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Postfire extracellular enzyme activity in a temperate montane forest

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Abstract

Wildfire is a disturbance expected to increase in frequency and severity, changes that may impact carbon (C) dynamics in the soil ecosystem. Fire changes the types of C sources available to soil microbes, increasing pyrogenic C and coarse downed wood, and if there is substantial tree mortality, decreasing C from root exudates and leaf litter. To investigate the impact of this shift in the composition of C resources on microbial processes driving C cycling, we examined microbial activity in soil sampled from an Oregon burn 1 year after fire from sites spanning a range in soil burn severity from unburned to highly burned. We found evidence that postfire rhizosphere priming loss may reduce soil C loss after fire. We measured the potential activity of C-acquiring and nitrogen (N)-acquiring extracellular enzymes and contextualized the microbial resource demand using measurements of mineralizable C and N. Subsurface mineralizable C and N were unaltered by fire and negatively correlated with hydrolytic extracellular enzyme activity (EEA) in unburned, but not burned sites. EEA was lower in burned sites by up to 46%, but only at depths below 5 cm, and with greater decreases in sites with high soil burn severity. These results are consistent with a subsurface mechanism driven by tree mortality. We infer that in sites with high tree mortality, subsurface EEAs decreased due to loss of rhizosphere priming and that inputs of dead roots contributed to mineralizable C stabilization.

Plain Language Summary

Wildfires are expected to become more severe and frequent, which may change how much carbon is stored in the soil. Fire changes the relative amount of leaves, wood, and charcoal available for soil microbes to decompose, which may affect soil microbial activity and soil carbon as a result. In this study, we evaluated the effect of fire on soil microbial decomposition activity. We found burned areas had less microbial decomposition activity than unburned areas, but only below soil depths of 5 cm in

Abbreviations: BG, β-1,4-glucosidase; CBH, cellobiohydrolase; CUE, carbon use efficiency; EEA, extracellular enzyme activity; LAP, leucine amino peptidase; MAOM, mineral associated organic matter; NAG, β-1,4-*N*-acetyl-glucosaminidase; PER, peroxidase; PHEN, phenol oxidase; PMC, potentially mineralizable carbon; PMN, potentially mineralizable nitrogen; SBS, soil burn severity; SOC, soil organic carbon; TN, total nitrogen.

areas where most trees died after the fire. This was a surprising result because fire heat and combustion only directly affects the surface soil. We attribute the lower activity in higher burn severity subsurface soils to greater dead roots and a loss of root secretions, which are known to boost decomposition. Reduced decomposition could partly offset fire-caused carbon loss from the ecosystem. More research is needed to clarify the long-term effect on soil carbon.

1 | INTRODUCTION

There are large uncertainties in characterizing soil organic carbon (SOC) response to wildfire, a disturbance expected to increase in frequency and severity due to historic land use change, fire suppression policy, and climate change (Halofsky et al., 2020). Many studies have speculated that increases in wildfire intensity, duration, and frequency will destabilize accumulated soil C via changes to soil structure, vegetation, and the soil microbial community, threatening global SOC stocks (Walker et al., 2019). However, alterations to the form of C inputs (i.e., dead roots in place of live root exudates) may slow decomposition rates, a change that would favor C accumulation (Pellegrini et al., 2022).

Fire effects on SOC can be better understood by studying soil microbial activities. C transformations in soil are largely mediated by the microbial community, which contributes to SOC decomposition to access nutrients (Liao et al., 2024; Luo et al., 2017) and contributes to SOC accumulation via production of microbial residues (i.e., exudates and necromass) (Geyer et al., 2020; Horwath, 2022; Liao et al., 2022). Microbial activity properties can provide insight into the drivers of decomposition and accumulation, and are often used as indicators of future changes in SOC stocks because they respond more rapidly to disturbance than SOC (O'Kelley & Myrold, 2022). To improve understanding of postfire SOC dynamics, we investigated the effect of fire on microbial resource acquisition activity.

To do this, we measured a suite of potential extracellular enzyme activities (EEAs) to assess decomposition and microbial nutrient demand (Caldwell, 2005; Carreiro et al., 2000; Sinsabaugh et al., 2009). We measured EEA associated with C acquisition (C-acquiring) and N acquisition (N-acquiring) to assess microbial nutrient demand for C and N. We also investigated whether the relative quantity of hydrolase EEA and oxidase EEA differed after fire. Hydrolases are associated with the decomposition of cellulose, chitin, and proteins, whereas oxidases are associated with the decomposition of lignin (Dove, Arogyaswamy et al., 2020; Men et al., 2023). Previous studies have found varying EEA responses to fire—from increases to decreases or no response (Adkins et al., 2020; Barreiro & Díaz-Raviña, 2021; Fultz et al., 2016; Taş et al., 2014), but few studies have investigated soil EEA below a depth of 5 cm. EEA is chronically undermeasured in the subsoil, as are other biological soil property responses to fire (Dove, Safford et al., 2020). In this study, we assessed postfire effects on microbial activity and SOC in both surface and subsurface soil.

To better predict the outcomes of stand-replacing wildfires for microbial activity and SOC, we examined data from the Detrital Input and Removal Treatment (DIRT) network, an ecological network of long-term research sites where organic matter sources are chronically manipulated to assess how rates and sources of plant litter inputs influence organic matter stocks in forest soils (Lajtha et al., 2018). In the H.J. Andrews DIRT network site after 20 years of manipulation, sites where live roots were excluded had as much SOC and more mineral associated organic matter (MAOM) as those with roots (Pierson et al., 2021). One possible mechanism was that the absence of root exudates caused a loss of rhizosphere priming. Alternatively, inputs of dead root material may have provided a high-quality source of organic matter that contributed to MAOM formation (Pierson et al., 2021). Stand replacing fires also cause a loss of live root exudates and a large influx of dead roots belowground, which may yield similar SOC dynamics to those observed by Pierson et al. (2021). Alternatively, the influx of dead roots may stimulate organic matter decomposition in the short term (Men et al., 2023).

We took advantage of the parallels between the DIRT experiment and fire disturbances to study the microbial response to resource changes in soil (i.e., loss of fresh litter and live root inputs and influx of dead roots and pyrogenic C) after a large wildfire in the Oregon Cascade Range in 2020. We characterized microbial resource acquisition in burned and unburned soils by measuring potential EEA using a suite of extracellular enzyme assays. To assess available microbial resources in these soils, we measured potentially mineralizable nitrogen (PMN) and potentially mineralizable carbon (PMC), indicators of the organic C and N available to microbes under standardized incubation conditions (Hurisso et al., 2016; O'Kelley & Myrold, 2022; Sprunger & Martin, 2023).

We hypothesized that due to changes to the quantity, accessibility, and composition of organic matter inputs—specifically, increased coarse woody debris and dead roots, and decreased leaf litter and root exudates—EEA will decrease for hydrolytic C and N scavenging and increase for oxidative enzymes. We further hypothesized that the rapid shifts in accessibility and quantity of nutrients after fire would weaken the interdependency between EEA and mineralizable nutrients, mirroring the abiotic–biotic decoupling that has been previously observed following fire, CO_2 enrichment, and nutrient additions (Ochoa-Hueso, 2016, 2019; Qin et al., 2022). Specifically, we predicted that PMC and C-associated enzymes and PMN and N-associated enzymes would be positively correlated in unburned sites and be uncorrelated in burned sites.

2 | METHODS

2.1 | Willamette National Forest and H.J. Andrews Experimental Forest

We selected sites from the 2020 Holiday Farm Fire burn in H.J. Andrews Experimental Forest (HJA) and the part of Willamette National Forest immediately surrounding HJA (Figure 1).

The HJA is an ecological research forest established in 1948 and is jointly managed by the US Department of Agriculture Forest Service's Pacific Northwest Research Station, Oregon State University, and the Willamette National Forest (Andrews Forest Program, 2017). The study area is an old-growth and second-growth coniferous forest in the western Cascade Range of Oregon. The topography is steep (sampling location slopes were 8.6%–40%; see Table S1), typical for the western Cascade Mountain Range (Andrews Forest LTER Site & Spies, 2013; United States Geological Survey, 2021). Precipitation follows a xeric moisture regime, with 80% of annual precipitation occurring between October and March (Waichler et al., 2003). The mean annual precipitation is 2.3 m and the mean annual temperature is 9°C (Waichler et al., 2003). In this region, large stand replacing fires were estimated to return on an interval of 231 years (Cissel et al., 1999). The most recent recorded wildfires in the study area occurred in 1893 and 1952 (Burke, 1979; Heyerdahl, 2013; Teensma, 1987). Additionally, in 2000, logging slash was burned on part of the study area after a clearcut as part of the forest research activities (Hawk & Biome, n.d.).

