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Fire severity influences large wood and stream ecosystem responses in western Oregon watersheds

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Abstract

Background Wildfire is a landscape disturbance important for stream ecosystems and the recruitment of large wood (LW; LW describes wood in streams) into streams, with post-fire management also playing a role. We used a stratified random sample of 4th-order watersheds that represent a range of pre-fire stand age and fire severity from unburned to entirely burned watersheds to 1) determine whether watershed stand age (pre-fire) or fire severity affected riparian overstory survival, riparian coarse wood (CW; CW describes wood in riparian areas), LW, or in-stream physical, chemical, and biological responses; and 2) identify relationships of LW with riparian vegetation and in-stream physical, chemical, and biological factors.

Results At higher fire severities, LW and CW diameter was smaller, but volume did not change in the first year post-fire. Larger size of CW in riparian areas versus LW in streams suggests potential future recruitment of larger-diameter wood into streams from riparian zones in severely burned watersheds. Fire severity exerted strong control on stream responses across watersheds, explaining more of the variation than stand age. At higher fire severities, riparian tree mortality, salvage logging, light, and dissolved organic matter (DOM) concentrations were higher, whereas canopy cover, LW diameter, macroinvertebrate diversity, and fish density were lower. In watersheds with older stand ages, elevation and mean annual precipitation were greater but mean annual temperature, specific ultra-violet absorption at 254 nm, and phosphorus concentrations were lower. Overstory mortality in burned riparian areas was lower for red alder (12%) than western redcedar (69%).

Conclusions Our results link forested streams, fire, and LW by identifying key relationships that change with fire severity and/or watershed stand age. Severe fires burn more overstory riparian vegetation, leading to increased light, DOM concentrations, and macroinvertebrate densities, along with reduced canopy cover, LW diameter, macroinvertebrate diversity, and fish densities. We highlight an important function of red alder in riparian zones—as a fire-resistant species, it may help facilitate a more rapid recovery for streams in fire-prone landscapes. Continued comprehensive aquatic and riparian ecosystem monitoring of these watersheds will aid in understanding long-term effects of post-fire management activities (salvage logging) on aquatic ecosystems.

Keywords Dissolved organic matter, Fish and amphibians, Large wood, Macroinvertebrate, Nutrients, Periphyton, Riparian coarse wood, Riparian mortality, Stream ecosystem response, Temperature

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Resumen

Antecedentes Los incendios son disturbios del paisaje importantes para los ecosistemas de arroyos y el reclutamiento de material leñoso (LW por sus siglas en inglés; LW describe el material leñoso en los arroyos) dentro de los arroyos, en los cuales también el manejo post-fuego juega un rol importante. Nosotros utilizamos una muestra al azar estratificada de ríos de 4to orden, que representa un rango de edades del bosque y severidades antes de incendios desde cuencas sin quemar hasta cuencas completamente quemadas, para 1) determinar si la edad del rodal en la cuenca (pre-fuego) o la severidad del fuego afectó la supervivencia del estrato superior ribereño, la madera gruesa ribereña (CW; CW), el LW, o las respuestas físicas, químicas o biológicas dentro del arroyo; y 2) identificar las relaciones del LW con la vegetación riparia y los factores físicos, químicos y biológicos dentro del arroyo.

Resultados A altas severidades de fuego, los diámetros de LW y CW fueron menores, pero el volumen no cambió primer año luego del fuego. Tamaños mayores de CW comparados con LW en áreas ribereñas sugieren un futuro potencial de reclutamiento de maderas de mayor diámetro en arroyos desde zonas ribereñas en cuencas severamente quemadas. La severidad del fuego ejerce un fuerte control en las respuestas de los arroyos a través de las cuencas, explicando más la variación que la edad del rodal. A severidades del fuego más altas, la mortalidad de los árboles ribereños, las cortas de recuperación, la luz, y las concentraciones de la materia orgánica disuelta (DOM) fueron más altas, donde la cobertura del dosel, el diámetro del LW, la diversidad de los macroinvertebrados, y la densidad de los peces fue más baja. En cuencas con rodales de mayores edades, la elevación y la precipitación media anual fueron mayores, pero la temperatura media anual, la absorción ultravioleta específica a 254 nm y las concentraciones de fósforo fueron menores. La mortalidad del estrato superior en áreas ribereñas quemadas fue más baja para el aliso rojo (12%) que para el cedro rojo del oeste (69%).

Conclusiones Nuestros resultados hacen la conexión entre arroyos forestados, fuego y LW por medio de la identificación de relaciones clave que cambian con la severidad del fuego y/o la edad del rodal en la cuenca. Los fuegos severos queman más el estrato superior de la vegetación ribereña, conduciendo a un incremento de la luz, concentraciones de DOM, y densidades de macroinvertebrados, junto con una reducción de la cobertura del dosel, el diámetro de LW, la diversidad de los macroinvertebrados, y la densidad de peces. Destacamos una función importante del aliso rojo en zonas ribereñas –como una especie resistente al fuego, que puede ayudar a facilitar una recuperación más rápida para los arroyos en paisajes propensos al fuego. El monitoreo contínuo y comprensivo de los ecosistemas acuáticos y ribereños de éstas cuencas ayudará a entender los efectos de largo plazo de las actividades de manejo post-fuego (talas rasas) en ecosistemas acuáticos.

Introduction

In-stream large wood (LW) influences the dynamics and functions of streams by providing refugia for fish and amphibians, affecting channel geomorphology and flow regimes, and enhancing storage of sediment and organic matter (Bilby and Bisson 1998; Olson et al. 2022; Short et al. 2015; Wohl 2020). LW consists of downed, dead pieces of wood found in streams, which can affect channel morphology by increasing channel width, channel meandering, bank stability, pools, and waterfalls (Bilby and Bisson 1998; Wohl 2020). Increases in LW and associated aggradation (Short et al. 2015; Wohl et al. 2022), are well known to affect macroinvertebrate, amphibian, and fish populations (House and Boehne 1986; Fausch and Northcote 1992; Welsh Jr and Hodgson 2008); the same populations can also be negatively affected by fine sediment (Ashton et al. 2006; Jones et al. 2012; Kemp et al. 2011; Welsh and Hodgson 2008).

Recruitment of LW to streams is influenced by wildfire, a landscape-scale disturbance process (Grette 1985; Lienkaemper and Swanson 1986; Murphy and Koski 1989; Bilby and Bisson 1998), and forest successional stage (Martens et al. 2020). As with fire, forest harvest can increase LW volume or biomass in adjacent streams relative to streams flowing through old-growth forests, although declines likely occur over longer timescales owing to an increased rate of decay, transport, and reduced recruitment (Chen et al. 2005; Martens et al. 2020). However, as with fire, LW volume response to harvest is context dependent and can be lower in streams in logged than in old-growth boreal forested watersheds (Liljaniemi et al. 2002; Turunen et al. 2017). Fire severity and pre-fire forest stand conditions are important determinants of in-stream LW and riparian coarse wood (CW) response within the first few years after a fire (Short et al. 2015; Spies et al. 1988), whereas post-harvest salvage logging can also affect LW recruitment (Reeves et al. 2006). Fire and forest harvest can also affect water quality, stream temperature, periphyton, macroinvertebrates, and amphibian and fish populations (Gresswell

1999; Minshall et al. 1997; Richardson and Béraud 2014; Shah et al. 2022).

Unlike other short-lived responses to fire (i.e., discharge or stream temperature), LW recruitment can be affected for decades after a fire because of its influence on the vegetation continuum in stream corridors (Gresswell 1999; Reeves et al. 1995; Scheidt 2006; Spies et al. 1988; Wohl 2020). This vegetation continuum refers to wood from live to dead standing trees to downed CW, and eventually LW in streams (Wohl 2020). Hereafter, to distinguish location of wood, we define coarse wood (CW) as wood in riparian areas, and large wood (LW) as wood in streams. Thus, fire-induced overstory mortality of riparian areas and salvage logging will determine potential future LW recruitment in streams. Wildfire has the potential to increase or decrease LW in streams. Increased LW delivery occurs from fire-induced tree mortality and from increases in bank instability, streamflow, and landslide or debris flow risk (Bêche et al. 2005; Bragg 2000; Pettit and Naiman 2007). Decreased LW delivery may occur when LW is reduced or completely combusted during a high-severity fire or exported during post-fire flood events (Rieman et al. 2012; Young 1994).

Fire-induced riparian tree mortality also enhances solar radiation reaching the stream, resulting in elevated thermal conditions that can be stressful for native coldwater salmonids (Gresswell 1999; Rieman et al. 2012). When fish experience high-temperature stress, they must consume more food to meet their metabolic demands. Greater light availability after wildfire can also increase primary production (periphyton), which can enhance basal resources for macroinvertebrates and apex predators (fish and amphibians) via autochthonous trophic pathways (Minshall et al. 1989; Gresswell 1999; Spencer et al. 2003). Increases in basal resources that translate to increased consumption may offset the adverse effects of thermal stress for apex predators after fire. However, increased flow (magnitude, velocity) after wildfire can also decrease streambed stability and increase scour of benthic biofilms, reducing periphyton biomass. These changes associated with post-fire flows may also affect macroinvertebrate recolonization after wildfire (Verkaik et al. 2015). Whereas autotrophic pathways are often expected to alter macroinvertebrate communities after wildfire, macroinvertebrate responses have yielded mixed results from relatively undisturbed systems (Minshall et al. 1997, 2001; Minshall 2003). In previously disturbed watersheds macroinvertebrate density was greater and diversity was lower in burned than unburned forested headwater streams (Mellon et al. 2008), suggesting that macroinvertebrate responses to fire may differ in relatively undisturbed versus managed forest ecosystems.

On 7 September 2020, strong winds in western Oregon spread many small fires, and led to ignition and expansion of multiple simultaneous megafires (fires > 404 km^2), leading to a widespread landscape, across multiple ownerships, that was affected by fire (Abatzoglou et al. 2021). The Oregon Labor Day fires burned more than 1242 km^2 of private institutional forest land, including low- and mid-elevation forests, offering an opportunity to evaluate aquatic responses to fire across ownerships that vary in elevation, forest stand age, and forest-management strategies. Megafires in temperate moist forests of the western Cascades have been rare in recent decades, but are not unprecedented (Reilly et al. 2017, 2022). For example, comparisons with regional fire history obtained from paleo-ecological records suggest these 2020 wildfires were similar to the largest historical wildfires (Reilly et al. 2017, 2022). With severe fires burning 11% of the Oregon Cascades ecoregion in 2020 (Abatzoglou et al. 2021), combined with existing regional LW deficiencies (Martens et al. 2020), future recruitment of LW may be severely limited. Understanding the response of LW, CW, and corresponding aquatic ecosystem responses to the range of fire conditions experienced is important to understanding the role of fire in aquatic-riparian ecosystems.

To investigate these questions, we quantified LW, riparian standing and downed wood, and in-stream physical, chemical, and biological responses to wildfire ranging from unburned to entirely burned watersheds and to pre-fire mean watershed stand age conditions ranging from 45 to 194 years old. Our objectives were to 1) determine whether watershed means of pre-fire stand age or fire severity affected riparian overstory survival, CW, and LW, or in-stream physical, chemical, and biological responses; and 2) identify relationships of LW with riparian vegetation and in-stream physical, chemical, and biological factors known to co-vary with LW and canopy cover. We hypothesized LW volume and fine-sediment storage would be greater in more severely burned than less burned watersheds regardless of pre-fire stand age. We expected fire-induced overstory mortality to increase with fire severity and elicit increases in stream temperature and light, with negative consequences for biota.

Methods

Study design

The majority of annual precipitation in western Oregon typically falls between October and June, and summer months are typically dry. Precipitation affects flow conditions and therefore can influence transport of large wood or sediment between the time of the fire and our summer sample period. In the first winter/spring following the fires, rainfall was below average as observed at Cougar Dam (USC00351914, located near Holiday Farm fire, https://www.ncdc.noaa.gov/cdo-web/). This rain monitoring location received 1789.8 mm in water year 2021 (WY2021, 1 October 2020 to 30 September 2021), relative to 1873 mm mean annual precipitation (MAP) (WY2007–WY2022).

During summer 2021, 8–11 months after the Oregon Labor Day fires, we inventoried aquatic ecosystem responses across 24 streams that encompass a range of pre-fire stand age and fire severity (Table 1; Fig. 1). We used a stratified random sampling design of pre-fire stand age and fire severity to select 24 watersheds of Strahler stream order of 4^{th} order (Strahler 1957) within 6 km of three fire boundaries (Riverside, Beachie Creek, Holiday Farm). We selected these three fire boundaries because they included both public and private land. Beachie Creek fire burned 783.3 km^2 comprising 41% private, 47% federal, and 12% state land, Holiday Farm burned 701.7 km^2 comprising 70% private and 30% federal land, and Riverside burned 558.7 km^2 comprising 30% private and 69% federal land. We acquired flow-accumulation and flow-direction layers from the National Hydrography Dataset Plus (version 2) to determine Strahler stream order (Strahler 1957) for all streams within the area of interest and then delineated watersheds for all 4^{th}-order streams (streams below a junction of two 3^{rd}-order streams). These analyses were performed using the Spatial Analyst hydrology tool in ArcGIS (v. 10.8.1 ESRI, Redlands, CA). From this pool of 4^{th}-order watersheds we selected a stratified random sample to ensure sites encompassed a range of pre-fire stand age and fire severity. We selected the scale of 4^{th}-order watersheds to ensure salmonid fish presence at all sites because Coastal Cutthroat Trout (*Oncorhynchus clarkii clarkii*) occurred in only 37% of 3^{rd}-order streams in the Cascade Range (Bjornn and Reiser 1991). We determined mean annual temperature (MAT) and MAP for the downstream sampling location using historical data available from WorldClim (Fick and Hijmans 2017) in R (R Core Team 2021).

