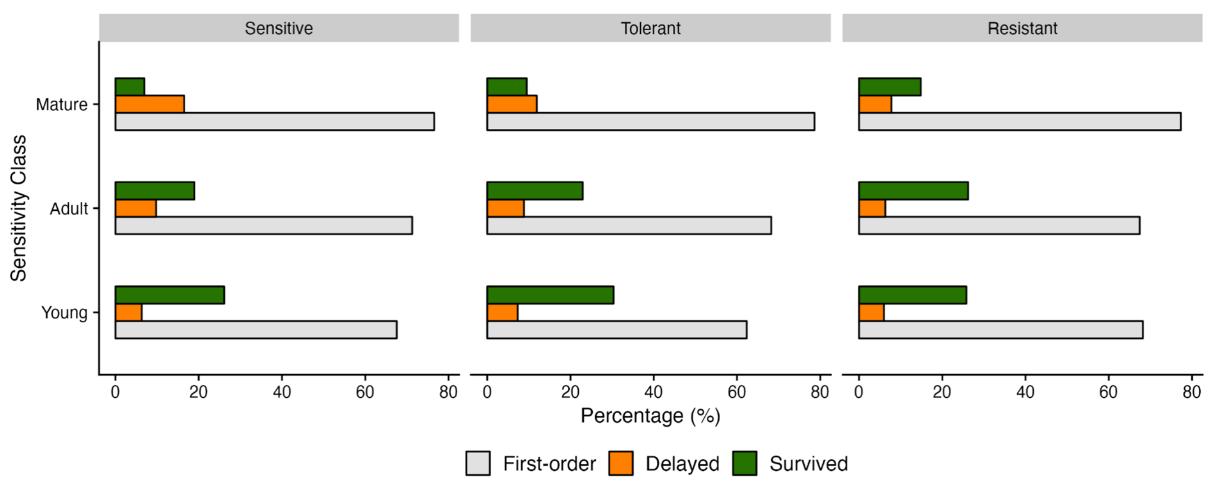

Fig. 6 Comparison of first-order mortality, delayed mortality, and survival (as of June 2023) for sensitive, tolerant, and resistant fire traits and their life stage within sections of the study area (Table 1) with an immediate RdNBR value greater than zero to isolate trees that were directly affected by the fire

recruitment in areas burned at high-severity. However, fire refugia patches large enough to encompass core areas were resilient to second-order fire effects, providing critical habitats for species dependent on shaded and cool conditions for nesting and foraging. Further analysis of the structure and composition of the forests revealed important considerations for the physiological traits and fitness of stress-sensitive tree species populations within fire refugia.

Spatiotemporal patterns of delayed mortality

The landscape metrics analysis of post-fire annual forest cover provided insight into the spatiotemporal patterns of delayed mortality, and by focusing on the first three post-fire years, we were able to largely remove the detection of regrowth, which was noted to have occurred in a similar analysis (using 5 years post-fire; Busby et al. 2024), and focus solely on the patch dynamics of fire refugia and delayed mortality. Annual reductions in refugia patch area revealed that the extent and rate of forest area loss within 3 years post-fire at the fire perimeter scale were similar to those reported in previous studies of coniferous forests in the western US (Brown et al. 2013; Whittier and Gray 2016; Jeronimo et al. 2020; Reilly et al. 2023; Busby et al. 2024). Overall, the five 2020 Labor Day Fires lost approximately 19% of the first-order fire refugia within 3 years post-fire, which is within the same range compared to previous studies on delayed mortality in western Cascade fires (Reilly et al. 2023; Busby et al. 2024).

Patches with core areas were more resilient to delayed mortality than patches that were not large enough to encompass core habitat. These core forest areas are critical for supporting habitats for tree species adapted to shaded and cool conditions (Andrus et al. 2021), including suitable nesting sites for bird species such as the northern spotted owl (Davis et al. 2016) and the Pacific marten (USFSW 2015; Reilly et al. 2021), both of which are on the threatened species list. The core areas that were found to be resilient to first- and second-order fire effects may be potential areas with persistent fire refugia that survive through multiple fires, whereas non-core patches may instead be ephemeral fire refugia that survive only a single fire (Meddens et al. 2018). Furthermore, a lack of core forest area following high-severity fires may be problematic for species of flora and fauna that are core-dependent.