Dominant tree species in the study area are Douglas-fir (*Pseudotsuga menziesii*) and western hemlock (*Tsuga heterophylla*). Typical understory species are red huckleberry (*Vaccinium parvifolium*), rhododendron (*Rhododendron macrophyllum*), and vine maple (*Acer circinatum*) (Sollins, 2006). Soils in the study area are Inceptisols classified as Andic, lithic, and typic humudepts, typically stony–cobbly loams with approximately 20% clay and 40% sand in the A horizon (Soil Survey Staff, n.d.). Additional site topographic and edaphic properties are listed in Tables S1 and S2.

The Holiday Farm Fire ignited on September 7, 2020, and spread rapidly before its eventual containment on October 29. Driven by strong desiccating winds and dry biomass, the fire burned over 70,000 ha, including 12,530 ha in Willamette National Forest and 162 ha within H.J. Andrews Experimental Research Forest (2.5% of HJA) (USFS, 2020). After containment, federal agencies dispatched Burned Area Emergency Response teams to assess postfire landscape changes. The fire burned in a heterogeneous pattern through mixed conifer forest, creating a mosaic of soil burn severity (SBS) and vegetation mortality levels throughout the burn area (Figure 1; USFS, 2020). SBS is a classification system used to estimate the impact of fire on soil properties. Soils are categorized as having an SBS of "unburned or very low," "low," "moderate," and "high." For the first category, we only selected sites that were entirely unburned, yielding SBS categories of "unburned," "low," "moderate," and "high" (USDA Forest Service, 2020). There are a number of characteristics that define each of these categories, but the amount of visible remaining surface litter, duff, and fine roots are key variables (Parson et al., 2010). Soils with low SBS have intact and recognizable litter, and soils with high SBS have lost all surface organic matter, exposing bare mineral soil and ash. In mixed conifer forests, sites classified as low SBS have a partially scorched understory and unaltered canopy, and in sites classified as high SBS both the understory and canopy have been completely consumed (Parson et al., 2010). SBS is mapped using geospatial information and ground-truthing as quickly as possible following fire, with recommended map polygon sizes ranging from 4 to 40 ha (Parson et al., 2010). Typical in forest wildfires, burn severities were highly varied across elevations and slope aspects. The USFS reported that 63% of the Holiday Farm Fire burned area in Willamette National Forest had high or moderate SBS (USFS, 2020).

Core Ideas

- Postfire extracellular enzyme activity decreases were observed only in sub-soils of higher burn severity sites.
- In high tree mortality burns, loss of rhizosphere priming may slow decomposition and mitigate carbon loss.
- This work challenges conventional views that fire affects only the surface of soils via direct heat and combustion.

2.2 | Study design

We sampled soil 7–10 months after the fire was contained from a range of burn severities and landscape positions

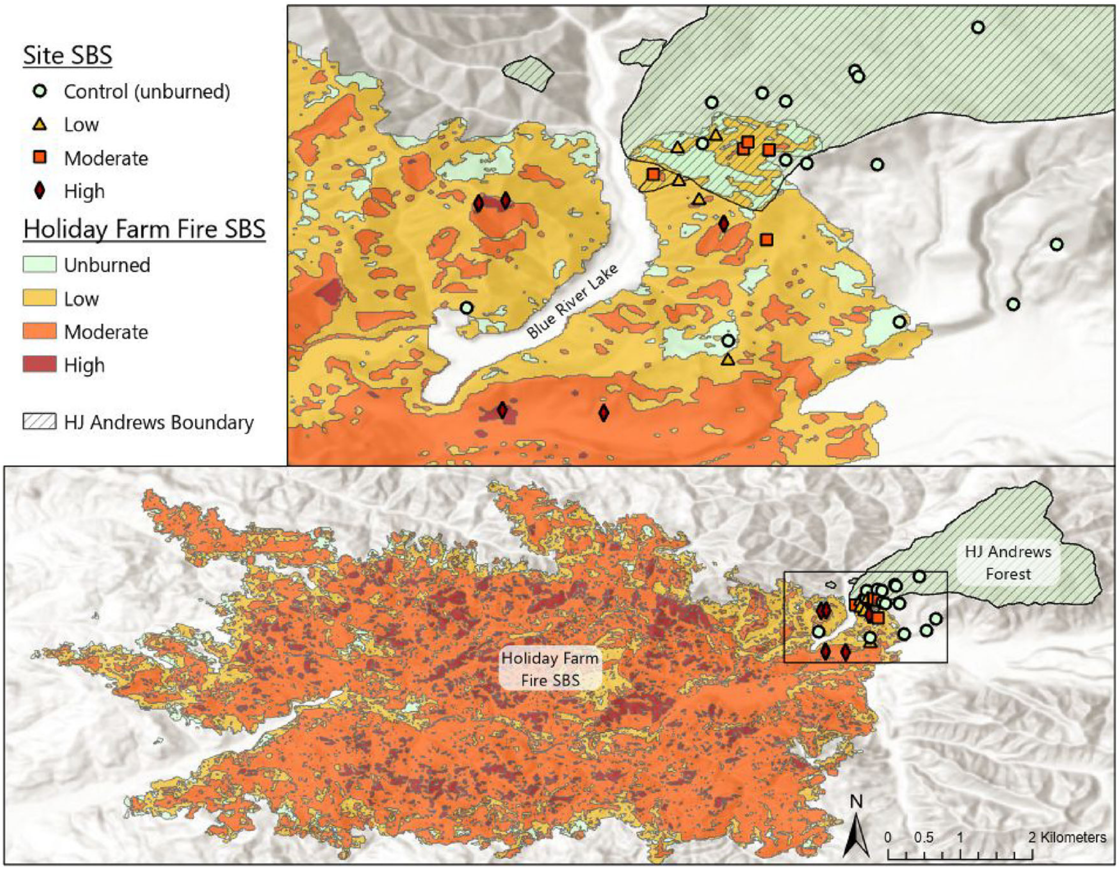

FIGURE 1 Map of soil sampling sites. Soil sampling sites were selected within and nearby the Holiday Farm Fire using soil burn severity (SBS) data mapped by Burn Area Emergency Response (BAER) teams post burn. Sites were within Willamette National Forest and H.J. Andrews Experimental Forest.

(Figure 1). Prior to sampling, we chose sites from each of the four SBS categories, stratified by a range of slope, aspect, and elevation. Sites were a minimum of 200 m from roads and distributed across an area of approximately 2575 ha. There were five burned sites from each burn severity (low, moderate, and high) and one control site at similar slope and elevation for each burn site, for a total of 15 burn sites and 15 unburned control sites. Upon arrival at each site, we verified the mapped SBS before collecting samples. If a site SBS was different than the mapped SBS, we selected a new site with the targeted SBS, elevation, and slope class. If a site mapped as "unburned to very low" was not entirely unburned, we selected a new unburned location for the site with the targeted elevation and slope class.

2.3 | Sample collection and processing

Sample collection was conducted between late May and early August 2021, immediately after access to the burn area was granted. If present, we measured the depth of the organic layer, placed a 13 cm by 14 cm rectangle on the sampling point and collected the organic material under this rectangle. Intact soil samples were collected from the 0 to10 cm and 10 to 30 cm layers of mineral soil. The 0–10 cm sample was collected by driving a 12-cm-long by 5.2-cm-diameter polyvinyl chloride pipe into the soil to a depth of 10 cm. This core was removed and capped. We then drove a second longer pipe section into the same hole to a depth of 30 cm and removed and capped it. Intact cores were stored in coolers on ice cold packs until they were returned to the lab for bulk density analysis and sample processing. At each site, we collected three subsamples for each depth for the EEA, PMC, and PMN analyses, for a total of 90 sampling locations with two depths. We also collected three additional cores for SOC and total nitrogen (TN) analyses at each site using the same protocol. This set of cores was primarily collected for a related study (Peter-Contesse et al., 2024). Polyvinyl chloride pipe sections were beveled at one end to minimize compaction and sanitized with 70% ethanol prior to sample collection.

Soil samples were processed under field moist conditions, sieved to <8 mm, and air-dried to a constant mass. Briefly, we dissected intact cores from the 0–10 cm layer into the 0–5 cm and 5–10 cm layers by cutting the polyvinyl chloride pipe crosswise with a reciprocating saw and separating the two layers with a putty knife. For the cores used for SOC and

TABLE 1 Substrates, standards, and their chemical abstracts service (CAS) numbers used in enzyme assays.