We summarized forest age, and fire severity relevant to each study reach across the entire watershed area, defined as the most-downstream sampling point. Watershed characteristics may be more influential on aquatic ecosystems and better predicted by remote sensing techniques than at the reach scale (i.e., adjacent riparian characteristics). Characteristics of the entire watershed can influence post-fire streamflow response, and associated changes in delivery of LW, changes in solute delivery of nutrients and sediment, and species assemblages (Schlosser 1991; Gresswell 1999; Saxe et al. 2018). Watershed-scale characteristics encompass variation in characteristics at the landscape scale of pre-fire forest management and fire extent. To quantify mean watershed stand age, we used a remote sensing data layer of the gradient nearest-neighbor data of forest attributes based on 30-m Landsat imagery, Forest Inventory and Analysis field data, and other geospatial data products (Bell et al. 2015; Davis et al. 2015; Ohmann et al. 2012; Ohmann and Gregory 2002). These GNN maps were developed for landscape-scale analyses (i.e., the scale of our 4^{th}-order watersheds) and at these scales model and map agreement were moderate for the Oregon Cascades; lower prediction accuracy occurs at finer (i.e., reach-scale) spatial scales (Ohmann et al. 2012). Therefore, we focused on watershed means in our analysis (data available at https://lemma.forestry.oregonstate.edu/data/structure-maps). Using the most recent information available on pre-fire stand conditions (2016 upon initial selection, 2017 for analysis), we initially stratified mean watershed stand age as < 85 years or > 85 years because half of all 4^{th}-order watersheds within the three fire boundaries were < 85 years and half were > 85 years. For each mean watershed stand age category, we had a sample size of 12 watersheds. For analyses we used pre-fire stand age as a continuous predictor variable.

To ensure a range of fire severities representative of 4^{th}-order watersheds, we initially categorized all basins by their overlap with the fire boundary, resulting in four categories ($n = 6$) of watershed burned area as: completely (100%), majority (> 50 to < 100%), minority (0 > to < 50), and reference (0%). We obtained final fire boundary shapefiles from the National Interagency Fire Center (NIFC; https://data-nifc.opendata.arcgis.com/pages/new_firehistory_services).

We quantified additional metrics of fire severity to better characterize this variation within and across watersheds. We quantified fire severity using the rapid assessment of vegetation condition (RAVG), which provided an estimate of basal area tree mortality resulting from fire (https://burnseverity.cr.usgs.gov/ravg/data-access). RAVG uses Landsat (or similar multispectral satellite imagery) and change-detection methods to compare pre-fire and post-fire conditions for fires that burn > 1000 ac of national forest land. Near-infrared and short-wave infrared bands are used to determine the normalized burn ratio (NBR), differenced NBR (dNBR), and relative dNBR (RdNBR), and then regression equations based on field tree-mortality data are used to determine RAVG metrics. RAVG is reported as a 7-class basal area percent change for each raster value (Fig. 1) or is also available in a continuous format (0 to 100%). In a post-fire landscape, we expected overstory mortality for the entire watershed to affect changes in water quantity, delivery of solutes (sediment, DOM, nutrients), and LW source and delivery (e.g., Gresswell 1999; Reeves

Table 1 Pre-fire stand age and percent of watershed burned for selected 4th-order watersheds

Stream name	Watershed characteristics					Fire characteristics				
	Watershed area (km^2)	MAP (mm)	Elevation (m)	MAT (°C)	Mean pre-fire stand age (y)	Fire	Fire area (km^2)	Percent burned	Mean RAVG	Soil burn severity RMA
Biggs	9.27	2004	368	8.3	61.96	Holiday Farm	0	0	0	unburned
Buck	4.81	1727	654	7.8	159.62	Holiday Farm	0	0	0	unburned
Cook	21.71	1950	652	7.5	194.22	Holiday Farm	0	0	0	unburned
Ella	11.08	1927	420	9.7	76.50	Beachie Creek	0	0	0	unburned
Quartz	26.51	1727	699	7.8	164.03	Holiday Farm	0	0	0	unburned
Hands	7.09	2004	476	8.3	73.66	Holiday Farm	0.03	0.48	0.01	unburned
Norhorn	15.7	2399	877	6.8	173.87	Beachie Creek	0.56	3.54	0.05	unburned
Hugh	13.64	2399	903	6.8	168.40	Beachie Creek	1.24	9.09	0.11	unburned
Cripple	12.78	2211	432	7.4	189.11	Riverside	3.10	24.26	0.69	moderate
Haagen	8.04	1655	205	9.6	45.17	Holiday Farm	2.92	36.31	1.03	low
Canyon	19.71	2079	335	9.0	71.68	Riverside	6.40	32.46	1.21	unburned
Molalla	15.11	2399	647	6.8	116.83	Beachie Creek	7.01	46.37	1.55	low
Doe	5.65	1727	741	7.8	80.84	Holiday Farm	3.65	64.67	2.03	low
Clear	50.54	1665	303	10.6	84.13	Riverside	39.38	77.92	2.22	unburned
Mad	10.72	1981	528	9.8	81.70	Beachie Creek	8.46	78.96	2.37	low
Cougar	16.04	2079	608	9.0	82.78	Riverside	16.04	100	2.61	low
Big	7.03	2211	610	7.4	146.48	Riverside	7.03	100	2.91	low
Coal	21.50	1543	269	10.7	59.21	Beachie Creek	19.96	91.78	3.10	moderate
NF Molalla	23.59	2079	608	9.0	80.16	Riverside	20.57	87.20	3.73	low
Lukens	15.68	2471	759	6.7	156.59	Riverside	15.64	99.77	3.66	low
Stout	10.91	1927	470	9.7	81.31	Beachie Creek	10.91	100	3.97	moderate
Wycoff	6.49	1727	576	7.8	82.91	Holiday Farm	5.98	92.15	4.42	low
Finn	9.76	1762	276	9.0	67.89	Holiday Farm	9.76	100	5.94	moderate
Elkhorn	33.48	2182	343	8.8	140.47	Beachie Creek	33.48	100	6.36	moderate

Characteristics of 4th-order watersheds selected using a stratified random sampling design (Category) of pre-fire stand age (< 85 or > 85 y based on 2016 LEMMA layer) and percent of watershed burned (0%, < 50%, > 50%, 100%). Soil burn severity in the riparian-management areas includes the area within 30.48 m (100 ft) of the stream, with values of unburned to very low, low severity, and moderate severity. Mean rapid assessment vegetation condition (RAVG) reflects watershed mean values; higher values are associated with greater % overstory mortality as predicted from remote sensing. Mean pre-fire stand age represents an updated version of pre-fire stand-age information rather than the age included in our initial selection (2017; mean pre-fire stand age). We do not have stand-age information for 2020, immediately prior to the fire, and instead rely on the best available information

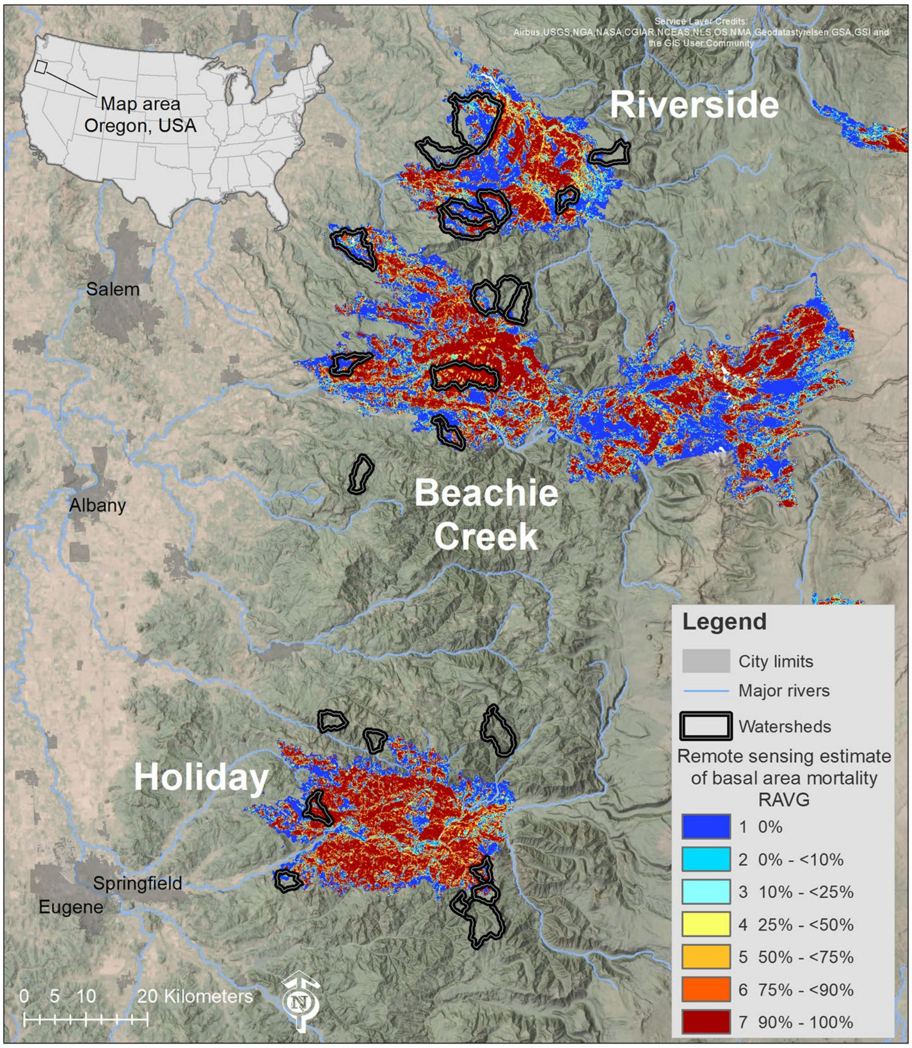

Fig. 1 Location of 24 4th-order study watersheds in Oregon's western Cascade Range. All sites were within 6 km of Riverside, Beachie Creek, and Holiday Farm wildfire boundaries

et al. 2006). A recent study also compared riparian and watershed scale burn severity metrics (RAVG, SBS) and found watershed RAVG was most strongly correlated with stream temperature response (Sanders et al. 2022). RAVG was developed to determine overstory mortality at landscape scales to prioritize post-fire restoration and revegetation initiatives. Therefore, we calculated means of RAVG raster values within each watershed area. We also used riparian (clipped within 30.48 m of stream) soil burn severity (SBS) obtained from the Burned Area Emergency Response (BAER) database to determine if the riparian area adjacent to our measurement reach was burned (low, moderate, or high severity) or not (https://burnseverity.cr.usgs.gov/baer/baer-imagery-support-data-download). SBS is based on 30-m Landsat imagery and uses field data to verify its accuracy. Hereafter, we refer to the variables pre-fire stand age and RAVG as watershed means.

We received post-fire forest management information on salvage logging from federal, state, and private forest landowners within our study basins. We compiled this information and calculated the total percent that was salvage logged in each watershed and riparian area. This data reflects salvage logging that occurred in the first year post-fire, with salvage ongoing during our sampling campaign. Therefore, we include these data in our analyses, but acknowledge that effects of salvage may be better explored in subsequent years.

Large wood, coarse wood, and overstory mortality

We defined LW as any fallen piece of wood in streams ≥ 10 cm in diameter and ≥ 1 m in length extending into or above the bankfull channel. We selected this size because it is the most commonly applied size definition (Wohl 2020). We measured all wood within the established 100 m reach. We sought to include a minimum of 50 pieces to ensure adequate sampling for volume estimation (Bilby and Ward 1991), and if that value was not met within the 100-m reach, we continued measurements until 50 pieces were quantified. This criterion meant that the length of stream channel surveyed depended on LW abundance, ranging from 100 to 485 m, with 50 to 202 pieces of LW surveyed per stream. We measured and estimated length and diameter for the first 20 pieces, then we measured every 10th piece and estimated all other pieces. Based on linear regression analyses of estimated versus measured values, individual large wood pieces were estimated with high precision for length ($r^2 = 0.94$, $n = 662$) and (diameter $r^2 = 0.94$, $n = 594$). Across all sites, 28 to 31% of all large wood pieces were measured, more than has been reported in other studies (e.g., Beechie and Sibley 1997). We estimated the percentage of each piece within 4 geomorphic zones (Robison and Beschta 1990; Gregory et al. 2017) (Supporting information). Geomorphic zone 1 includes wood within the wetted channel at low flow; zone 2 includes the stream channel at bankfull width; zone 3 refers to the area above the stream prism at bankfull width; and zone 4 is lateral to bankfull and is equivalent to the floodplain (Gregory et al. 2017). We compared average size of LW among sites with a volume index (Bilby and Ward 1989, 1991), which was calculated by determining the geometric mean diameter and geometric mean total length. Geometric means are used for large wood when frequency distributions reveal large wood diameters and lengths are skewed towards smaller size classes (Bilby and Ward 1989, 1991; Beechie and Sibley 1997), which applied to all of our sites. Volume index for LW was standardized for reach length in all analyses.