Delayed mortality was most prevalent in low- and moderate-burn severity areas with less than 75% first-order mortality (Hood et al. 2018), supporting findings by Reilly et al. (2023) that a large portion of delayed mortality occurring in low-burn severity areas extends the size of high-severity burned areas. However, in areas with high immediate burn severity from the first-order effects of fires, 77% of the combined remaining refugia was lost. This relatively small change in relation to the total area of mortality had drastic effects on the isolation of the patches and therefore their ecological function of seed dispersal, showing that there was a disproportionate influence on fire refugia in the areas burned immediately at high severity. The increased isolation of fire refugia patches over time is an important factor for the reduced dispersal of seeds to high-burn severity areas, which are essential for repopulating forests after fires. Limited seed source availability following wildfires is a key driver of fire-induced forest conversion (Stevens-Rumann and Morgan 2019; Coop et al. 2020; Stevens-Rumann et al. 2022), and a reduction in seed supply to high burn severity areas may increase the likelihood of such forest conversions, especially under drier and warmer conditions that are unsuitable for seedling establishment (Davis et al. 2019; Stevens-Rumann and Morgan 2019; Coop et al. 2020; Stevens-Rumann et al. 2022). The isolation metrics utilized in this study begin to characterize the magnitude of how impactful delayed mortality is on seed dispersal, with an 11% increase in area with zero seed dispersal probabilities within 3 years post-fire based on refugia density (D^2WD) across all fires (Fig. 5c). The changes to reduced seed availability from delayed mortality are likely more severe for true fir and other species since a generous maximum threshold for seed dispersal distance of 400 m was utilized in this study based on *Pseudotsuga menziesii* (Donato et al. 2009; Laughlin et al. 2023).

Our isolation metrics fail to account for the release of a seed bank prior to delayed mortality (i.e., stress crop) found for obligate seeding conifers through delayed or stressed-induced reproduction (Pausas and Keeley 2014), which has been found to be especially prevalent for *Pseudotsuga menziesii* (Larson and Franklin 2005). In mesic and cool subalpine forests within the western Cascades, Busby and Holz (2022) reported that the extent of fire refugia 1 year post-fire was a better predictor of tree establishment than were all other parameters assessed. These findings indicate that under suitable climate conditions, post-fire seed development prior to delayed mortality controls the provision of seeds for seedling establishment. However, if post-fire climate conditions are not suitable for cone production, seedling germination, or juvenile establishment (e.g., Stevens-Rumann et al. 2018; Davis et al. 2019), delayed mortality may hinder forest regeneration. Therefore, an additional disturbance following a high-severity fire, such as drought, heatwaves, or reburns, may have the greatest effect on forest resiliency in forests that have a high dominance of obligate seeding conifers (Busby et al. 2020; Stevens-Rumann et al. 2022). While the release of seeds during stress has been acknowledged (e.g., Russell 2017; Pokorny 2019), additional research investigating the timing and abundance of seeds released prior to delayed mortality under varying post-fire climate conditions is necessary to fully characterize the availability of seeds across a post-fire landscape, with a special focus on fire-injured trees within fire refugia.

The 2020 Labor Day Fires were unique due to a post-fire heatwave in June 2021, which contributed to the combined disturbance effect. This study expanded the typical 12-month window for assessing fire effects to include secondary disturbance from the heatwave, although no clear evidence of an exceptionally strong effect was detected within the analysis period. Delayed mortality percentages aligned with previous findings (e.g., Busby et al. 2024), suggesting that the heatwave's role, while notable, did not result in unusually high delayed mortality levels. If extreme heatwave events become more common under climate change (Heeter et al. 2023), future studies should apply appropriate controls to discern between tree mortality caused by either heatwaves or second-order fire effects.