Enzyme	Group	Substrate	Substrate CAS	Standard	Standard CAS
B glucosidase (*BG*)	Hydrolytic	4-MUB-b-D-glucoside	18997-57-4	4-MUB-sodium salt	5980-33-6
Cellobiohydrolase (*CBH*)		4-MUB-b-D-cellobioside	72626-61-0	4-MUB-sodium salt	5980-33-6
N-Acetyl-glucosaminidase (*NAG*)		4-MUB-N-acetyl-b-glucosaminide	37067-30-4	4-MUB-sodium salt	5980-33-6
Leucine amino peptidase (*LAP*)		L-Leucine 7-amido-4-MC	62480-44-8	7-amino-4-MC	26093-31-2
Phenol oxidase (*PHEN*)	Oxidative	L-DOPA	59-92-7	L-DOPA	59-92-7
Peroxidase (PER)		L-DOPA	59-92-7	L-DOPA	59-92-7

Abbreviations: L-DOPA, L-3,4-dihydroxyphenylalanine; MC, methyl coumarin; MUB, methylumbelliferone.

TN analyses, we also separated intact 10–30 cm cores into 10–20 cm and 20–30 cm layers with the same technique. We then massed and composited subsamples from each site by depth layer such that there was one set of composited samples from 0- to 5-cm, 5- to 10-cm, and 10- to 30-cm depths for the EEA, PMC, and PMN analyses, and a second set from 0- to 5-cm, 5- to 10-cm, 10- to 20-cm, and 20- to 30-cm depths for the SOC and TN analyses. We composited samples to allow analysis of a greater number of sites and account for spatial heterogeneity within each site.

We measured the total organic C and N content of soil that was air-dried, sieved to <2mm, and ground to a fine powder with an Elementar Vario MACRO Cube elemental analyzer (Elementar Americas Inc.).

2.4 | Soil analyses

We measured the potential EEA of a suite of enzymes associated with C and N cycling using a previously described protocol (McGinnis et al., 2014), which was adapted from earlier EEA quantification work (German et al., 2011; Sinsabaugh et al., 2013). In brief, we suspended air-dried soil in acetate buffer, then allowed the soil slurry to incubate with fluorometrically or colorimetrically tagged enzyme substrates. We quantified the fluorescence and absorbance released by enzymes with a Biotek Synergy microplate reader (Agilent). We calculated activity in nmol activity per gram of dry soil per hour (nmol EEA $\times$ g soil^{-1} $\times$ h^{-1}). For C, we measured the EEAs of β-1,4-glucosidase (BG) and cellobiohydrolase (CBH), which are associated with cellulose decomposition. For N, we measured the EEA of β-1,4-*N*-acetyl-glucosaminidase (NAG) and leucine amino peptidase (LAP). For EEA associated with lignin decomposition, we measured the EEA of two oxidases, phenol oxidase (PHEN) and peroxidase (PER). See Table 1 for a complete list of substrates and standards used and McGinnis et al. (2014) for complete details of the method.

We assessed PMC and PMN over a 28-day aerobic incubation (Danielson et al., 2017; Kersey & Myrold, 2021). Incubation soil moisture content was optimized to maximize microbial access to resources and the quantities measured are therefore related to the *potential* quantity of mineralizable C and N, not the actual activity rates in the field (Hurisso et al., 2016; O'Kelley & Myrold, 2022). We added 7.5 g of air-dried soil to 50 mL uncapped centrifuge tubes placed upright in 1-L glass jars. Immediately before closing the jars, we added water to each sample to bring the water content to 50% of the water-filled pore space. We covered the tops of the jars with polyethylene bags to reduce water loss from the sample and simultaneously permit gas exchange to prevent anaerobic conditions from developing. We checked the mass of each incubation tube weekly and added water to maintain initial incubation water content.

We measured PMC nondestructively using a Picarro gas analyzer with multiport valve sampler (Picarro Inc.). We measured the CO_2 release rate of the samples on day 1, 7, 14, 21, and 28 of the incubation. To measure the release rate of CO_2, we replaced the polyethylene bags with jar lids fitted with rubber septa on days 0, 6, 13, 20, and 27, and measured the CO_2 content of the jars immediately after fitting the lid. We measured the CO_2 content of the jars 24 h later and replaced the lids with the polyethylene bags.

We calculated PMC as the total CO_2-C released during the incubation. For each sample, we fit a power function to the CO_2-C emission data by fitting a linear regression model to the log-transformed day and CO_2-C emissions. We integrated each power function from 0 to 28 days.

To assess the mineralizable N, we extracted and measured NH_4-N and NO_3-N in the soils before and at the end of the 28-day incubation. Extractions were performed by adding 30 mL of 2 M KCl to each 7.5 g soil sample (either a separate air-dried sample or the sample incubated for 28 days), shaking for 1 h, and filtering through #1 Whatman qualitative filter paper.

We measured NO_3-N colorimetrically using the vanadium reduction method (Hood-Nowotny et al., 2010). We measured NH_4-N colorimetrically using a protocol commonly used for ammonium analysis, scaled for microplate usage (Bower & Holm-Hansen, 1980).

2.5 | Data analysis

We conducted statistical analyses and generated figures using R version 4.2.1 and packages from the Tidyverse (R Core Team, 2021; Wickham et al., 2019). We carried out one-way analysis of variance tests to assess the effect of burn severity on SOC, TN, EEA, PMC, and PMN in each depth using the aov(), anova(), and lm() functions in R (R Core Team, 2021). For each test, the main effect was burn severity, there were 3 degrees of freedom between burn severity groups (unburned, low, moderate, and high), and there were 26 degrees of freedom within groups. We used Type II sum of squares in analysis of variance (ANOVA) tests to account for the unequal sample sizes between burn severity levels (15 observations for unburned sites, five for each level of burned site). We log-transformed data where necessary to satisfy normality assumptions. To assess whether the interdependencies between EEA and microbial resources differed after fire, we calculated Pearson correlation coefficients and *p*-values for correlations between individual EEA, PMC, and PMC in unburned sites and burned sites using the rstatix and ggcorrplot packages (Kassambara, 2022, 2023). To explore the drivers of nutrient acquisition stoichiometry, we calculated the effect size of burn severity, site, and soil characteristics on C-acquiring (BG + CBH) and N-acquiring (NAG + LAP) EEA and the C:N-aquiring ratio (C-acquiring:N-acquiring), using Spearman's rank correlation coefficients for burn severity (with control [C], low [L], moderate [M], and high [H] ranked 1, 2, 3, and 4, respectively) and Pearson correlation coefficients for all other factors. Spearman's rank correlation and Pearson correlation coefficients have the same range of values and interpretation, but Spearman's rank correlation is recommended for discrete, ordered variables (Yu & Hutson, 2024). To further identify factors driving differences between EEA, and avoid spurious conclusions about the effect of burn severity, we explored the effect of environmental factors on the relative abundances of EEA using dimension reduction analyses (Chuan et al., 2020; Gao et al., 2021). Specifically, we calculated Bray–Curtis dissimilarity matrices and conducted nonmetric multidimensional scaling (NMDS) analyses using metaMDS() using the Vegan package in R (Oksanen et al., 2024). The NMDS had two dimensions, a maximum of 100 random starts, and no auto-transformation, which is not recommended for noncommunity data (Gao et al., 2021; Oksanen et al., 2024). We then fit site and soil characteristics (environmental factors) to this ordination as vectors with the envfit() function, using even weighting and 999 permutations. We tested the significance of each factor's effect within burn classes with permutation multivariate analysis of variance (PERMANOVA) tests and adonis2() functions, with statistical significance determined at the $p < 0.05$ level, and non-euclidified Bray–Curtis distances (Oksanen et al., 2024).

3 | RESULTS

Unburned sites had a mixed canopy of Douglas-fir (*P. menziesii*), western hemlock (*T. heterophylla*), and big-leaf maple (*Acer macrophyllum*). Common understory shrubs and trees were red huckleberry (*V. parvifolium*), rhododendron (*R. macrophyllum*), salal (*Gaultheria shallon*), and vine maple (*A. circinatum*). In unburned sites, litter and organic matter at the surface ranged from a light duff layer to a 12-cm thick horizon (9–46.5 t ha^{-1}), based on samples we collected at each unburned site.