At each study site, we completed 4 perpendicular transects (at 20, 40, 60, and 80 m along the 100-m reach), each running 50 m upslope into the riparian zone on alternating sides of the stream. We measured length and diameter of each piece of downed CW (also ≥ 10 cm in diameter and ≥ 1 m in length) that intersected each transect. We collected overstory data in a 10×10 m plot extending from 10–20 m along each upslope transect, on alternating sides of each transect. We recorded the species, diameter at breast height (dbh), and status (live or dead) of every standing tree or snag in each plot.

Abiotic and biotic co-variates

To record stream temperature at 15-min intervals, we deployed a temperature and dissolved oxygen sensor (miniDOT, Precision Measurement Engineering, Vista, CA, with accuracy of ± 0.1 °C) secured to the stream bottom in the center of the channel in a polyvinyl chloride housing at the downstream end of each reach. Prior to deployment, we used side-by-side logging for miniDOT sensors to ensure appropriate calibration of dissolved oxygen and temperature across all sensors. We report temperature response as 7-day moving average maximum temperature ($T_{7daymax}$) and DO as 7-day moving average minimum concentrations ($DO_{7daymin}$) for simultaneous logging periods.

We collected replicate water samples from each study site at the downstream end of each reach. We filtered samples through pre-combusted Whatman glass fiber filters (GF/F, 0.7 µm pore size) into acid-washed Nalgene high density poly-ethylene bottles and kept samples frozen until analysis. We determined total nitrogen (TN), ammonia/ammonium (NH_4^+), nitrate (NO_3^-), total phosphorus (TP), ortho-phosphate (PO_4^{3-}), dissolved organic carbon (DOC), and specific UV absorbance at 254 nm ($SUVA_{254}$) in water samples following standard methods. Hereafter, for inorganic nutrients our descriptions of NH_4^+, NO_3^-, and PO_4^{3-} refer to the atomic portion of N (NH_4^+-N, NO_3^--N) or P (PO_4^{3-}-P), respectively. We determined nitrogen and phosphorus concentrations in water samples using a SEAL AutoAnalyzer 3 HR (SEAL Analytical Inc., Mequon, WI, USA). We quantified total nitrogen following U.S. Environmental Protection Agency (USEPA) method 363.2, nitrate/nitrite (NO_3^-) following USEPA method 363.2/353.2, and ammonia/ammonium (NH_4^+) following USEPA method 350.1 (USEPA 1983; O'Dell 1993a, b). Total phosphorus was determined following USEPA method 365.4 and 365.1 and ortho-phosphate (PO_4^{3-}) followed USEPA method 365.1 (USEPA 1974; O'Dell 1993c). Dissolved organic carbon (DOC) was determined using high-temperature catalytic oxidation with a Shimadzu TOC-L combustion TOC analyzer. Minimum detection limits were 0.01 mg L^{-1} for each nutrient analyte, and values below detection were observed only for PO_4^{3-} and NH_4^+. Ultra-violet (UV) absorption at 254 nm was determined using a spectrophotometer (Agilent Cary 100). Specific UV absorbance at 254 nm ($SUVA_{254}$), an indicator of C aromaticity, was determined by dividing the UV absorbance at 254 nm by DOC concentration (Weishaar et al. 2003).

We used a spherical densiometer and photosynthetically active radiation (PAR; miniPAR, Precision Measurement Engineering, Vista, CA) to quantify forest cover and light over the stream every 20 m along the thalweg. At each transect, four readings were taken with one in each of four directions (upstream, downstream, left bank, and right bank). At each of these transect locations, in the thalweg, we quantified light as photosynthetically active radiation (PAR) with a miniPAR (Precision Measurement Engineering, Vista, CA) logging at 1-min intervals. We held the miniPAR sensor vertically while facing upstream, uncapped the sensor, held it for a minimum of four minutes, and then re-capped the logger prior to the next reading. We measured bankfull width, wetted width to the nearest 0.1 m at each of six transects, and for each transect cross-section we measured depth at 5 equidistant locations determined by wetted width. We determined discharge using the dilution gaging method (Kilpatrick and Cobb 1985) with a HOBO conductivity data logger (Onset, Bourne MA) recording specific conductivity at 5-s intervals.

To determine surface substrate size, we used a modified Wolman pebble count in which 18 random rock samples were collected and measured along each 20-m transect ($n = 108$/stream). Pebbles > 2 mm were measured along their median axis using a ruler. Substrate < 2 mm with gritty texture was assumed to be sand and recorded as 1 mm, whereas substrate < 2 mm with a smooth texture was assumed to be silt and recorded as 0.031 mm. From these data, we determined percent surface fines (< 2 mm). For each transect, we visually estimated substrate embeddedness at 5 locations (Peck et al. 2006). For sand, silt, and clay, embeddedness was recorded as 100%, whereas for bedrock embeddedness was recorded as 0%. We collected subsurface fines from the center 2/3rds of the stream at three locations (20, 60, 100 m) within each stream reach using a bulk shovel with a portable stilling well (Schuett Hames et al. 1996). To determine size of subsurface fines, bulk samples were placed in plastic bags, kept cool until returned to a lab where they were oven dried at 60 °C for 24 h and then sieved for particle-size analysis (Plumb Jr 1981). We used a 10-sieve stack to separate streambed particles into Wentworth size categories of cobbles (> 63.5 mm), two sizes of pebbles (> 15.875 mm; > 4 mm), and fines < 2 mm. Sand and fines were further divided into smaller fractions (1 mm, 0.5 mm, 0.25 mm, 0.125 mm, 0.063 mm).

We collected periphyton samples on natural substrates at three locations (0, 40, 80 m) within each stream reach by randomly selecting three similarly sized rocks representative of the sampling area. Rocks were scraped, brushed, and washed into a graduated cylinder. Subsamples of a known volume of homogenized slurry were filtered onto pre-combusted Whatman GF/F 0.7-µm filters for chlorophyll α analysis and ash-free dry mass. Filters were wrapped in foil, labeled, immediately placed on ice, and frozen until analysis. To estimate rock area, the planar surface area of each rock surface was traced onto paper, and then quantified using image analysis. Rock outlines were digitized, and planar surface area was quantified using Image J software (US National Institutes of Health). Chlorophyll α concentration was determined on a Genesys 8 Spectrophotometer (Thermo Scientific, Waltham, MA, USA) and followed standard methods (APHA 2005). Ash-free dry mass (AFDM) was quantified as the difference between filters dried at 60 °C for 24 h and combusted at 500 °C for 2 h.

We collected macroinvertebrate samples with a surber sampler (0.09 m^2, 243-µm mesh) from 3 locations (0, 40, 80 m) within each stream reach. At each location, the surber sampler was placed on the streambed facing upstream. Large rocks were vigorously scrubbed, and substrate was disturbed to a depth of 10 cm for 2 min. Samples from all three locations were then composited into a single sample per stream and stored in HDPE sample bottles and preserved in 95% ethanol. We sorted, enumerated, and identified macroinvertebrates to lowest practical taxon level (genus for most individuals) for the entire sample (range: 68 to 3087 individuals). We determined density (individuals m^{-2}), Shannon–Weaver diversity index (Shannon and Weaver 1963), fine-sediment biotic index (FSBI) (Relyea et al. 2012), percent tolerant, intolerant, and fine-sediment sensitive (sensitive) taxa, and percent of each functional feeding group (collector-gatherer (CG), collector-filterer (CF), shredder (SH), scraper (SC)). We also determined the percent abundance of Ephemeroptera, Plecoptera, and Trichoptera (EPT). Relative abundance of EPT taxa is typically high when water quality is high and declines with increasing stress (Barbour et al. 1996). We calculated fine-sediment biotic index (FSBI) because it has been shown to predict fine-sediment storage. Higher FSBI values indicate greater abundance of taxa sensitive to fine-sediment deposition (Relyea et al. 2012). Tolerant taxa were defined as taxa with tolerance values > 5, whereas intolerant taxa had tolerance values < 3. Tolerant taxa increase in response to stress while intolerant taxa decrease. We calculated all macroinvertebrate indices in Microsoft Access (NCASI, Inc. 2007).

We quantified fish and stream-living amphibians using triple-pass depletion backpack electrofishing in two sections of contiguous 40-m stream reach where we separated each 20-m section with block nets. We identified and measured all captured fish and amphibians for total length (1 mm) and wet weight (0.1 g) under an anesthetic (buffered MS-222; 40 mg L^{-1}). Snout-to-vent length (SVL) was also measured for amphibians. We placed fish in an aerated bucket for recovery prior to being released in the reach where they were captured.

Statistical methods

To understand susceptibility of riparian vegetation to fire-induced mortality, we parsed our dataset of species most common to burned riparian areas (riparian soil burn severity = low, moderate, or high, $n = 12$ sites) or unburned riparian areas (riparian soil burn severity = unburned, $n = 12$ sites). We excluded species that occurred at ≤ 3 sites from analysis. We first explored whether mortality rates differed between burned and unburned riparian areas using a generalized regression with a beta binomial response distribution. Then we performed separate generalized regressions with a beta binomial response distribution on burned and unburned riparian areas to determine whether mortality rates differed by species in the presence or absence of riparian fire. A beta binomial response requires $n > 1$ for each species, therefore sites with only one observation of a species were excluded from analysis. When models were significant, we used post-hoc pairwise comparisons (Tukey–Kramer) to elucidate significant differences among groups. These analyses were performed in JMP Pro (v16, SAS Institute, Inc., Cary, NC).

Physical, chemical, and biological variables per site (averaged for some metrics) were analyzed using principal components analysis (PCA) to evaluate covariation among variables and to decompose this variation into fewer components for subsequent analysis. We selected PCA as a variable reduction technique because we sought to understand how the entire stream ecosystem responded to fire severity and pre-fire stand age, and to understand correlations among physical, chemical, and biological covariates. We transformed some variables as necessary, and centered and scaled all variables prior to PCA analysis. Variables included in this analysis were: LW geometric mean diameter (m), CW geometric mean diameter (m), canopy cover (%), light (PAR; μmol m^{-2} s^{-1}), subsurface fines (%), temperature ($T_{7daymax}$; °C), TP (mg L^{-1}), PO_4^{3-} (mg L^{-1}), NH_4^+ (mg L^{-1}), NO_3^- (mg L^{-1}), DON (mg L^{-1}), DOC (mg L^{-1}), $SUVA_{254}$ (mg C L^{-1} m^{-1}), macroinvertebrate Shannon–Weaver diversity, density (no. m^{-2}), scrapers (%), sensitive (%), intolerant taxa (%), amphibian density (no. m^{-2}) and biomass (g m^{-2}), fish density (no. m^{-2}) and biomass (g m^{-2}), overstory riparian vegetation (% mortality), mean annual precipitation (MAP; mm), mean annual temperature (MAT; °C), elevation (m), and salvage (% watershed and riparian). We extracted the loading values for the PC axes representing the most variation in the data, and then used these PC axes as response variables in generalized regression models with fire severity and pre-fire stand age as predictors (as described below). These analyses were performed in JMP Pro (v16, SAS Institute, Inc., Cary, NC).

To determine whether pre-fire stand age, fire severity, or their interaction affected physical (LW and CW volume index, LW and CW geometric mean diameter, geometric mean length, position by geomorphic zone, canopy cover, PAR, $T_{7daymax}$, fines, subsurface fines, embeddedness, FSBI, watershed and riparian salvage), chemical (TN, NO_3^-, NH_4^+, DON, TP, PO_4^{3-}, DOC, $SUVA_{254}$), or biological (chlorophyll α, AFDM, macroinvertebrate density, diversity, scrapers, collector-gatherers, collector-filterers, shredders, EPT, tolerant, intolerant, and sensitive taxa, and amphibian and fish density and biomass) responses we applied generalized regression with pre-fire stand age and watershed mean RAVG, and their two-way interaction as predictors for each response variable. Only NH_4^+ and PO_4^{3-} concentrations had values below detection limits, thus for these variables we applied generalized regression for limit of detection of left-censored data. For each response variable, we selected an appropriate distribution, and these were: normal (CW volume index, FSBI, CG), gamma (fish biomass density, LW volume index, $SUVA_{254}$, NO_3^-, macroinvertebrate density, CF, SC) zero inflated gamma (surface fines, zone 1, watershed salvage), log normal (amphibian biomass density), standing live dbh, standing dead dbh, CW diameter, LW diameter, zone 2, DOC, TN, TP, AFDM, subsurface fines, tolerant, intolerant, and sensitive macroinvertebrate taxa, SH), Cauchy (fish density, $T_{7daymax}$, DON, riparian salvage), Weibull (amphibian density, canopy cover, chlorophyll α, embeddedness, EPT), and exponential (PAR). We assessed model terms for significance ($p < 0.05$) and applied a lasso estimation method with Akaike Information Criterion (AICc) to select the best model (full, reduced, or null model) for each response variable.

Results

Watershed characteristics

Across our 24 4^{th}-order watersheds, watershed area ranged from 4.81 to 50.54 km^2, mean watershed fire severity (RAVG) ranged from 0 to 6.36, percent of watershed burned ranged from 0 to 100%, and mean pre-fire stand age ranged from 45 to 194 y (Table 1). Salvage logging occurred in 14 of our 18 burned watersheds and ranged from 0 to 35.6% of total watershed area with a mean of 10.12% and median of 5.54%. Riparian salvage logging occurred in 10 of our 18 burned watersheds, ranging from 0 to 1.70% of the watershed, with a mean 0.16% and median of 0.02% (Additional file 1).