Delayed mortality increases the distance between refugia and results in a more fragmented landscape (Reilly et al. 2023), contributing to the long-standing debate on fragmentation and biodiversity (Valente et al. 2023). In this work, the authors highlight the effect of the scale of the study (i.e., landscape vs. patch) on whether "fragmentation per se" either increases or decreases biodiversity. What remains to be examined is how further fragmentation of fire refugia due to delayed mortality influences biodiversity across these burned landscapes over time. This study revealed that delayed mortality can result in both habitat loss and habitat loss combined with fragmentation. Fragmentation likely has species-dependent effects. For example, patch fragmentation due to delayed mortality was found to reduce isolation (i.e., increase proximity) for distances up to 250 m (Fig. 4), improving the likelihood of colonization events within this distance threshold, especially in areas burned at low-severity. Species adapted to edges that move short distances between patches, such as select bird species (e.g., Kotliar et al. 2002), may therefore benefit from this type of fragmentation. However, all species' habitats may be endangered or lost as positive feedback loops between fire, fragmentation, and flammability may lead to ecosystem transitions (Driscoll et al. 2021).

Delayed mortality varies by species life stage and fire traits

In addition to first-order fire effects, delayed mortality has disproportionate effects depending on the forest structure and individual species' fire adaptations. Among both fire-sensitive and fire-tolerant species, adult (60–120 years) and mature (> 120 years) trees were more vulnerable to delayed mortality than surviving young (10–60 years) individuals (Fig. 6). This finding supports the difference in high-burn severity within first-order effects reported by Evers et al. (2022) and Reilly et al. (2022) for the same 2020 Labor Day Fires. While the former study used the October 2020 date to map the 2020 Labor Day Fires and found disproportionate high-severity burns of young stands, the latter study used the traditional post-fire season summer (summer 2021) date to map the high severity of fires and reported no differences among young, adult, and mature stands. This study using October 2020 as a date for assessing first-order effects suggests that young timber stands are more likely to be killed by first-order fire effects and, therefore, do not survive long enough to experience delayed mortality. As a result, a greater probability of delayed mortality was associated with refugia patches of adult to mature trees, especially for fire-sensitive species. While certain conifer species in the western Cascades may have fire-tolerant and fire-resistant traits, previous results suggest that under extreme fire conditions, even individual species with fire-resistant traits are not sufficient to defend against first-order fire-induced mortality (Evers et al. 2022; Reilly et al. 2023). In contrast, under low- and mixed-severity burn conditions, traits related to self-pruning, bark thickness, and maximum tree height to prevent crown scorching were found to be significant resistance mechanisms against delayed mortality for thin-barked, obligate seeding conifers (Cansler et al. 2020).

Conclusions

A revised perspective that treats fire refugia as a dynamic system that is continuously changing will provide influential information to aid in pre- and post-fire forest management planning, identify current knowledge gaps, and further understand the role of fire refugia in forest resiliency. With our results indicating a reduction in seed supply to high-severity burned areas, developing more accurate assessments and tools of the quantity and quality characteristics of fire refugia over space and time will be critical to support post-fire seed planting strategies. However, the release of a seed bank prior to delayed mortality (i.e., stress crop) may play an important mediating role in patch isolation. Furthermore, fire refugia patches with core areas are resistant to secondary fire effects and provide critical habitats for core species, and post-fire salvage logging should prioritize abundant refugia patches without core areas while avoiding cutting rare but important refugia patches with core areas. By integrating these ideas with management applications, we can work toward fostering resilient forest ecosystems capable of withstanding the growing threats of increasing wildfire activity.

Acknowledgements We thank the Global Environmental Change Lab and the Department of Geography at Portland State University for their support of this work.

Author contributions All the authors contributed to the conceptualization and methodology. Formal analysis and investigation: ASD, SB. Writing—original draft and final manuscript: ASD. Writing—review and editing: SB, CE, MR, AZ, AH. Funding acquisition: AH. Supervision: AH, CE. All the authors have read and approved the final manuscript..

Funding Alec S. Dyer and Andrés Holz were partially funded by NSF award #1832483.

Data availability Due to the copyrights of imagery sourced from Planet Labs and the large file size, PlanetScope imagery data utilized in this publication are not available. The imagery from the National Agriculture Imagery Program utilized in this publication is not available because of the large file size of the data. Select geospatial data representing boundaries and pseudo-invariant point locations as well as source code utilized for data processing and analysis in this publication have been made available in a GitHub repository available at https://github.com/dyeralec/PostFireDelayedTreeMortality.

Code availability The source code utilized for data processing and analysis in this publication has been made available in a GitHub repository.

Declarations

Competing interests The authors have no relevant financial or nonfinancial interests to disclose.

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