High SBS sites did not have a living canopy. In these sites, we observed some vegetation recovery of small herbs (*Galium* and *Collomia* spp.), ferns (*Polystichum* and *Pterdium* spp.), and shrubs (*Ribes* and *Mahonia* spp.), with the herbs being the most common. Most of these sites had very sparse vegetation (covering less than 10% of the surface, by ocular estimate), but one site had abundant bracken fern (*Pteridium aquilinum*) and spreading herbaceous plants (*Galium* sp. and *C. heterophylla*) covering at least 60% of the surface, by ocular estimate. Low SBS sites had intact canopies of Douglas-fir (*P. menziesii*), western hemlock (*T. heterophylla*), and big-leaf maple (*A. macrophyllum*), and had sparse understory with Oregon grape (*Mahonia aquifolium*), sword fern (*Polystichum munitum*), bracken fern, and salal as the most common species. Moderate SBS sites had a partly burned canopy and similar understory to low SBS sites. None of the low or moderate SBS sites had an O-horizon, but sparse needle litter was present in several sites for both burn classes.

For the 0- to 5-cm depth, SOC was higher in low SBS sites than in unburned ($p = 0.032$) and high SBS sites ($p = 0.033$) and did not differ between burn severities in other depths (Table 1). For the 0- to 5-cm depth, TN was higher in low SBS sites than high SBS sites ($p = 0.041$) and did not differ between any burn severities in other depths (Table 2).

In the 0–5 cm layer, potential EEA did not differ between burned and unburned soils (Figure 2), nor between burn severity levels for any of the enzymes ($p > 0.1$, one-factor ANOVA) (Figure 2).

Mass-specific potential EEA data in nmol EEA × g $soil^{-1}$ × h^{-1} are listed in Table S3. BG, associated with C, did not differ between burn severity levels in the 5- to10-cm or 10- to 30-cm depths, but the burn severity level term in the model for 10–30 cm was slightly significant ($p = 0.061$; Table 3). CBH, also associated with C, was lower in burned sites in the 5–10 cm ($p = 0.0025$) and 10–30 cm ($p < 0.0001$) layers (Table 3). Additionally, in the 5- to 10-cm depth, CBH was lower in high SBS than in unburned ($p = 0.021$), low ($p = 0.0026$), and moderate ($p = 0.0098$) burn sites, with no other differences between the other burn severity levels and unburned sites ($p > 0.1$; Table 3; Figure 2).

TABLE 2 Mean and standard error for soil organic carbon (SOC) and total nitrogen (TN) content in control (C), low (L), moderate (M), and high (H) severity burn sites in each depth.

Depth (cm)	Burn class	SOC (%) (SE)	Pair	*p*-value	TN (%) (SE)	Pair	*p*-value
0–5	C	6.21 (0.488)A	C–L	0.032	0.235 (0.021)AB	C–L	0.079
	L	9.05 (0.216)B			0.292 (0.03)B		
	M	6.13 (1.05)AB	M–L	0.058	0.23 (0.034)AB		
	H	5.88 (0.512)A	H–L	0.033	0.2 (0.006)A	H–L	0.041
5–10	C	4.56 (0.562)A			0.17 (0.021)A		
	L	4.91 (0.152)A			0.184 (0.026)A		
	M	3.83 (0.667)A			0.14 (0.024)A		
	H	5.59 (0.673)A			0.182 (0.026)A		
10–20	C	3.64 (0.461)A			0.131 (0.017)A		
	L	4.22 (0.298)A			0.162 (0.005)A		
	M	3.12 (0.521)A			0.13 (0.02)A		
	H	3.12 (0.195)A			0.118 (0.011A)		
20–30	C	2.96 (0.461)A			0.114 (0.016)A		
	L	3.14 (0.299)A			0.148 (0.024)A		
	M	2.58 (0.036)A			0.118 (0.019)A		
	H	2.22 (0.339)A			0.1 (0.006)A		

Note: Compact letter display shows comparisons between burn severity classes within each depth.

Specifically, in the 5- to 10-cm depth of high SBS sites, CBH was 26% lower than the unburned sites, 67% lower than moderate sites, and 36% lower than low sites (Figure 2). In the 10- to 30-cm depth, CBH was lower in moderate ($p = 0.046$) and high ($p = 0.034$) burn sites than in unburned sites by 17% and 18%, respectively (Figure 2; Table 3). In the 10- to 30-cm depth, CBH was higher in low SBS sites compared to unburned ($p = 0.032$), moderate ($p = 0.0004$), and high ($p = 0.0003$) burn sites by 18%, 43%, and 44%, respectively (Figure 2; Table 3).

LAP and NAG, associated with N, did not differ between burn severities in the 0- to 5-cm depth. For the 5- to 10-cm depth compared to unburned sites, LAP was lower in the moderate ($p = 0.008$) and high SBS sites ($p = 0.083$) by 51% and 37%, respectively (Figure 2; Table 3). For the 10- to 30-cm depth, LAP was lower in high SBS sites than unburned ($p = 0.0003$), low ($p = 0.0005$), and moderate ($p = 0.019$) burn sites by 46%, 50%, and 41%, respectively (Figure 2; Table 2). In the 5- to 10-cm depth, NAG was greater in low SBS sites than in high SBS sites ($p = 0.012$) by 9% and did not otherwise differ between any burn severities (Figure 2; Table 3). For the 10- to 30-cm depth, compared to control sites, NAG was lower in moderate ($p < 0.0001$) and high ($p < 0.0001$) burn sites by 30% for both (Figure 2; Table 3). Compared to low SBS sites in the same depth, NAG was lower in moderate ($p < 0.0001$) and high ($p < 0.0001$) burn sites by 26% for both (Table 2). NAG did not differ between control sites and low SBS sites in any depth ($p > 0.1$; Table 2).

Overall, greater burn severity was negatively correlated with C-acquiring EEA (BG + CBH) in the 10- to 30-cm depth (effect size = −0.54, $p = 0.002$), as did greater PMC in each depth (effect size = −0.36, −0.45, and −0.37 for the 0- to 5-cm, 5- to 10-cm, and 10- to 30-cm depths, respectively) and elevation in the 10- to 30-cm depth (effect size = −0.38). Other soil and site properties did not have a significant effect on C-acquiring EEA (Figure 3A). N-acquiring EEA (LAP + NAG) were negatively correlated with increasing burn severity in the 5- to 10-cm and 10- to 30-cm depths (effect size = −0.39, −0.80; $p = 0.038$, 8.8×10^{-8} for 5- to 10-cm and 10- to 30-cm depths, respectively). N-acquiring EEAs were also negatively correlated with PMC in the 5- to 10-cm depth (effect size = −0.53, $p = 0.0039$) and PMN in the 0- to 5-cm (effect size = −0.55, $p = 0.0017$) and 5- to 10-cm depths (effect size = −0.46, $p = 0.013$) (Figure 3A).

EEA stoichiometry was affected by burn severity in the 10- to 30-cm depth and nutrient availability in the 0- to 5-cm depth. Specifically, the C:N-acquiring EEA ratio (BG + CBH:LAP + NAG) was 25% greater in high SBS sites than unburned sites in the 10- to 30-cm depth ($p = 0.021$; Table 3), but did not differ between other SBS levels (Table 3). Burn severity had an effect size of 0.51 on the C:N-acquiring ratio ($p = 0.0037$) for the 10- to 30-cm depth and was not significant ($p > 0.05$) for the 0- to 5-cm or 5- to 10-cm depths (Figure 3A), indicating relatively greater C-acquiring EEA activity with greater burn severity. Besides burn severity, the only significant effect on EEA stoichiometry was a positive correlation between the C:N-aquiring ratio and PMN in the 0- to 5-cm depth (effect size = 0.51, $p = 0.0041$), with all other site and soil property effect sizes insignificant (Figure 3A).