Wood response to fire and stand age along the continuum of vegetation

Across all riparian zones, two deciduous tree species, red alder (*Alnus rubra*) and bigleaf maple (*Acer macrophyllum*) were most abundant and present at most sites (16). The most abundant conifer species were western redcedar (*Thuja plicata;*15), western hemlock (*Tsuga heterophylla;* 12), and Douglas-fir (*Pseudotsuga menziesii*; 9). Other overstory species were present at fewer than 3 sites. Deciduous trees dominated riparian areas at most sites (68%), followed by conifer-dominated riparian areas (27%), and the remainder of sites had equal occurrence of deciduous and conifer trees (5%).

Similar proportions of deciduous and conifer tree species occurred in the burned and unburned riparian categories, and we found higher tree-mortality rates in burned than unburned riparian areas ($X^2=9.71$, df = 1, $p=0.0018$). Mortality differed by species in burned riparian areas ($X^2=11.62$, df = 4, $p=0.0204$). Post-hoc Tukey–Kramer pairwise comparisons revealed red alder mortality rates (12.29%) were lower than for western redcedar (68.57%) in burned riparian areas by a factor of 5.6X ($p=0.0360$). Mortality rates did not differ among any other species in burned riparian areas (Fig. 2). Across sites with unburned riparian zones, we found similar mortality rates across species ($X^2=1.90$, df = 4, $p=0.7526$).

In the first post-fire year, wood volume (as volume index) did not vary with fire severity, pre-fire stand age, or their interaction for either CW or LW (Fig. 3; Additional file 2). Diameter across the vegetation continuum did not vary with fire severity for live and dead standing trees (as dbh) (Fig. 4a), but did vary significantly for CW and LW (as diameter geometric mean; Fig. 4b,c; Additional file 2). Smaller-diameter wood occurred in more severely burned watersheds both in riparian areas (as CW) and in streams (as LW; Fig. 4b,c). Diameters of riparian CW and stream LW were positively related, with CW diameter greater than LW diameter for most sites (below 1:1 line; Fig. 4d). Length of LW and proportion of LW in each geomorphic zone did not vary significantly with fire severity (Additional file 3). The interaction term of pre-fire stand age and fire severity and the main effect of pre-fire stand age were not significant contributors in the models for any of these CW or LW response variables (Additional file 2).

Principal components analysis

Physical, chemical, and biological variables were best explained by fire severity (and correlated variables) followed by pre-fire stand age (and correlated variables). Principal component 1 (PC1) explained 26.1% of the variation and was positively related to canopy cover, LW diameter geometric mean, and macroinvertebrate sensitive and intolerant taxa, and negatively related to overstory tree mortality, PAR, watershed salvage logging, DOC, and stream temperature (Fig. 5a). Principal component 2 (PC2) explained 15.7% of the variation and was positively related to $SUVA_{254}$, MAT, PO_4^{3-}, and TP, but negatively related to MAP and elevation.

Fire severity was a significant predictor of PC1 revealing more severely burned watersheds had greater tree mortality, salvage logging, light availability, DOC, DON, NH_4^+, and stream temperature, and had lower canopy cover, fish density, sensitive and intolerant macroinvertebrate taxa, percent scrapers, and smaller-diameter wood in streams and riparian areas (Fig. 5b; Additional File 2). Pre-fire stand age best predicted variation in PC2. Watersheds draining older forests were located at higher elevations, where they received more precipitation and experienced lower air temperatures, with stream water having less aromatic carbon ($SUVA_{254}$) and lower concentrations of phosphorus (Fig. 5c).

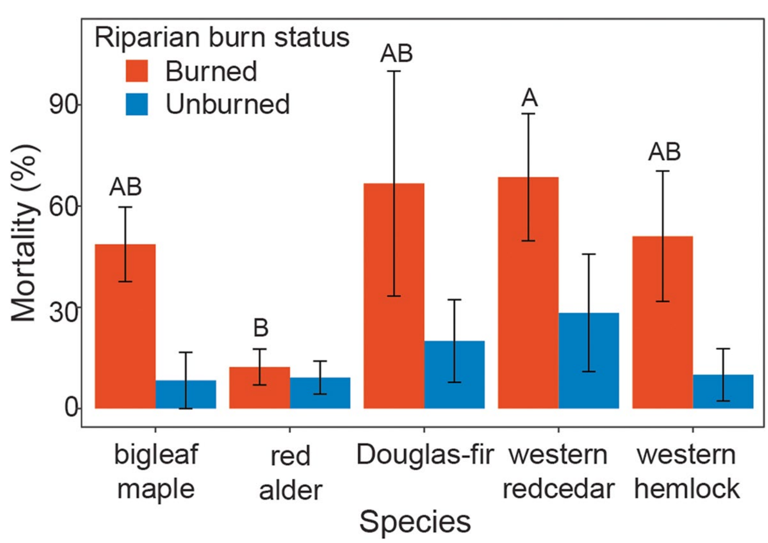

Fig. 2 Overstory mortality (%) for the most common species in burned and unburned riparian areas. Different letters denote significant differences among species in burned riparian zones

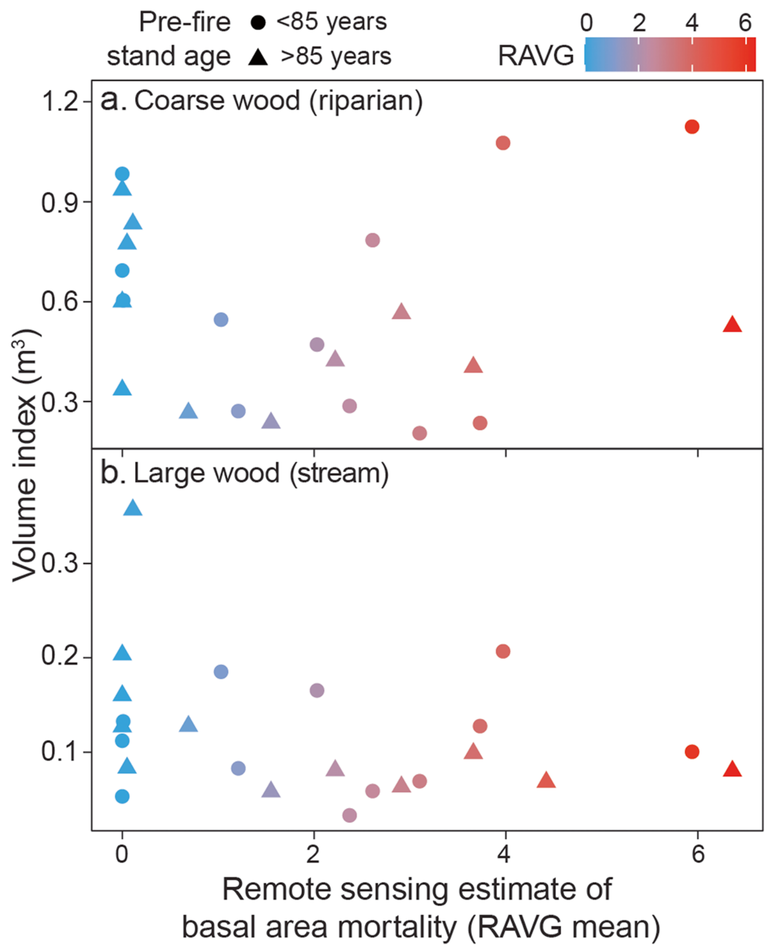

Fig. 3 Volume index (m^3) as a function of fire severity. Volume index (m^3) for (**a**) CW (riparian) and (**b**) LW (stream). Fire severity refers to watershed mean rapid assessment vegetation condition (RAVG), which provides a remote sensing estimate of basal area mortality (Fig. 1)

Covariate response to fire severity or pre-fire stand age

Fire severity (RAVG) was an important predictor of several physical characteristics across our study streams, including canopy cover, light, and temperature (Fig. 5; Additional file 2). Canopy cover (%) decreased in more severely burned watersheds, whereas light (photosynthetic active radiation [PAR]; μmol m^{-2} s^{-1}) increased exponentially in more severely burned watersheds. Neither canopy cover nor light varied with pre-fire stand age or an interaction term. Stream temperature (7-day moving average maximum; [$T_{7day\ max}$]; °C) varied significantly as an interaction between fire severity and pre-fire stand age; both main effects revealed stream temperature maxima were greater in more severely burned watersheds and lower in watersheds draining older pre-fire stand ages (Fig. 5e,h; Additional File 4). Given these large differences in overstory canopy and light availability, we also expected to observe a benthic periphyton response with fire severity. Chlorophyll α varied significantly as an interaction of fire severity and pre-fire stand age, and also as a main effect of pre-fire stand age alone (Additional file 4), but not with fire severity alone. Ash-free dry mass did not vary with any of these predictors (Additional file 5).

Stream DOM and nutrients varied in response to fire severity and pre-fire stand age. For DOM, both DOC and DON concentrations increased in more severely burned watersheds (Fig. 6; Additional file 2), whereas $SUVA_{254}$ decreased in watersheds with older pre-fire stand age (Additional file 4). No significant interaction was observed for DOC, DON, or $SUVA_{254}$. Both NO_3^- and TN exhibited significant interactions with fire severity and pre-fire stand age, but main effects were not significant contributors to these models (Additional file 2). No significant responses were observed for TP, NH_4^+, or PO_4^{3-} (Additional file 6).

We expected fire-induced changes in LW to affect sediment storage across our study sites. Although we quantified multiple metrics of sediment, only FSBI and sensitive taxa varied significantly with fire severity. FSBI did not

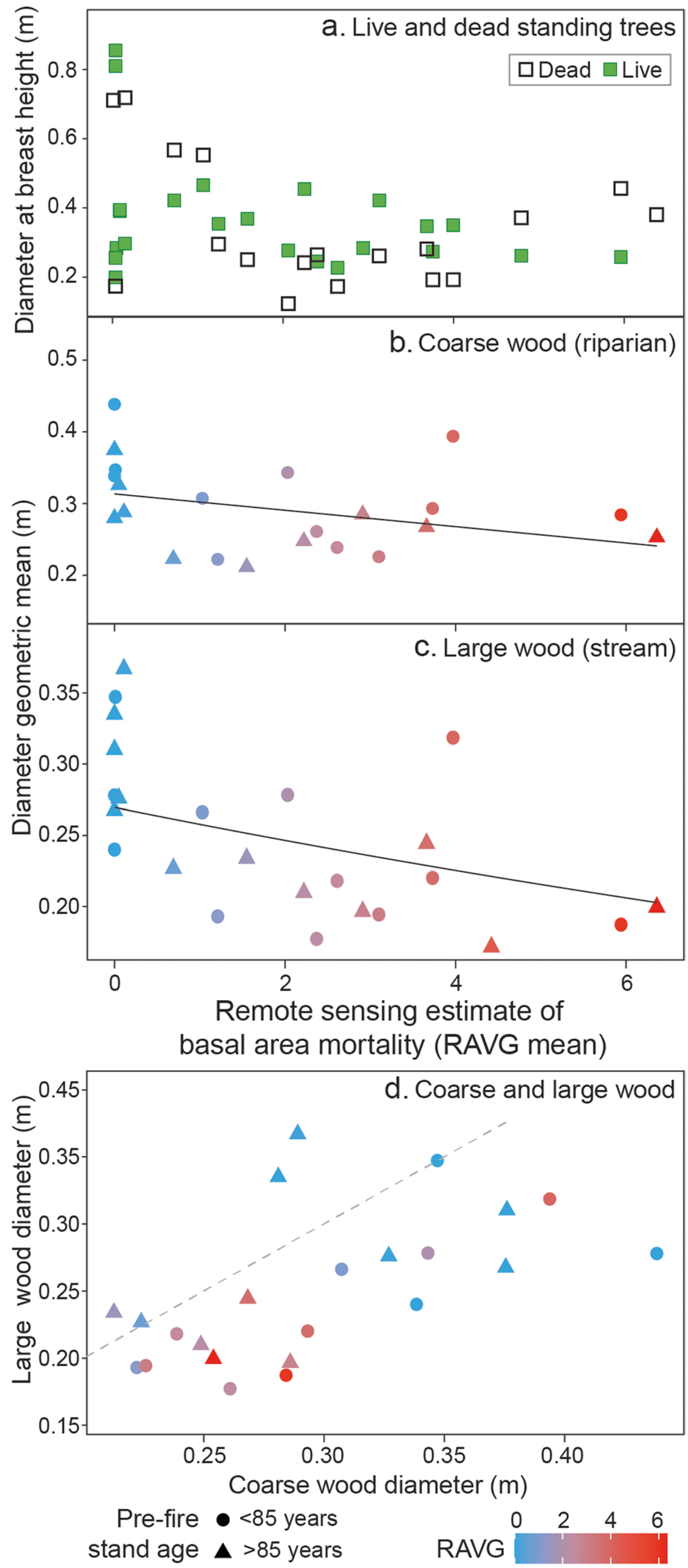

Fig. 4 Diameter as a function of fire severity for vegetation continuum. Diameter as (**a**) mean diameter at breast height (dbh) for live (green) and dead (black) standing trees (m); **b** CW diameter geometric mean of downed wood in riparian area (m); **c** LW diameter geometric mean (m) in streams as a function of fire severity, and (**d**) LW diameter (m) (stream) plotted against CW diameter (m) (riparian); Dashed line represents 1:1 line with values above this line indicating wood in streams is larger than in riparian area

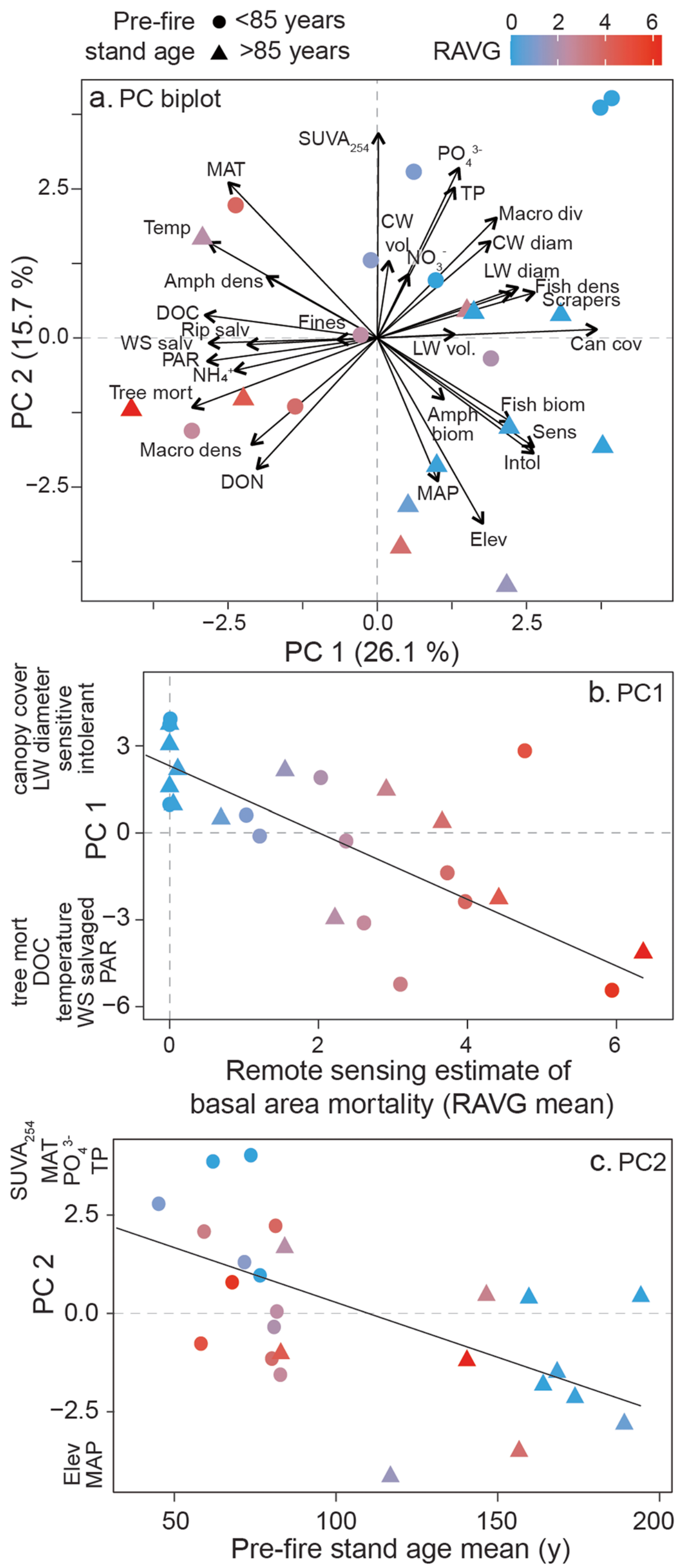

Fig. 5 Principal components analysis (PCA) and relationships of axes with fire severity and pre-fire stand age. **a** PCA with scores and loadings of physical, chemical, biological, and watershed characteristics. **b** Principal component 1 (PC1) varied as a function of fire severity as RAVG mean. **c** Principal component 2 (PC2) varied as a function of pre-fire stand age

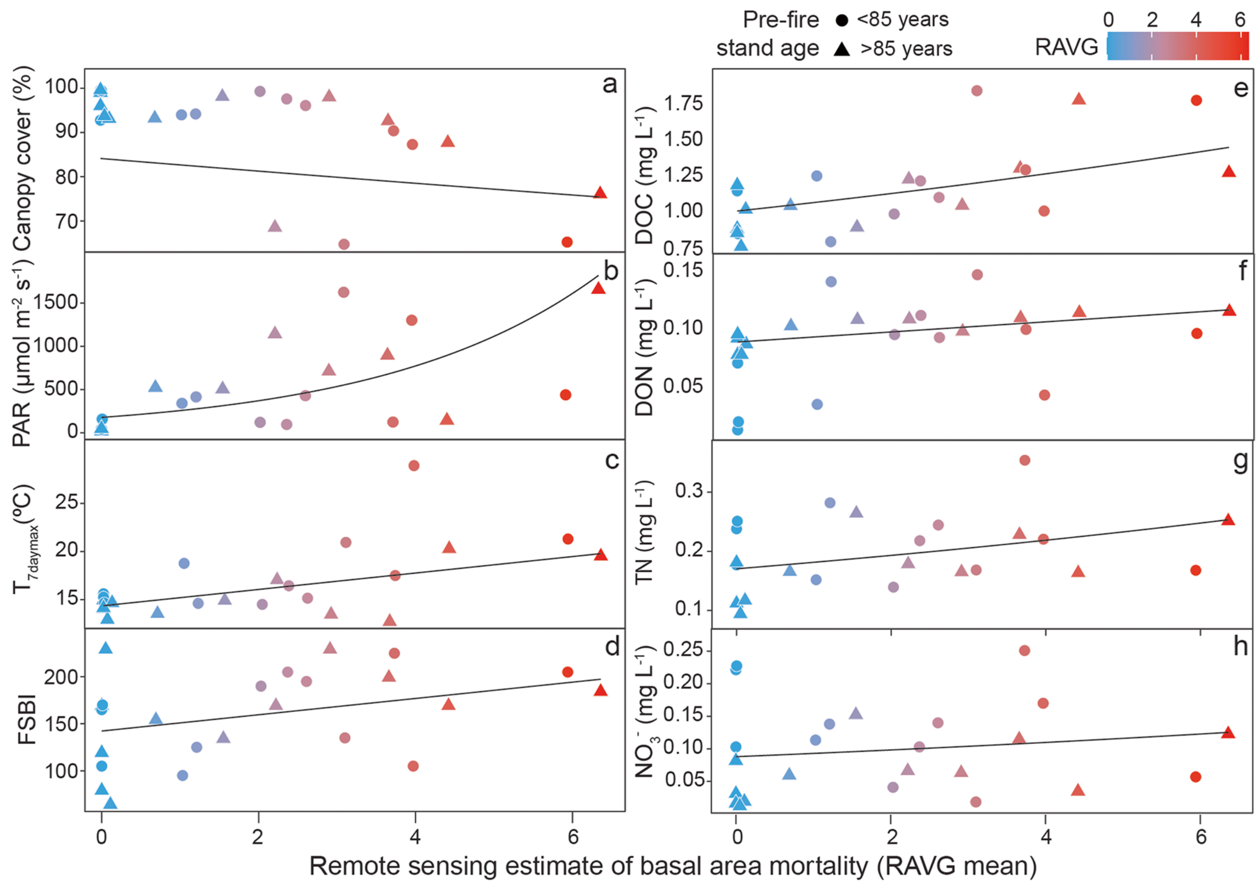

Fig. 6 Physical characteristics that varied as a function of fire severity (RAVG). Physical characteristics included: **a** canopy cover (%); **b** photosynthetically active radiation (PAR, μmol m^{-2} s^{-1}); **c** temperature ($T_{7daymax}$, °); **d** fine sediment biotic index (FSBI); **e** dissolved organic carbon (DOC, mg L^{-1}); **f** dissolved organic nitrogen (DON, mg L^{-1}); **g** total nitrogen (TN, mg L^{-1}); and (**h**) nitrate (NO_3^-, mg $L.^{-1}$)

differ with pre-fire stand age or an interaction, whereas sensitive taxa varied as an interaction and with individual main effects (Fig. 6d, Additional file 2). FSBI was greater in more severely burned watersheds, indicating the presence of more macroinvertebrates that are sensitive to high sediment loads and suggesting these streams have lower sediment storage (Larson et al. 2019; Relyea et al. 2012). Fewer taxa sensitive to fine sediment occurred in more severely burned watersheds. However, surface fines, subsurface fines, and % embeddedness did not vary significantly with fire severity, pre-fire stand age, or their interaction (Additional files 2 and 6).

Several macroinvertebrate indices varied in response to fire severity and/or pre-fire stand age. Macroinvertebrate density was greater in more severely burned watersheds, but diversity (Shannon–Weaver diversity) and relative abundance of scrapers were lower (Fig. 7, Additional file 2). Relative abundance of EPT taxa, collector-filterers, shredders, and tolerant taxa did not vary with fire severity, pre-fire stand age, or their interactions. Percent collector-gatherers decreased in watersheds draining older pre-fire stand ages. Intolerant macroinvertebrate taxa varied with fire severity and pre-fire stand age as an interaction and as individual main effects. As with sensitive taxa, there were fewer intolerant taxa in more severely burned watersheds and more intolerant taxa in watersheds with older pre-fire stand ages.

We hypothesized that stream biota would respond negatively to streams exposed to greater fire severity, and our results are consistent with this hypothesis for some top predators. Of top predators (fish or amphibians), we found that only fish density and fish biomass density varied with fire severity and pre-fire stand age, whereas amphibian density and amphibian biomass density did not vary with any predictors (Fig. 5). We observed a significant interaction of fish density to fire severity and pre-fire stand age, and to their individual main effects. Fish biomass density varied with fire severity, but not pre-fire stand age or their interaction. Fish density and fish biomass density were lower in more severely burned watersheds, but fish density was greater in watersheds draining younger pre-fire stand ages.

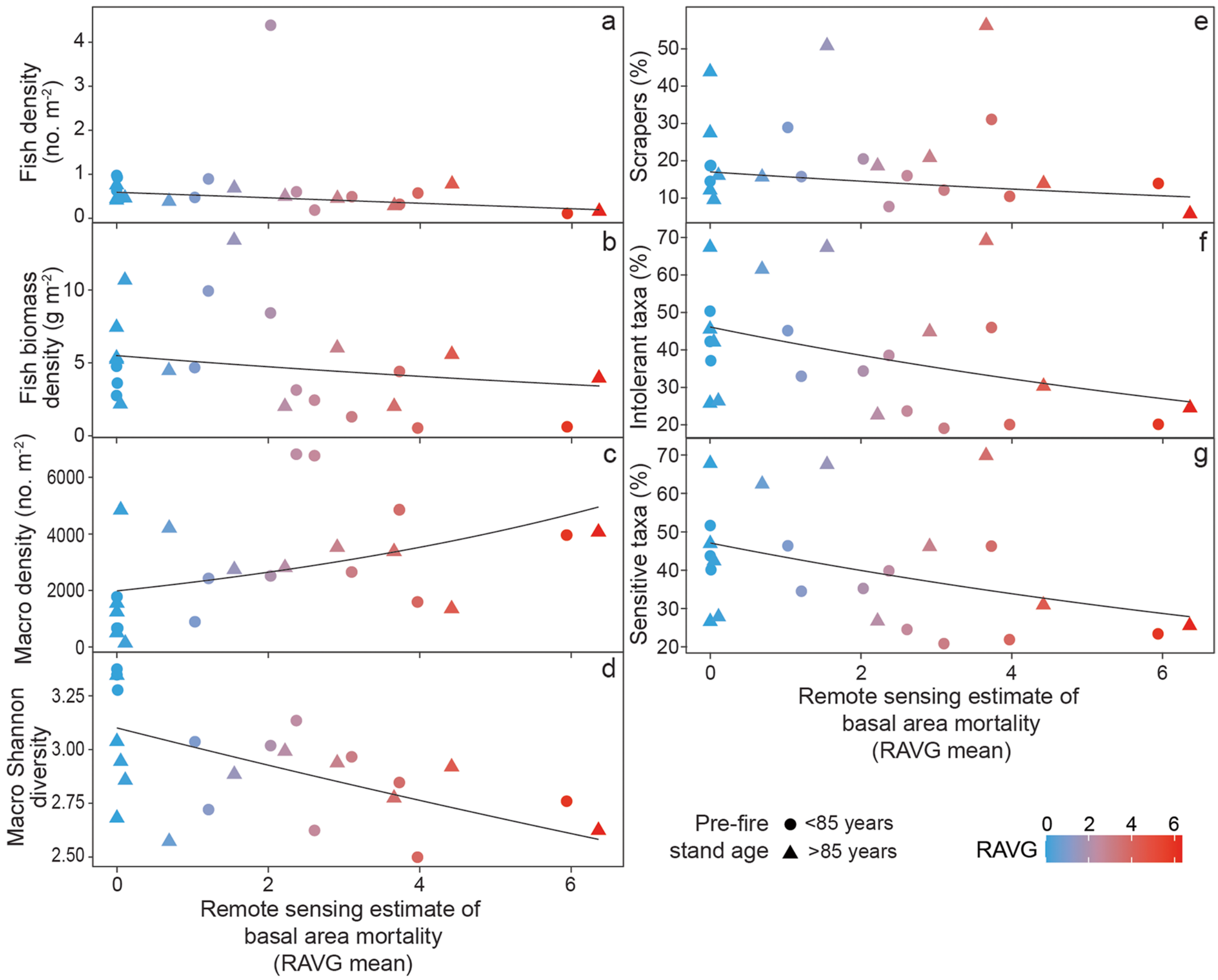

Fig. 7 Biological responses that varied as a function of fire severity (RAVG). Biological responses included: **a** fish density (no m^{-2}); **b** fish biomass density (g m^{-2}); **c** macroinvertebrate density (no m^{-2}); **d** macroinvertebrate Shannon–Weaver diversity (Shannon diversity); **e** scrapers (%); **f** intolerant taxa (%); and (**g**) sensitive taxa

Discussion

Large and coarse wood response to fire severity

We expected increases in LW delivery and sediment storage in more severely burned watersheds (Martens et al. 2020; Short et al. 2015), but our results revealed LW diameter was smaller and sediment (as % surface or subsurface fines, % embeddedness) did not vary in more severely burned watersheds. These findings suggest that streams experienced increased loading of younger fire-killed trees (Zelt and Wohl 2004) and no change in fine sediment storage in more severely burned watersheds. Smaller diameter LW has been observed previously in Wyoming, where LW diameter was 10% smaller in a burned than an unburned watershed 11 years after a fire (Zelt and Wohl 2004). Interestingly, as with sediment, we also did not observe statistically significant differences in other metrics of LW (volume, position, density) in the first post-fire year. LW volume, position, or density may have a greater effect on sediment storage than LW diameter, which likely explains the lack of a sediment response with fire severity. During the first winter/spring, these watersheds received less precipitation than average and events were characterized by low-intensity rainfall. The lack of high-intensity events likely limited transport of large wood and sediment in the time between the fires and the timing of our sampling (8 to 11 months). We expect these responses to change over time when large flood events transport riparian CW to streams in the most severely burned watersheds.