The NMDS ordination of EEAs was selected after 66 tries, and had a stress of 0.097. In the visualized ordination, the

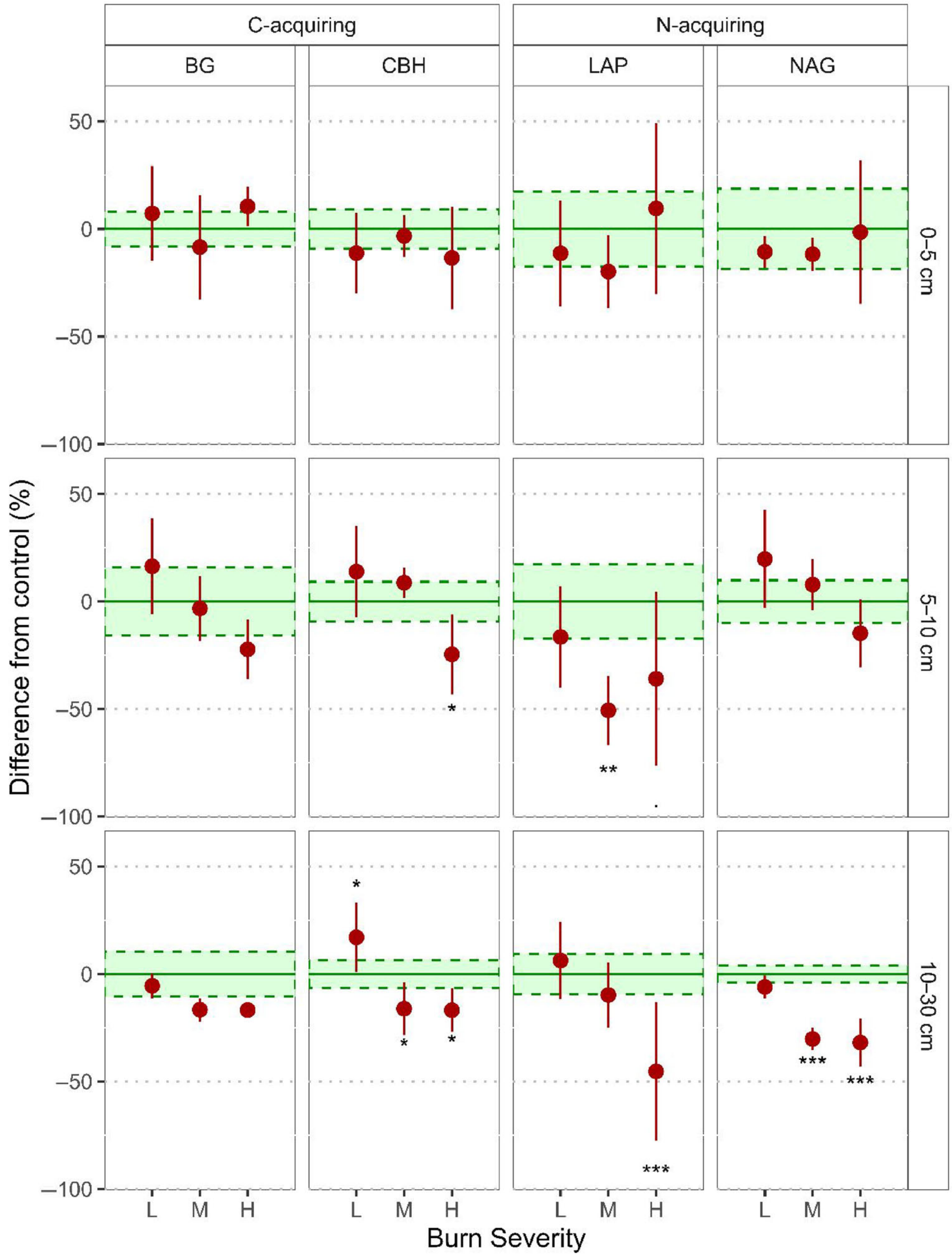

FIGURE 2 Extracellular enzyme activities (EEAs) for β-1,4-glucosidase (BG), cellobiohydrolase (CBH), β-1,4-*N*-acetyl-glucosaminidase (NAG), and leucine amino peptidase (LAP), associated with C (BG and CBH) and N (NAG and LAP) acquisition. Red points and lines show the mean (±95% confidence intervals) EEA in soil from low (L), moderate (M), and high (H) burn severity sites at each depth, scaled as the % difference from the mean EEA of the unburned sites for each enzyme and depth. Green lines denote the unburned control mean (solid) and 95% confidence interval (dashed) for each depth. *$p < 0.05$; **$p < 0.01$; ***$p < 0.0001$.

greatest separation can be observed between unburned and high SBS sites in the 10- to 30-cm depth, and poor separation among low SBS, moderate SBS, and the 0- to 5-cm depths. PERMANOVA tests indicated a significant effect of burn severity on EEA composition ($p = 0.001$). Site and soil properties fit to the ordination as vectors showed no clear association with the visualized SBS or depth categories (Figure 3B). PERMANOVA tests identified PMC, PMN, and elevation as having a significant effect on EEA composition after controlling for burn severity ($p = 0.002$, 0.002, and 0.032, respectively), but not depth, aspect, slope, or soil pH (Figure 3B).

PMC, calculated as the total mineralized C released during the 28-day incubation, did not differ between burn severity levels ($p = 0.3$; Figure 4A), nor did mineralized C during the first 24 h of the incubation ($p = 0.6$, ANOVA, data not shown). There were no significant differences in mineralized C between burn severity levels after 1, 2, 3, and 4 weeks

TABLE 3 p-values and F-values of the burn class coefficient in one-way analysis of variance (ANOVA) tests for each depth and enzyme, nonsignificant comparisons ($p > 0.1$) are not shown.

EEA	Depth (cm)	*p* (*F*-value)	Pair	*p*-value
BG	10–30	0.0609 (2.78)$^{\#}$		
CBH	5–10	0.00248 (6.23)**		
			C > H	0.0218*
			L > C	0.0026**
			M > H	0.00984**
	10–30	0.000106 (10.5)**		
			L > C	0.0321*
			C > M	0.046*
			C > H	0.0349*
			L > M	0.000436**
			L > H	0.000335**
NAG	5–10	0.0173 (4.05)*		
			L > H	0.0123*
	10–30	3.03×10^{-10} (43.2)***		
			C > M	2.42×10^{-8}***
			C > H	8.42×10^{-9}***
			L > M	3.54×10^{-5}***
			L > H	1.31×10^{-5}***
LAP	5–10	0.00659 (5.1)**		
			C > M	0.00798**
			C > H	0.0826$^{\#}$
	10–30	0.000199 (9.55)**		
			C > H	0.000205**
			L > H	0.00051**
			M > H	0.0187*
PHEN	10–30	0.0982 (2.32)$^{\#}$		
			M > C	0.0965$^{\#}$
C:N-acquiring	10–30	0.0227 (3.77)*		
			H > C	0.0208*

Note: p-values for post hoc pairwise comparisons (Tukey HSD) of severity levels are shown, omitting nonsignificant comparisons ($p > 0.1$).

Abbreviations: BG, β-1,4-glucosidase; C, control; CBH, cellobiohydrolase; H, high; L, low; LAP, leucine amino peptidase; M, moderate; NAG, β-1,4-*N*-acetyl-glucosaminidase; PHEN, phenol oxidase.

$^{\#}p < 0.1$; $^{*}p < 0.05$; $^{**}p < 0.01$; $^{***}p < 0.0001$.

during the 28-day incubation ($p > 0.1$, data not shown). PMC decreased with depth ($p < 0.0001$) among all sites (ANOVA; Figure 4A). PMC was greater in the 0- to 5-cm depth than the 5- to 10-cm ($p = 0.002$) and 10- to 30-cm ($p < 0.0001$) depths, and greater in the 5- to 10-cm depth than the 10- to 30-cm depth at the slightly significant level ($p = 0.07$).

PMN was greater in the soil of low ($p = 0.014$) and high ($p = 0.044$) SBS sites compared to unburned sites in the 0- to 5-cm depth (Figure 4B). Low SBS sites had a mean PMN of 7.32 mg kg^{-1} compared to 1.62 mg kg^{-1} for unburned sites. PMN did not significantly differ between depths in a two-factor ANOVA test ($p > 0.1$). However, the difference for high SBS appears to be caused by greater PMN in a single high SBS site, which had much greater evolved NO$_3$ than other high SBS samples in all three depths. For example, NO$_3$-N was 63.6 mg kg^{-1} soil in this site compared to 0.13–17.1 mg kg^{-1} for the other high SBS sites in the 0- to 5-cm depth. We compared results of analyses with and without this site, and included the site in the results presented here. If this site was excluded from analyses, PMN did not differ between high SBS and unburned sites, but the significance level of correlations between quantitative properties was not altered.