Similar to the LW response, riparian CW response (diameter) to fire severity suggests younger (smaller-diameter) trees were killed in more severely burned watersheds, whereas volume did not differ. Diameter of CW in most sites exceeded diameter of LW, which suggests the size of in-stream wood is likely to increase in the future, potentially improving stream characteristics for biota (Martens et al. 2020). In the three watersheds where LW diameter exceeded riparian CW diameter, pre-fire stand ages were 116, 159, and 168 y, evidence that older forests upstream have been an important source of wood in these streams. Upstream riparian fire severity, therefore, will be an important determinant for whether continued contributions of larger-diameter wood will occur in these watersheds. Recruitment of standing dead trees to riparian CW or stream LW is expected to occur on longer timescales and likely will occur as episodic pulses due to species-specific timing of treefall (Bendix and Cowell 2010).

The distribution of LW in streams may be affected by fire, as LW may be more likely to move and may move further downstream in burned than in unburned watersheds (Young 1994). The position of LW may be an important determinant of its stability in streams post-fire. We did not observe significant differences in the location of LW across these fire severities, but smaller-diameter LW found in our severely burned sites may be less stable, more prone to transport, more mobile in winter, and less likely to contribute to habitat structure (Ralph et al. 1994). Notably, we found the percent of salvage harvest in a watershed was also associated with severely burned watersheds and smaller-diameter LW. High-flow conditions were not observed in the first winter post-fire, and therefore we expect the conditions we captured represent a baseline post-fire condition. Timing and intensity of wet-winter precipitation during early forest regeneration may contribute to future post-fire debris flows, landslides, or hydrological transport of riparian CW to streams, which will have important consequences for aquatic-riparian ecosystems. Continued monitoring of these locations will aid in understanding transport and long-term stability of LW and aquatic ecosystems with fire severity.

Fire severity and pre-fire stand age influence aquatic ecosystems

Responses of aquatic ecosystems to fire are context-dependent owing to fire characteristics, stream features, and the local biological community. Using our extensive dataset of stream and riparian characteristics, we found within the first year, fire severity exerted a stronger control on ecosystem responses than stand age. In watersheds that burned at higher severity, overstory mortality, light availability, DOM concentrations, salvage logging, and stream temperature increased whereas canopy cover, LW diameter, sensitive and intolerant macroinvertebrate taxa, functional feeding group of scrapers, fish density, and fish biomass density decreased. Pre-fire stand age was related to elevation, mean annual precipitation, and mean annual temperature, which collectively explained variation in phosphorus concentrations, C aromaticity ($SUVA_{254}$), and stream temperature. These relationships with pre-fire stand age and geophysical characteristics reflect the geographic distribution of forest ownerships in the region, with private forests typically restricted to low to mid elevations. Post-fire research should encompass the full range of aquatic-riparian ecosystems affected by fire to capture differences in forest stand age and forest-management strategies that may differ by ownership and geophysical position.

Across watersheds, we found elevated DOM concentrations (as DOC and DON) in more severely burned watersheds. This finding is consistent with some prior research that found greater DOC concentrations after wildfire (McEachern et al. 2000; Olivares et al. 2019), but others have found decreases (Rodríguez-Cardona et al. 2020; Wei et al. 2021). In our study, the most severely burned watersheds were also correlated with salvage logging in the watershed (0 to 35.6%), potentially contributing to DOM responses. Soil erosion, regeneration of vegetation, ash deposition, and reductions in canopy interception or transpiration after a fire can contribute to enhanced DOC availability (Loiselle et al. 2020; Wei et al. 2021), and these factors may have greater contributions in more severely burned drainages. For example, in California elevated DOC concentrations occurred in the first year post-fire in severely burned watersheds and then declined with time since fire (Santos et al. 2019). In contrast, in less severely burned watersheds low initial DOC concentrations increased with time since fire (Santos et al. 2019). Our spatial analysis, taken together with the Santos et al. (2019) temporal analysis reveal that elevated DOC concentrations occur in the most severely burned watersheds in the first post-fire year, but are expected to decline with time since fire.

Our results further suggest interactions between pre-fire stand age (and elevation, climate) and fire severity explain variation in post-fire NO_3^- response, whereas DON response was explained by fire severity alone. Both NO_3^- and TN concentrations were higher in more severely burned watersheds, but lower concentrations also occurred in watersheds draining older stands. Post-fire increases in NO_3^- and TN concentrations have been attributed to increases in N mineralization and soil leaching (Wan et al. 2001; Turner et al. 2007). Others have also found NO_3^- response to fire is variable and dependent on amount of vegetation cover loss and watershed structure (Rhea et al. 2022). Root decomposition of trees killed by fire can release DON, which may be delivered to streams or mineralized to inorganic N (Smithwick et al. 2005). NH_4^+ concentrations in our study remained low regardless of fire severity, which suggests that if fire increased NH_4^+ concentrations immediately, NH_4^+ was quickly immobilized (Turner et al. 2007).

Complete removal of riparian vegetation enhances light availability, thereby increasing primary and secondary production (Spencer et al. 2003), which may counter negative effects of elevated thermal conditions on coldwater-adapted species. Consistent with our expectations, fire severity explained variation in riparian overstory mortality, thereby enhancing stream light availability and thermal conditions. However, we did not observe associated increases in periphyton biomass in the first year in more severely burned watersheds, as Spencer et al. (2003) observed 5 years after a fire in Montana and Swartz and Warren (2022) observed at a few sites in Oregon one year after fire. Periphyton standing crop does not account for the amount of periphyton removed by grazing, and it is unclear whether algal growth is limited by resources (e.g., nitrogen or phosphorus) in addition to light across these sites, which may explain the lack of a periphyton response to fire severity despite elevated light conditions in our sites. Periphyton response varied as a function of both fire severity and pre-fire stand age (as revealed by a significant interaction) suggesting post-fire responses can differ depending on location of study sites and associated differences in pre-fire stand age, elevation, and climate. Similarly, the lack of response of $SUVA_{254}$ to fire severity indicated no decrease (or change) in the relative proportion of allochthonous versus autocthonous sources of DOM in more severely burned watersheds.

Macroinvertebrates, as secondary producers, responded to fire severity exhibiting an increase in density, but decrease in diversity, scrapers, intolerant, and sentitive taxa in more severely burned watersheds. Similarly, on the Colville National Forest, macroinvertebrate diversity declined but density increased, and scrapers did not vary after wildfire (Mellon et al. 2008). Mellon et al. (2008) found that macroinvertebrate responses after wildfire may be greater in managed forests than in undisturbed ecosystems (Minshall et al. 1989, 2001). Our results suggest pre-fire forest management or associated differences in elevation and climate contributed to variation in macroinvertebrate responses (collector-gatherers, intolerant, and sensitive taxa). For example, collector-gatherers had greater relative abundance in streams draining younger watersheds with more allochthonous DOM sources ($SUVA_{254}$). We expect temporal variability in macroinvertebrate response to fire as post-fire floods alter sediment and large wood inputs in our study reaches, and potentially limit recolonization of macroinvertebrates in some of these burned watersheds (Mellon et al. 2008). Enhanced future LW recruitment in severely burned watersheds increasing structure may also lead to greater macroinvertebrate diversity (Minshall 2003; Vaz et al. 2014).

When severe fires burn riparian zones, resulting in high tree mortality, fish typically experience high mortality or emigration owing to increased stream temperatures, adverse stream chemistry, or higher winter streamflow (Minshall et al. 1997; Rieman and Clayton 1997; Gresswell 1999; Spencer et al. 2003). We found that fish density and biomass density decreased in more severely burned watersheds across our study area, which includes 24 sites and multiple fires. Declines were also observed for Coastal Cutthroat Trout and Coastal Giant Salamander (*Dicamptodon tenebrosus*) biomass density in two of three severely burned watersheds in the Holiday Farm fire (Swartz and Warren 2022), revealing consistent fish, but not amphibian, responses to these wildfires. Fish have also been found to be resilient to post-fire temperature increases that exceed 20 °C (Warren et al. 2022), and $T_{7daymax}$ reached as high as 28.9 °C in our study. Our results reveal that streams draining the most severely burned watersheds experienced greater exposure to direct sunlight and associated summer stream temperature maxima, smaller-diameter large wood, altered stream chemistry, and altered macroinvertebrate taxa in the first year post-fire. These changes likely collectively contributed to declines in fish density and fish biomass density. Despite immediate declines observed in our study, these native populations are expected to recover quickly (Rieman and Clayton 1997; Dunham et al. 2003; Rieman et al. 2012; Gomez Isaza et al. 2022), and ongoing monitoring will aid in our understanding of recovery across a range of fire severity across sites from different fires.

Implications for forest management

Contemporary forest management in the Pacific Northwest has prioritized establishment of conifers in riparian areas to enhance stream shading and for LW recruitment. However, our results suggest red alder may be important for fire resilience of stream ecosystems with greater riparian overstory survival associated with larger-diameter LW, lower temperature, and greater fish density and macroinvertebrate diversity. Our results are consistent with prior research demonstrating greater survival rates of some deciduous than conifer species during fires (Cumming 2001; Halofsky and Hibbs 2008; Rupasinghe and Chow-Fraser 2021), and the presence of these species may be an important determinant of riparian area resilience to fires. Our results highlight an important function of red alder in riparian zones that may facilitate faster stream and riparian ecosystem recovery in increasingly fire-prone landscapes.

Riparian areas are primary determinants of LW delivery to streams, with 70 to 90% of LW originating within 30 m of the stream (McDade et al. 1990; Bilby and Bisson 1998), and post-fire management strategies near streams influence near and long-term LW responses. Salvage activities may remove fire-killed trees and replant to more rapidly re-establish vegetation, thereby enhancing rooting strength and soil stability adjacent to streams and promoting faster thermal recovery (Reeves et al. 2006). In contrast, retaining legacies (dead and live trees, coarse sediment) after a fire may lead to greater recruitment of in-stream LW, organic matter, or may provide habitat for some terrestrial and aquatic species (Reeves et al. 2006). Data assessing these post-fire approaches on aquatic ecosystems remains scarce (Barrett and Reilly 2017; Reeves et al. 2006). Across our randomly selected watersheds, we found salvage activities affected 0 to 36% of the watershed, including 0 to 1.7% within riparian areas. Although salvage activities were strongly correlated with fire severity, overstory mortality, and other stream characteristics, we cannot elucidate the effects of salvage from fire severity.

Conclusions

Our results link forested streams, fire, and LW by identifying key relationships that change with fire severity and/or pre-fire watershed stand age. Within the first 8 to 11 months after western Cascades mega-fires, we found more severe fires burned more overstory riparian vegetation, leading to increased light, DOM concentrations, and macroinvertebrate densities, along with reduced canopy cover, LW diameter, macroinvertebrate diversity, and fish densities. However, we did not observe expected increases in CW or LW volume or associated increases in fine sediment likely due to a lack of high intensity winter rainfall. Greater survival of red alder in severely burned riparian zones may serve an important function of shade and bank stability immediately following wildfire, and may facilitate more rapid recovery for forested streams in fire-prone landscapes. Continued comprehensive aquatic and riparian ecosystem monitoring of these watersheds will aid in understanding long-term effects of post-fire management activities (salvage logging) on aquatic ecosystems, which is expected to affect LW recruitment to streams for decades.

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s42408-023-00192-5.

Additional file 1: Figure 1. Salvage logging versus fire severity for the entire watershed and for riparian areas. Both are expressed as a percent of the entire watershed.

Additional file 2. Generalized regression model details with fire severity as RAVG and pre-fire stand age as predictors.

Additional file 3. Percent of large wood in each stream geomorphic zone as a function of fire severity. Geomorphic zone 1 includes wood within the wetted channel at low flow, zone 2 includes the stream channel at bankfull width, zone 3 refers to the area above the stream prism at bankfull width, and zone 4 is lateral to bankfull and is equivalent to the floodplain (Gregory et al., 2017).

Additional file 4. Physical, chemical, and biological variables as a function of pre-fire stand age (y). Characteristics included: a) temperature (°, $T_{7daymax}$), b) $SUVA_{254}$ (L mg $C^{-1}m^{-1}$) c) TN (mg L^{-1}), NO_3^- (mg L^{-1}), Chlorophyll α (g m^{-2}), and macroinvertebrate metrics including: f) Collector-gatherers (%), g) Intolerant taxa (%), h) Sensitive taxa (%).