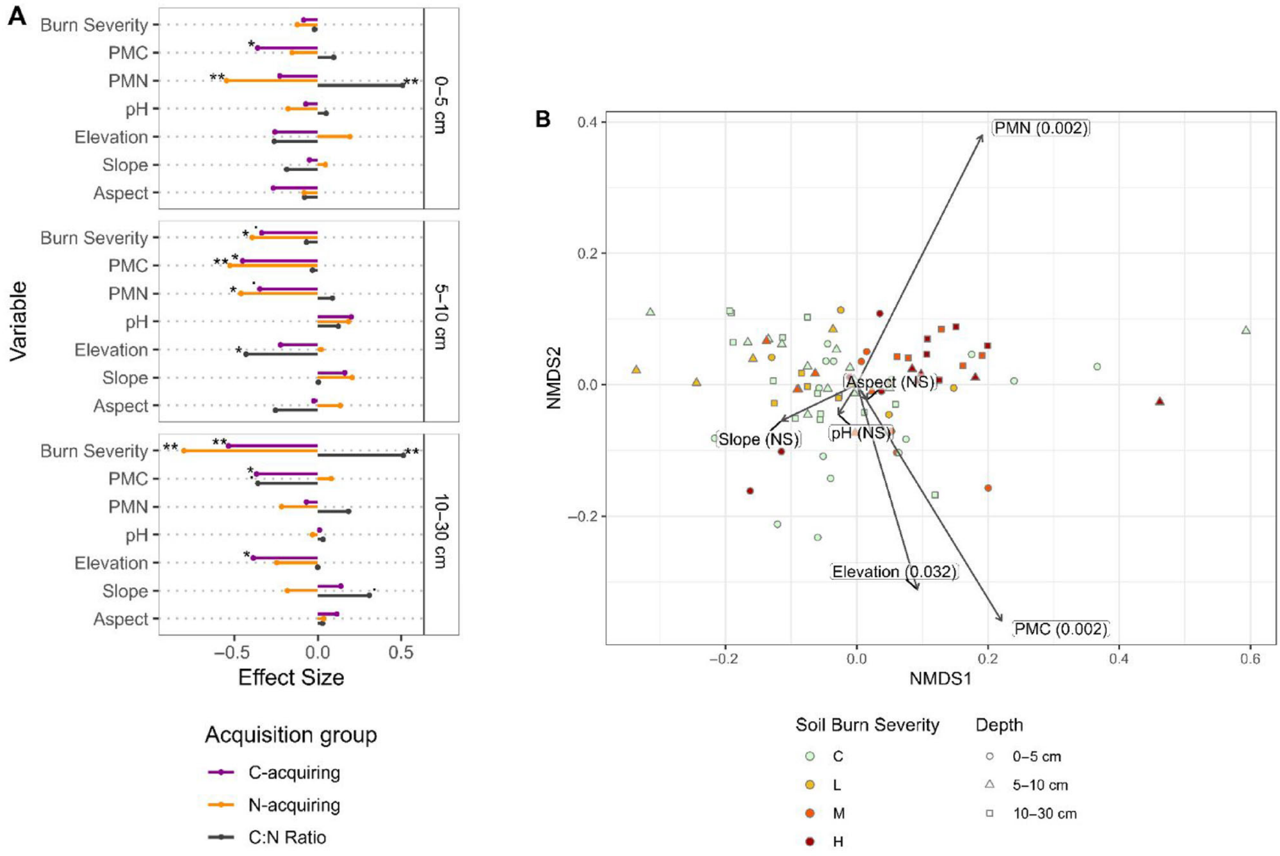

FIGURE 3 Impact of candidate predictor variables on soil extracellular enzyme activity (EEA) and stoichiometry. (A) Candidate predictor variables' effect size on C-acquiring and N-acquiring EEA. Effect size calculated as Spearman's rank (burn severity) and Pearson coefficients (all others) (**$p < 0.01$; *$p < 0.05$; ·$p < 0.1$). (B) Nonmetric multidimensional scaling (NMDS) ordination of hydrolytic EEA in soils by burn severity and depth. Arrows show vectors for each candidate predictor variables fitted to the ordination. p-values from permutation multivariate analysis of variance (PERMANOVA) tests are displayed next to each vector variable if $p < 0.05$ ("NS" shown otherwise). For burn severity, $p = 0.001$. C, control; H, high; L, low; M, moderate; PMC, potentially mineralizable carbon; PMN, potentially mineralizable nitrogen.

Correlation matrixes containing quantitative properties (EEA, PMC, and PMN) generated for control (Figure 5A) and burned sites (Figure 5B) showed that hydrolytic EEAs were often negatively correlated with PMC and PMN quantities in unburned control sites only.

For example, NAG was negatively correlated with PMN (Figure 5A; $R = -0.44$, $p < 0.0001$). In burned sites, hydrolytic EEAs were not significantly correlated with PMC or PMN ($p > 0.05$), while correlations between hydrolytic EEAs were largely significant (Figure 5B). Oxidases, by contrast, tended to have stronger correlations to PMC and PMN in the burned sites than the unburned control sites. PHEN was negatively correlated with microbial resource indicators in burned sites, but correlations were not significant for the unburned controls. For example, PHEN was negatively correlated with PMC in the burned sites only (Figure 5B; $R = -0.43$, $p = 0.0041$). PER, on the other hand, was positively correlated with PMC in both the unburned control ($R = 0.33$, $p = 0.0016$) and the burned sites ($R = 0.63$, $p < 0.0001$), but the correlation was stronger in the burned sites (Figure 5).

4 | DISCUSSION

We hypothesized that wildfire-induced increases in coarse woody debris and dead roots in tandem with decreases in leaf litter and root exudates would cause decreases in EEA for hydrolytic C and N scavenging, and increases for oxidative enzymes. As we expected, fire decreased hydrolytic C and N EEA, but only for moderate and high SBS sites and never for the 0- to 5-cm soil depth. Contrary to our hypothesis, oxidases generally did not differ between SBS levels. We expected that these postfire shifts in resources along with hypothesized shifts in microbial resource demand (i.e., EEA changes), would weaken the coupling between EEA and mineralizable nutrients. In agreement with this hypothesis, we observed that in burned sites PMN was decoupled from N-associated enzymes and PMC was decoupled from

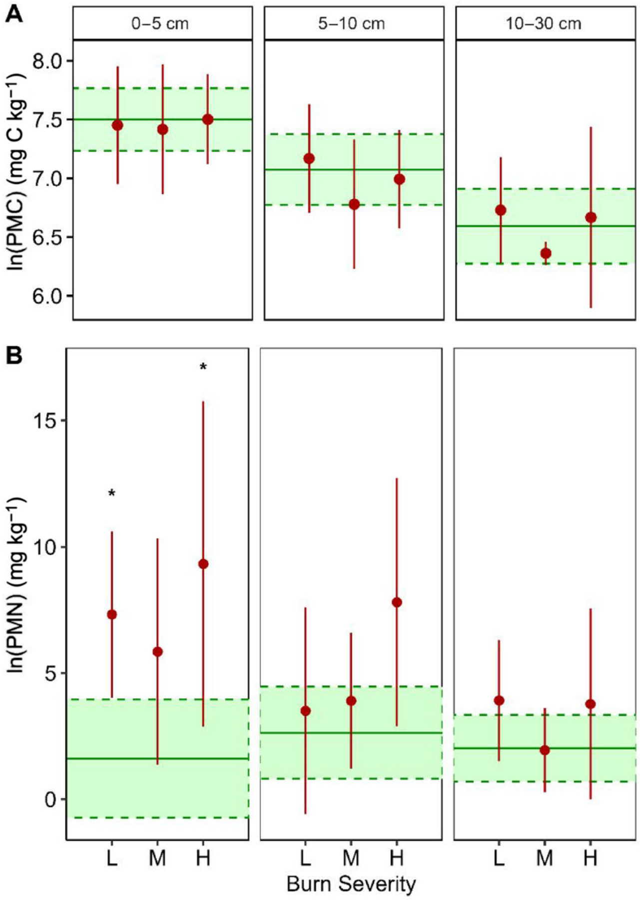

FIGURE 4 Log of potentially mineralizable (A) carbon (PMC) and (B) nitrogen (PMN) in burned and unburned soils based on 28-day aerobic incubation. Red points show the mean mineralized nutrient (±95% confidence intervals) in soil from low (L), moderate (M), and high (H) burn severity sites in three depths. Green lines denote the unburned control mean (solid) and 95% confidence interval (dashed) for each depth. Asterisks denote significant differences ($p < 0.05$) between burn severity levels and unburned sites within depths.

C-associated enzymes. Further, increasing SBS level shifted the ecoenzymatic stoichiometry toward greater C-acquiring EEA in the 10- to 30-cm depth. However, we did not observe co-occurring differences in PMC between burned and unburned sites, and only small differences in PMN between burned and unburned sites. PMC and PMN were both highly variable among samples from the same depth and SBS level, indicating that a higher sampling density may be required to capture differences between SBS levels.

4.1 | Lack of PMC response indicates resiliency to fire

A long-held assumption in soil ecology is that fire is expected to drive losses of C from the soil through the combustion of the organic layer during fire and reduced inputs from vegetation in the decade following fire (Walker et al., 2019). Our results contribute to a growing body of evidence that challenge this assumption (Pellegrini et al., 2022) and show instead that compensatory decreases in EEA may slow mineralization of C resources, even in high-severity fires. PMC, often used as an early indicator of changes to SOC (Lehmann et al., 2020), was consistent among burn severity treatments, demonstrating surprising resilience to a substantial disturbance (Figure 4A). The similarity between PMC in control and low SBS sites is in line with the results of Fultz et al. (2016), who showed in situ soil respiration returning to preburn levels within 24 h of a low-intensity prescribed burn. Given reductions in the quantity of leaf litter and root exudates after moderate and high severity fire, we expected that PMC would be lower. In subsurface horizons, EEAs were suppressed after fire, which could explain PMC remaining stable despite changes in organic matter input. C decomposition via the influx of dead roots could also compensate for the loss of root exudates in the subsurface and contribute to the lack of PMC response. In the 0–5 cm layer, however, EEA was consistent among burn SBS levels, a surprising result given that combustion of organic matter should be essentially limited to the surface (Figure 2). Soil collected simultaneously for a parallel study had more particulate organic C with increasing burn severity, without an effect of burn severity on bulk soil C (Peter-Contesse et al., 2024), consistent with a shift in the composition, but not quantity, of SOC. Although combustion of organic matter, particularly in moderate- and high-severity fires cause direct CO_2 release from the soil, pyrogenic C and coarse woody debris inputs may have compensated for this loss (Pellegrini et al., 2022).

Ecosystem coupling has previously been proposed as a unifying theory for describing consequences of disturbance, and detecting early changes to ecosystems under global change (Ochoa-Hueso et al., 2021). After fire, potential EEA became decoupled from the quantity of microbial resources (PMC and PMN). Decoupling of EEA from microbial resources in burn sites compared to control was a pattern across enzyme substrates (Figure 5), indicating that fire disrupts a regulated relationship between microbes and their resources. This result is in line with biogeochemical decoupling that other authors have observed postfire (Butler et al., 2018; Qin et al., 2022). However, the previous work was focused on stoichiometric ratios among elements, rather than the abiotic–biotic coupling we examined (see Ochoa-Hueso et al., 2021).

Identification of the mechanism responsible for this decoupling remains an open line of inquiry, as there are several potential explanations. One is that abiotic factors affected by fire, such as soil temperature and soil moisture, influenced the soil enzymatic production (Caldwell, 2005). These are difficult to disentangle from co-occurring differences in organic matter inputs. There was no response of EEA to several other

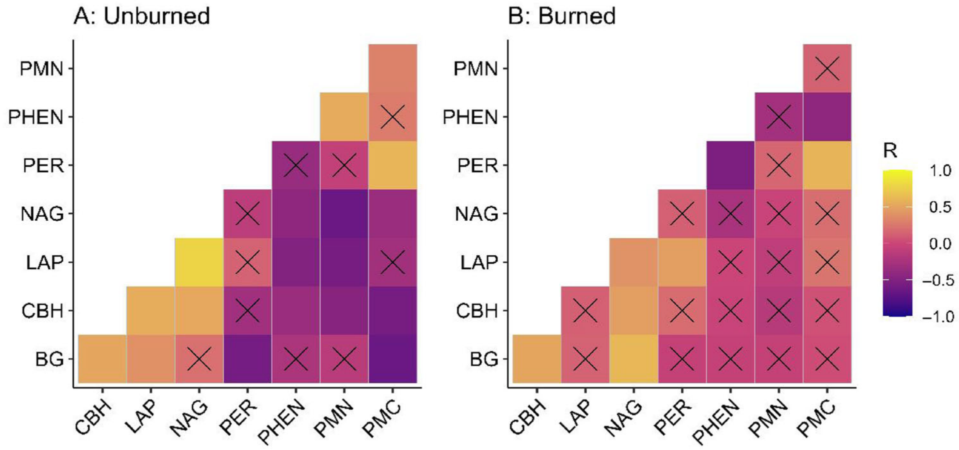

FIGURE 5 Correlation matrix for soil properties in (A) unburned control site soil and (B) burned site soil. Statistically nonsignificant correlations ($p < 0.05$) are marked with an "X." Properties are the extracellular enzyme activities (EEAs) for B glucosidase (BG), cellobiohydrolase (CBH), β-1,4-*N*-acetyl-glucosaminidase (NAG), leucine amino peptidase (LAP), peroxidase (PER), and phenol oxidase (PHEN). Also shown are potentially mineralizable nitrogen (PMN) and potentially mineralizable carbon (PMC).

environmental factors (slope, elevation, aspect, and soil pH), except for a negative elevation effect in the 10- to 30-cm depth (Figure 3), but there may be factors not included in this study with a greater effect. The correlation between EEA and soil nutrients is multifaceted due to intermediate processes between the secretion of enzymes and subsequent consumption of decomposition byproducts by the microorganisms responsible for their production (Allison, 2005; Nunan et al., 2020). Factors such as the degree of conformity between assay rates and corresponding field rates, protection of enzymes and organic matter on mineral surfaces, as well as the proximity of the enzyme to the microbe responsible for its production, all contribute to the complexity of this relationship (Allison & Jastrow, 2006). Fire is known to increase soil erosion and hydrophobicity (Girona-García et al., 2021), a physical disturbance that may affect extracellular enzymes that are stabilized on mineral surfaces (Allison & Jastrow, 2006). Postfire hillslope stabilization techniques were recently shown to improve the recovery of EEA rates, indicating erosion plays a role in microbial activity rates postfire (Lucas-Borja et al., 2022); however, we did not find an effect of slope on EEA (Figure 3).

Microbial C acquisition could change without PMC changing if the carbon use efficiency (CUE) also changed. For example, if microbes switched to decomposing a lower quality substrate, and CUE decreased (Cotrufo et al., 2013) along with the microbial population, overall CO_2 generation could remain constant. Although we did not measure microbial biomass, previous work has generally found that microbial biomass decreased in the short term, with variable recovery rates within the following year (Barreiro & Díaz-Raviña, 2021). Another possibility is that microbial decomposition activity was more driven by demand (i.e., nutrient scarcity relative to the microbial population) than by the supply of C. PMC is an indicator of both the availability of SOC and the functional capacity of the microbial community to mineralize it (Fierer et al., 2021). In this case, the demand and ability of the microbial community to mineralize C appears to be a more important driver of PMC than the quantity or composition of the resource.

4.2 | Potentially mineralizable nitrogen increased in low SBS sites

Changes to N availability have long been observed following fire (Fultz et al., 2016; Pellegrini et al., 2020; Raison, 1979). Fire releases N previously held in biomass to the soil, in part through volatilization. This can lead to large N losses (Homann et al., 2011), however, some of the released N remains in the soil, making it rapidly available for microbial mineralization while simultaneously reducing plant uptake (Dove, Safford et al., 2020). In particular, a pulse of ammonia is commonly observed after fire, which can support nitrification rates and aid in supplying N to heterotrophic microbes (Fultz et al., 2016).

Long-term impacts of fire on microbial N transformations are less understood. A meta-analysis of fire effects in forest ecosystems found that PMN was lower in burned soils more than three months after a fire, following an initial spike, but the magnitude of this change depended on forest type, climate, and fire type (Wang et al., 2012). Their result is in contrast to our results, where PMN was higher in the 0- to 5-cm depth of low SBS sites compared to unburned sites (Figure 4B). Wang et al. did not differentiate results between burn severity, a factor which may explain the discrepancies between our results. Previous work has found that in the intermediate term, burn severity continues to drive differences in microbial activity, soil nutrients, and microbial communities after fire (Adkins et al., 2020; Fernández-García et al., 2019). Given this prior literature, the decreased EEA observed may be an early indicator that PMN will similarly decrease as recovery from the fire proceeds.

PMN was greater in the 0- to 5-cm depth of high SBS sites compared to unburned sites, but this was likely an artifact of a single high SBS site with greater evolved NO_3-N than the other four, so we are hesitant to place undue emphasis on this finding. This site exhibited rapid regrowth of herbaceous vegetation that may have stimulated the microbial community and lead to increased N mineralization. Excluding the site from analyses did not alter our overall interpretation, and it is included in the results of analyses presented here.