Additional file 5. Biological variables as a function of pre-fire stand age (y). Variables included: a) Ash-free dry mass (g m^{-2}), b) Collector-filterer (%), c) Shredders (%), d) EPT (%), e) Amphibian density (no. m^{-2}), and f) Amphibian biomass density (g m^{-2}).

Additional file 6. Physical and chemical variables as a function of fire severity (RAVG). Variables included: a) Fines (%), b) Subsurface fines (%), c) Visual embeddedness, d) NH_4^+ (mg L^{-1}), e) PO_4^{3-} (mg L^{-1}), f) TP (mg L^{-1}), g) $SUVA_{254}$ (L mg C^{-1} m^{-1}). Dashed horizontal lines for panels d and e represent minimum detection limits. No other analytes had sample concentrations below detection.

Additional file 7. Dataset of physical, chemical, and biological variables used in this study.

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Authors' contributions

A.A.C. wrote the original draft of the manuscript and completed formal analysis. All authors contributed to methodology, data collection, and funding acquisition. All authors provided input and assisted with revisions on the final version of the manuscript, and approved the final manuscript.

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Availability of data and materials

All data generated or analysed during this study are included in this published article [and its supplementary information files].

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare they have no competing interests.

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References

Abatzoglou, J.T., D.E. Rupp, L.W. O'Neill, and M. Sadegh. 2021. Compound extremes drive the Western Oregon wildfires of September 2020. *Geophysical Research Letters* 48 (8): e20212520. https://doi.org/10.1029/2021GL092520.

American Public Health Association [APHA]. 2005. Standard methods for the examination of water and wastewater. American Public Health Association.

Ashton, D.T., S.B. Marks, and H.H. Welsh Jr. 2006. Evidence of continued effects from timber harvesting on lotic amphibians in redwood forests of northwestern California. *Forest Ecology and Management* 221 (1–3): 183–193. https://doi.org/10.1016/j.foreco.2005.09.015.

Barbour, M.T., J. Gerritsen, G.E. Griffith, R. Frydenborg, E. McCarron, J.S. White, and M.L. Bastian. 1996. A framework for biological criteria for Florida streams using benthic macroinvertebrates. *Journal of the North American Benthological Society* 15 (2): 185–211. https://doi.org/10.2307/1467948.

Barrett, S.W., and M. Reilly. 2017. *Effects of salvage logging on riparian zones in coniferous forests of eastern Washington and adjacent regions. Washington State Forest Practices Adaptive Management Program CMER #17–100*. Olympia, WA: Washington Department of Natural Resources.

Bêche, L.A., S.L. Stephens, and V.H. Resh. 2005. Effects of prescribed fire on a Sierra Nevada (California, USA) stream and its riparian zone. *Forest Ecology and Management* 218 (1–3): 37–59. https://doi.org/10.1016/j.foreco.2005.06.010.

Beechie, T.J., and T.H. Sibley. 1997. Relationships between channel characteristics, woody debris, and fish habitat in northwestern Washington streams. *Transactions of the American Fisheries Society* 126 (2): 217–229. https://doi.org/10.1577/1548-8659(1997)126%3c0217:RBCCWD%3e2.3.CO;2.

Bell, D.M., M.J. Gregory, and J.L. Ohmann. 2015. Imputed forest structure uncertainty varies across elevational and longitudinal gradients in the western Cascade Mountains, Oregon, USA. *Forest Ecology and Management* 358: 154–164. https://doi.org/10.1016/j.foreco.2015.09.007.

Bendix, J., and C.M. Cowell. 2010. Fire, floods and woody debris: Interactions between biotic and geomorphic processes. *Geomorphology* 116 (3–4): 297–304. https://doi.org/10.1016/j.geomorph.2009.09.043.

Bilby, R.E., and P.A. Bisson. 1998. Function and distribution of large woody debris. In *River Ecology and Management. Lessons from the Pacific Northwest*, ed. R.J. Naiman, R.E. Bilby, and S. Kantor, 324–346. New York, NY: Springer-Verlag.

Bilby, R.E., and J.W. Ward. 1989. Changes in characteristics and function of woody debris with increasing size of streams in western Washington. *Transactions of the American Fisheries Society* 118: 368–378.

Bilby, R.E., and J.W. Ward. 1991. Characteristics and function of large woody debris in streams draining old-growth, clear-cut, and second-growth forests in southwestern Washington. *Canadian Journal of Fisheries and Aquatic Sciences* 48 (12): 2499–2508. https://doi.org/10.1139/f91-291.

Bjornn, T.C., and D.W. Reiser. 1991. Habitat requirements of salmonids in streams. In *Influences of Forest and Rangeland Management of Salmonid Fishes and Their Habitat*, ed. W.R. Meehan, 83–138. Special Publication 19. Bethesda, Maryland: American Fisheries Society.

Bragg, D.C. 2000. Simulating catastrophic and individualistic large woody debris recruitment for a small riparian system. *Ecology* 81 (5): 1383–1394.

Chen, X., X. Wei, and R. Scherer. 2005. Influence of wildfire and harvest on biomass, carbon pool, and decomposition of large woody debris in forested streams of southern interior British Columbia. *Forest Ecology and Management* 208 (1–3): 101–114.

Cumming, S.G. 2001. Forest type and wildfire in the Alberta Boreal Mixedwood: What do fires burn? *Ecological Applications* 11 (1): 97–110. https://doi.org/10.1890/1051-0761(2001)011[0097:FTAWIT]2.0.CO;2.

Davis, R.J., J.L. Ohmann, R.E. Kennedy, W.B. Cohen, M.J. Gregory, Z. Yang, H.M. Roberts, A.N. Gray, and T.A. Spies. 2015. *Northwest Forest Plan: the first 20 years (1994–2013)—Status and trends of late-successional and old-growth forests. General Technical Report PNW-GTR-911*. Portland, OR: U.S. Dept. of Agriculture, Forest Service, Pacific Northwest Research Station.

Dunham, J.B., M.K. Young, R.E. Gresswell, and B.E. Rieman. 2003. Effects of fire on fish populations: Landscape perspectives on persistence of native fishes and nonnative fish invasions. *Forest Ecology and Management* 178 (1–2): 183–196. https://doi.org/10.1016/S0378-1127(03)00061-6.

Fausch, K.D., and T.G. Northcote. 1992. Large woody debris and salmonid habitat in a small coastal British Columbia stream. *Canadian Journal of Fisheries and Aquatic Sciences* 49 (4): 682–693. https://doi.org/10.1139/f92-077.

Fick, S.E., and R.J. Hijmans. 2017. WorldClim 2: New 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology* 37 (12): 4302–4315. https://doi.org/10.1002/joc.5086.

Gomez Isaza, D.F., R.L. Cramp, and C.E. Franklin. 2022. Fire and rain: A systematic review of the impacts of wildfire and associated runoff on aquatic fauna. *Global Change Biology* 28 (8): 2578–2595. https://doi.org/10.1111/gcb.16088.

Gregory, S.V., A. Gurnell, H. Piégay, and K. Boyer. 2017. Dynamics of wood. In *Methods in Stream Ecology Volume 2: Ecosystem Function*, 3rd ed., eds. F. Hauer and G. Lamberti, 2:113–126. Elsevier.

Gresswell, R.E. 1999. Fire and aquatic ecosystems in forested biomes of North America. *Transactions of the American Fisheries Society* 129 (2): 128–193.

Grette, G.B. 1985. *The abundance and role of large organic debris in juvenile salmonid habitat in streams in second growth and unlogged forests. M.S. Thesis*. Seattle, WA: University of Washington.

Halofsky, J.E., and D.E. Hibbs. 2008. Determinants of riparian fire severity in two Oregon fires, USA. *Canadian Journal of Forest Research* 38 (7): 1959–1973. https://doi.org/10.1139/X08-048.

House, R.A., and P.L. Boehne. 1986. Effects of instream structures on salmonid habitat and populations in Tobe Creek Oregon. *North American Journal of Fisheries Management* 6 (1): 38–46.

Jones, J.I., J.F. Murphy, A.L. Collins, D.A. Sear, P.S. Naden, and P.D. Armitage. 2012. The impact of fine sediment on macro-invertebrates. *River Research and Applications* 28: 1055–1071. https://doi.org/10.1002/rra/1516.

Kemp, P., D. Sear, A. Collins, P. Naden, and I. Jones. 2011. The impacts of fine sediment on riverine fish. *Hydrological Processes* 25 (11): 1800–1821. https://doi.org/10.1002/hyp.7940.

Kilpatrick, F.A, and E.D. Cobb. 1985. *Measurement of discharge using tracers. Open-File Report 84–136*. Washington, DC: U.S. Geological Survey. https://pubs.usgs.gov/of/1984/0136/report.pdf

Larson, C.A., G. Merritt, J. Janisch, J. Lemmon, M. Rosewood-Thurman, B. Engeness, S. Polkowske, and G. Onwumere. 2019. The first statewide stream macroinvertebrate bioassessment in Washington state with a relative risk and attributable risk analysis for multiple stressors. *Ecological Indicators* 102: 175–185. https://doi.org/10.1016/j.ecolind.2019.02.032.

Lienkaemper, G.W., and F.J. Swanson. 1986. Dynamics of large woody debris in streams in old-growth Douglas-fir forests. *Canadian Journal of Forest Research* 17: 150–156.

Liljaniemi, P., K.-M. Vuori, B. Ilyashuk, and H. Luotonen. 2002. Habitat characteristics and macroinvertebrate assemblages in boreal forest streams: Relations to catchment silvicultural activities. *Hydrobiologia* 474: 239–251.

Loiselle, D., X. Du, D.S. Alessi, K.D. Bladon, and M. Faramarzi. 2020. Projecting impacts of wildfire and climate change on streamflow, sediment, and organic carbon yields in a forested watershed. *Journal of Hydrology* 590: 125403. https://doi.org/10.1016/j.jhydrol.2020.125403.

Martens, K.D., D.C. Donato, J.S. Halofsky, W.D. Devine, and T.V. Minkova. 2020. Linking instream wood recruitment to adjacent forest development in landscapes driven by stand-replacing disturbances: A conceptual model to inform riparian and stream management. *Environmental Reviews* 28 (4): 517–527. https://doi.org/10.1139/er-2020-0035.

McDade, M.H., F.J. Swanson, W.A. McKee, J.F. Franklin, and J. Van Sickle. 1990. Source distances for coarse woody debris entering small streams in western Oregon and Washington. *Canadian Journal of Forest Research* 20 (3): 326–330.

McEachern, P., E.E. Prepas, J.J. Gibson, and W.P. Dinsmore. 2000. Forest fire induced impacts on phosphorus, nitrogen, and chlorophyll a concentrations in boreal subarctic lakes of Northern Alberta. *Canadian Journal of Fisheries and Aquatic Sciences* 57: 73–81.

Mellon, C.D., M.S. Wipfli, and J.L. Li. 2008. Effects of forest fire on headwater stream macroinvertebrate communities in eastern Washington, U.S.A. *Freshwater Biology* 53: 2331–2343. https://doi.org/10.1111/j.1365-2427.2008.02039.x.

Minshall, G.W. 2003. Responses of stream benthic macroinvertebrates to fire. *Forest Ecology and Management* 178 (1–2): 155–161. https://doi.org/10.1016/S0378-1127(03)00059-8.

Minshall, G.W., J.T. Brock, and J.D. Varley. 1989. Wildfires and Yellowstone's stream ecosystems. *BioScience* 39 (10): 707–715.
Minshall, G.W., C.T. Robinson, and D.E. Lawrence. 1997. Postfire responses of lotic ecosystems in Yellowstone National Park, U.S.A. *Canadian Journal of Fisheries and Aquatic Sciences* 54: 2509–2525.
Minshall, G.W., C.T. Robinson, D.E. Lawrence, D.A. Andrews, and J.T. Brock. 2001. Benthic macroinvertebrate assemblages in five central Idaho (USA) streams over a 10-year period following disturbance by wildfire. *International Journal of Wildland Fire* 10 (2): 201–213. https://doi.org/10.1071/WF01018.
Murphy, M.L., and K.V. Koski. 1989. Input and depletion of woody debris in Alaska streams and implications for streamside management. *North American Journal of Fisheries Management* 9: 427–436.
NCASI, Inc. 2007. *A review of macroinvertebrate and fish metrics and indices of biotic integrity: spatial and temporal patterns in the long-term receiving water study rivers*. Technical Bulletin No. 941. Research Triangle Park, N.C.: National Council for Air and Stream Improvement, Inc. (NCASI).
O'Dell, J.W. 1993a. *Method 350.1: Determination of ammonia nitrogen by semi-automated colorimetry*. Cincinnati, OH: U.S. Environmental Protection Agency (USEPA).
O'Dell, J.W. 1993b. *Method 353.2, Revision 2.0: Determination of nitrate-nitrite nitrogen by automated colorimetry*. Cincinnati, OH: United States Environmental Protection Agency (USEPA).
O'Dell, J.W. 1993c. *Method 365.1, Revision 2.0: Determination of phosphorus by semi-automated colorimetry*. Cincinnati, OH: United States Environmental Protection Agency (USEPA).
Ohmann, J.L., and M.J. Gregory. 2002. Predictive mapping of forest composition and structure with direct gradient analysis and nearest-neighbor imputation in coastal Oregon, U. S. A. *Canadian Journal of Forest Research* 32 (4): 725–741. https://doi.org/10.1139/x02-011.
Ohmann, J.L., M.J. Gregory, H.M. Roberts, W.B. Cohen, R.E. Kennedy, and Z. Yang. 2012. Mapping change of older forest with nearest-neighbor imputation and Landsat time-series. *Forest Ecology and Management* 272: 13–25. https://doi.org/10.1016/j.foreco.2011.09.021.
Olivares, C.I., W. Zhang, H. Uzun, C.U. Erdem, H. Majidzadeh, C. Trettin, T. Karanfil, and A. Chow. 2019. Optical in-situ sensors capture dissolved organic carbon (DOC) dynamics after prescribed fire in high-DOC forest watersheds. *International Journal of Wildland Fire* 28 (10): 761–768. https://doi.org/10.1071/WF18175.
Olson, D.H., A.A. Coble, and J.A. Homyack. 2022. Beyond best management practices. In *Reflections on Forest Management: Can Fish and Fiber Coexist?*, ed. R.J. Danehy, C.A. Dolloff, and G.H. Reeves, 279–325. AFS Symposium 92. Baltimore, Maryland: American Fisheries Society. https://doi.org/10.47886/9781934874660.
Peck, D.V., A.T. Herlihy, B.H. Hill, R.M. Hughes, P.R. Kaufmann, D.J. Klemm, J.M. Lazorchak, et al. 2006. *Environmental monitoring and assessment program-surface waters Western Pilot Study: field operations manual for wadeable streams*. Washington, DC: U.S. Environmental Protection Agency. EPA 620/R-06/003.
Pettit, N.E., and R.J. Naiman. 2007. Fire in the riparian zone: Characteristics and ecological consequences. *Ecosystems* 10 (5): 673–687. https://doi.org/10.1007/s10021-007-9048-5.
Plumb, R.H Jr. 1981. *Procedures for handling and chemical analysis of sediment and water samples. Prepared for the U.S. Environmental Protection Agency/ Corps of Engineers Technical Committee on Criteria for Dredged and Filled Material. Technical Report EPA/CE-81–1*. Vicksburg, MS: Environmental Laboratory, U.S. Army Waterways Experiment Station.
R Core Team. 2021. *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. https://www.R-project.org/.
Ralph, S.C., G.C. Poole, L.L. Conquest, and R.J. Naiman. 1994. Stream channel morphology and woody debris in logged and unlogged basins of western Washington. *Canadian Journal of Fisheries and Aquatic Sciences* 51 (1): 37–51.
Reeves, G.H., L.E. Benda, K.M. Burnett, P.A. Bisson, and J.R. Sedell. 1995. A disturbance-based ecosystem approach to maintaining and restoring freshwater habitats of evolutionarily significant units of anadromous salmonids in the Pacific Northwest. *American Fisheries Society Symposium* 17: 334–349.
Reeves, G.H., P.A. Bisson, B.E. Rieman, and L.E. Benda. 2006. Postfire logging in riparian areas: Postfire logging in riparian areas. *Conservation Biology* 20 (4): 994–1004. https://doi.org/10.1111/j.1523-1739.2006.00502.x.
Reilly, M.J., C.J. Dunn, G.W. Meigs, T.A. Spies, R.E. Kennedy, J.D. Bailey, and K. Briggs. 2017. Contemporary patterns of fire extent and severity in forests of the Pacific Northwest, USA (1985–2010). *Ecosphere* 8 (3): e01695. https://doi.org/10.1002/ecs2.1695.
Reilly, M.J., A. Zuspan, J.S. Halofsky, C. Raymond, A. McEvoy, A.W. Dye, D.C. Donato, et al. 2022. Cascadia burning: the historic, but not historically unprecedented, 2020 wildfires in the Pacific Northwest, USA. *Ecosphere* 13 (6): e4070. https://doi.org/10.1002/ecs2.4070.
Relyea, C.D., G.W. Minshall, and R.J. Danehy. 2012. Development and validation of an aquatic fine sediment biotic index. *Environmental Management* 49 (1): 242–252. https://doi.org/10.1007/s00267-011-9784-3.
Rhea, A.E., T.P. Covino, C.C. Rhoades, and A.C. Brooks. 2022. Use of geostatistical models to evaluate landscape and stream network controls on post-fire stream nitrate concentrations. *Hydrological Processes* 36 (9): e14689. https://doi.org/10.1002/hyp.14689.
Richardson, J.S., and S. Béraud. 2014. Effects of riparian forest harvest on streams: A meta-analysis. *Journal of Applied Ecology* 51 (6): 1712–1721.
Rieman, B., and J. Clayton. 1997. Wildfire and native fish: Issues of forest health and conservation of sensitive species. *Fisheries* 22 (11): 6–15.
Rieman, B., R. Gresswell, and J. Rinne. 2012. *Fire and fish: a synthesis of observation and experience. General Technical Report RMRS-GTR-290*. Fort Collins, CO: U.S. Dept. of Agriculture, Forest Service, Rocky Mountain Research Station.
Robison, E.G., and R.L. Beschta. 1990. Characteristics of coarse woody debris for several coastal streams of Southeast Alaska, USA. *Canadian Journal of Fisheries and Aquatic Sciences* 47 (9): 1684–1693. https://doi.org/10.1139/f90-193.
Rodríguez-Cardona, B.M., A.A. Coble, A.S. Wymore, R. Kolosov, D.C. Podgorski, P. Zito, R.G.M. Spencer, A.S. Prokushkin, and W.H. McDowell. 2020. Wildfires lead to decreased carbon and increased nitrogen concentrations in upland Arctic streams. *Scientific Reports-UK* 10 (1): 8722. https://doi.org/10.1038/s41598-020-65520-0.
Rupasinghe, P.A., and P. Chow-Fraser. 2021. Relating pre-fire canopy species, fire season, and proximity to surface waters to burn severity of boreal wildfires in Alberta Canada. *Forest Ecology and Management* 496: 119386. https://doi.org/10.1016/j.foreco.2021.119386.
Sanders, A.M., A.A. Coble, A.G. Swartz, M. River, P. James, and D.R. Warren. 2022. Heat and smoke from wildfires influence water temperature and dissolved oxygen levels in headwater streams. *Freshwater Science* 41: 665–679. https://doi.org/10.1086/722632.
Santos, F., A.S. Wymore, B.K. Jackson, S. Mažeika, P. Sullivan, W.H. McDowell, and A.A. Berhe. 2019. Fire severity, time since fire, and site-level characteristics influence streamwater chemistry at baseflow conditions in catchments of the Sierra Nevada, California, USA. *Fire Ecolology* 15 (1): 3. https://doi.org/10.1186/s42408-018-0022-8.
Saxe, S., T.S. Hogue, and L. Hay. 2018. Characterization and evaluation of controls on post-fire streamflow response across western US watersheds. *Hydrology and Earth System Sciences* 22: 1221–1237. https://doi.org/10.5194/hess-22-1221-2018.
Scheidt, N.E. 2006. *Stream succession: Channel changes after wildfire disturbance. Thesis*. Moscow, ID: University of Idaho.
Schlosser, I. J. 1991. Stream fish ecology: a landscape perspective. *BioScience* 41 (10): 704-712.
Schuett Hames, D., B. Conrad, A. Pleus, and D. Smith. 1996. *Field comparison of the McNeil sampler with three shovel-based methods used to sample spawning substrate composition in small streams. TFW-AM-9–96–005*. Northwest Indian Fisheries Commission, TFW Ambient Monitoring Program. https://www.dnr.wa.gov/publications/fp_tfw_am9_96_005.pdf
Shah, N.W., B.R. Baillie, K. Bishop, S. Ferraz, L. Högbom, and J. Nettles. 2022. The effects of forest management on water quality. *Forest Ecology and Management* 522: 120397. https://doi.org/10.1016/j.foreco.2022.120397.
Shannon, C.E., and W.W. Weaver. 1963. *The Mathematical Theory of Communication*. Urbana, Illinois: University of Illinois Press.
Short, L.E., E.J. Gabet, and D.F. Hoffman. 2015. The role of large woody debris in modulating the dispersal of a post-fire sediment pulse. *Geomorphology* 246: 351–358. https://doi.org/10.1016/j.geomorph.2015.06.031.

Smithwick, E.A.H., M.G. Turner, M.C. Mack, and F.S. Chapin. 2005. Postfire soil N cycling in northern conifer forests affected by severe, stand-replacing wildfires. *Ecosystems* 8 (2): 163–181. https://doi.org/10.1007/s10021-004-0097-8.
Spencer, C.N., K. Odney Gabel, and F.R. Hauer. 2003. Wildfire effects on stream food webs and nutrient dynamics in Glacier National Park, USA. *Forest Ecology and Management* 178 (1–2): 141–153. https://doi.org/10.1016/S0378-1127(03)00058-6.
Spies, T.A., J.F. Franklin, and T.B. Thomas. 1988. Coarse woody debris in Douglas-fir forests of western Oregon and Washington. *Ecology* 69 (6): 1689–1702. https://doi.org/10.2307/1941147.
Strahler, A.N. 1957. Quantitative analysis of watershed geomorphology. *Eos, Transactions American Geophysics Union* 38 (6): 913–920.
Swartz, A., and D. Warren. 2022. Wildfire in western Oregon increases stream temperatures, benthic biofilms, and juvenile Coastal Cutthroat Trout size and densities with mixed effects on adult trout and Coastal Giant Salamanders. *Canadian Journal of Fisheries and Aquatic Sciences* 80 (3): 503–516. https://doi.org/10.1139/cjfas-2022-0053.
Turner, M.G., E.A.H. Smithwick, K.L. Metzger, D.B. Tinker, and W.H. Romme. 2007. Inorganic nitrogen availability after severe stand-replacing fire in the Greater Yellowstone Ecosystem. *Proceedings of the Academy of Natural Sciences of USA* 104 (12): 4782–4789. https://doi.org/10.1073/pnas.0700180104.
Turunen, J., J. Aroviita, H. Marttila, P. Louhi, T. Laamanen, M. Tolkkinen, P.-L. Luhta, B. Kløve, and T. Muotka. 2017. Differential responses by stream and riparian biodiversity to in-stream restoration of forestry-impacted streams. *Journal of Applied Ecology* 54 (5): 1505–1514. https://doi.org/10.1111/1365-2664.12897.
USEPA. 1974. *Methods for the chemical analysis of water and wastes; phosphorus, total (colorimetric, automated, block digester AA II). Method 365.4. E. EPA/600/4–79/020*. Cincinnati, OH: United States Environmental Protection Agency (USEPA).
USEPA. 1983. *Methods for chemical analysis of water and wastes. EPA-600/4–79–020*. Cincinnati, OH: United States Environmental Protection Agency (USEPA).
Vaz, P.G., S. Dias, P. Pinto, E.C. Merten, C.T. Robinson, D.R. Warren, and F.C. Rego. 2014. Effects of burn status and conditioning on colonization of wood by stream macroinvertebrates. *Freshwater Science* 33 (3): 832–846. https://doi.org/10.1086/676657.
Verkaik, I., M. Vila-Escale, M. Rieradevall, C.V. Baxter, P.S. Lake, G.W. Minshall, P. Reich, and N. Prat. 2015. Stream macroinvertebrate community responses to fire: Are they the same in different fire-prone biogeographic regions?". *Freshwater Science* 34 (4): 1527–1541.
Wan, S., D. Hui, and Y. Luo. 2001. Fire effects on nitrogen pools and dynamics in terrestrial ecosystems: A meta-analysis. *Ecological Applications* 11 (5): 1349–1365.
Warren, D.R., D.A. Roon, A.G. Swartz, and K.D. Bladon. 2022. Loss of riparian forests from wildfire led to increased stream temperatures in summer, yet salmonid fish persisted. *Ecosphere* 13: e4233. https://doi.org/10.1002/ecs2.4233.
Wei, X., D.J. Hayes, and I. Fernandez. 2021. Fire reduces riverine DOC concentration draining a watershed and alters post-fire DOC recovery patterns. *Environmental Research Letters* 16 (2): 024022. https://doi.org/10.1088/1748-9326/abd7ae.
Weishaar, J.L., G.R. Aiken, B.A. Bergamaschi, M.S. Fram, R. Fujii, and K. Mopper. 2003. Evaluation of specific ultraviolet absorbance as an indicator of the chemical composition and reactivity of dissolved organic carbon. *Environmental Science and Technology* 37 (20): 4702–4708. https://doi.org/10.1021/es030360x.
Welsh, H.H., Jr., and G.R. Hodgson. 2008. Amphibians as metrics of critical biological thresholds in forested headwater streams of the Pacific Northwest, USA. *Freshwater Science* 53 (7): 1470–1488. https://doi.org/10.1111/j.1365-2427.2008.01963.x.
Wohl, E. 2020. *Rivers in the Landscape*. John Wiley & Sons.
Wohl, E., A.E. Marshall, J. Scamardo, D. White, and R.R. Morrison. 2022. Biogeomorphic influences on river corridor resilience to wildfire disturbances in a mountain stream of the Southern Rockies. *Scienceof the Total Environment* 820: 153321. https://doi.org/10.1016/j.scitotenv.2022.153321.
Young, M.K. 1994. Movement and characteristics of stream-borne coarse woody debris in adjacent burned and undisturbed watersheds in Wyoming. *Canadian Journal of Forest Research* 24: 1933–1938.
Zelt, R.B., and E.E. Wohl. 2004. Channel and woody debris characteristics in adjacent burned and unburned watersheds a decade after wildfire, Park County. *Wyoming. Geomorphology* 57 (3–4): 217–233. https://doi.org/10.1016/S0169-555X(03)00104-1.

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