A positive relationship is often observed between PMN and N scavenging EEA (see, for instance, Danielson et al., 2017; McGinnis et al., 2014). Surprisingly, we instead observed a negative, significant, relationship between PMN and LAP in unburned control sites (Figure 5; $R^2 = 0.25$, $p < 0.01$) and a negative effect of PMN on N-acquiring EEA across sites (Figure 3A). This implies that N scavenging enzymes are induced in our system only when easily mineralizable N is unavailable, consistent with results from recent nutrient enrichment experiments (Rosinger et al., 2019).

4.2.1 | Fire effect on EEA was depth dependent

Previous studies on EEA postfire have shown conflicting results. Some studies report stimulation of enzymatic activity (Rietl & Jackson, 2012), while others found decreased activity, particularly for hydrolytic enzymes (Barreiro & Díaz-Raviña, 2021). It is unusual for studies to separate moderate severity burns, sample from control sites so close to burn sites, or sample below the surface soils. Our results support the idea that the impact of fire depends on both depth and burn severity.

According to conventional soil ecology theory, because heat transfer from fire decreases exponentially in the first 5 cm of soil (Certini, 2005), the impact of fire on soil microbes should be limited to this thin depth layer. Few fire studies, therefore, measure EEA below the first few centimeters (Barreiro & Díaz-Raviña, 2021; Dove, Arogyaswamy et al., 2020). However, an inventory of soil microbial properties showed that more than half of EEAs in the first meter of depth are found below 20 cm (Dove, Arogyaswamy et al., 2020); so, despite the greater concentration of EEA in surface soils, subsurface soils should not be ignored. In our study, we found fire-impacted EEA only below 5 cm, with the largest impacts between 10 and 30 cm (Table 2). This shows that the effect of fire is not limited to the soil surface or to direct heat experienced during a fire.

Although there is a paucity of literature reporting subsurface enzymatic responses to fire, there are a few studies that illustrate the importance of depth resolved sampling. For example, Fairbanks et al. (2020) found, in contrast to our study, hydrolytic enzymes increased after fire in the subsurface but decreased in the surface. Both studies were conducted in western-montane coniferous forests with similar fire severity levels, but Fairbanks and others collected samples almost immediately (18 days) after fire. We suggest that their study better captures the initial microbial response to fire, whereas our study with samples taken a year after fire represents the response after the microbial community has recovered somewhat from the earlier mortality event.

One reason decomposition may slow after fire is alteration of the balance of the soil priming effect and C addition that live vegetation provides. Inputs of root exudates are expected to lead to greater accumulation of MAOM because they are more efficiently processed by the microbial community (Cotrufo et al., 2013). MAOM is a slower cycling pool of organic matter believed to contribute strongly to long-term SOC accumulation (Cotrufo et al., 2013). However, exudates can also stimulate mineralization of native SOC through the rhizosphere priming effect (Kuzyakov, 2002; Zhu et al., 2014). Our research addresses the extent to which root exudate contributions to SOC result in net accumulation or mineralization and how the system responds to loss of live roots and root exudates (and simultaneous influx of dead roots) after stand-replacing fires.

We hypothesize that loss of priming from root exudates due to tree mortality in moderate and high SBS sites drove the loss of potential EEAs. Priming has most commonly been investigated by enriching soil with simple sugars to induce priming, and comparing microbial activity to baseline conditions lacking these additions (Brant et al., 2006). However, for rhizosphere microbes, priming via root exudates is the baseline. In the absence of this priming, a reduction of EEA around the roots could result, although the recently dead roots would provide a compensatory source of organic matter.

Another possibility is that inputs of pyrogenic material could compensate for reduced fresh leaf litter and root exudates and decrease the need for microbial investment in EEA. However, if this were the case, we would expect greater EEA changes in surface soil. However, EEA reductions were most pronounced in the 10- to 30-cm depth and for N-acquiring EEA (Figures 2 and 3). In high SBS burned soils, for example, NAG was 30% lower than the unburned sites in the 10- to 30-cm depth, and LAP was 52% lower in moderately burned sites compared to control for the 5- to 10-cm depth. This result is consistent with loss of rhizosphere priming driving EEA differences in the sub-soil, as the priming effect is often linked to N mining activity (Chen et al., 2014; Zhu et al., 2014).

We hypothesized that in burned soils, C acquisition would shift from enzymes associated with cellulose decomposition to those associated with lignin decomposition. Our results were overall not consistent with these results. PHEN activity was higher in moderate SBS sites compared to unburned sites in the 10- to 30-cm depth at the slightly significant level (Table 2). However, these differences were modest and not found in other depths or other SBS comparisons. In the parallel study characterizing postfire soil carbon composition at the same sites, Peter-Contesse et al. (2024) found coarse woody debris and pyrogenic C are controlled by the historic wildfire frequency, not the SBS of this most recent fire. In turn, the impact of the legacy of wildfire on coarse woody debris and pyrogenic C may control oxidase EEA, which is strongly associated with decomposition of both C sources. Although we did not assess the microbial community composition, the lack of oxidase response could also be explained by classic postfire shifts in the relative abundance of fungi and bacteria in combination with shifts in organic matter composition. Oxidases are generally associated with fungi, which have higher mortality during fire (Barreiro & Díaz-Raviña, 2021). Shifts in fungal abundance (decreasing oxidases) could have compensated for increases in lignin-rich material associated with oxidases.

4.3 | Sampling timing and establishment of future sampling dates

We sampled soil approximately 1 year after fire. Sampling on this timeline captured a relatively short-term burn response, characterizing differences at an early point in the ecosystem recovery trajectory. At this point, vegetation that either survived the initial burn or emerged during the first year of recovery had a spring season to produce root exudates that contribute to rhizosphere dynamics. Legacy effects on the soil microbiome should be characterized at the same sites going forward.

In the nearby DIRT study, where organic matter sources were manipulated to assess the effects of plant litter on organic matter accumulation in forest soils (Lajtha et al., 2018), root exclusion allowed accumulation of MAOM via loss of priming activity over decadal scales and an influx of dead roots to the soil matrix (Pierson et al., 2021). In line with these results, we observed decreased EEA in the subsurface of high SBS sites, where the comparable tree mortality observed in high SBS sites is likely to have ongoing impacts on the ecosystem because of reduced inputs of exudates and an influx of decomposing dead roots. The parallel study of postfire SOC composition found no change in MAOM with burn severity, but changes to this pool tend to be slower (Peter-Contesse et al., 2024). With respect to the shift in the composition of organic matter inputs, the Holiday Farm burn functions as a larger natural analog to the DIRT experiment at HJA, with additional inputs of pyrogenic C. However, vegetation recovery over the coming years will differentiate our postfire sites from the sustained removal treatments conducted in the DIRT experiments. We recommend resampling this burn at regular intervals to characterize microbial response to burns during vegetation recovery.

While EEA recovery following fire has not been well studied, vegetation recovery has (Halofsky et al., 2020; Nolan et al., 2021). Because our results suggest that microbial investment in EEA decreased in response to vegetation mortality, vegetation recovery research may provide insight into EEA recovery after fire. Regeneration of conifer seedlings occurs on variable timelines, but peak regeneration rates have been reported between four and six years after fire in Oregon (Hibbs & Jacobs, 2011). Plants begin recruiting microbes to their rhizosphere very early (Sasse et al., 2018), so it is plausible that priming responses, including enzyme production, would occur on a similar timeline. Burns with high vegetation mortality rates decrease canopy cover and increase light to the forest floor, resulting in early successional species establishing before conifers (Halofsky et al., 2020). Root secretions from these species can contribute to stimulating microbial communities prior to conifer regeneration, but the relative magnitude of rhizosphere priming in these stages of ecosystem recovery is unknown. Comparing any locations that reburn in later years to non-reburned sites is another strategy to dissect the influence of vegetation regrowth and living roots in general on post-burn soil microbial activity.

5 | CONCLUSIONS

Our finding that changes in EEA were limited to the subsurface contradicts conventional views of the effect of wildfire on the soil environment, which tend to be constrained to only the very surface of soils exposed to direct heating during fire. In this case, fire likely impacted microbial activity primarily through the loss of live roots rather than combustion of the organic layer and combustion of pyrogenic C and coarse woody debris at the surface. These components of the system may have a delayed effect on the soil microbial community, but in the first year after fire, the visible changes to organic matter inputs after fire did not appear to impact soil microbial activity.

The reduced enzymatic activity without reduction in PMC is corroborated by recent research showing that EEA is independent from nutrient availability (Rosinger et al., 2019). The authors conducted a nutrient loading incubation experiment with combinations of C, N, and P and found that microbial growth and EEA responded differently to nutrient loading treatment, demonstrating that EEAs are not equivalent to nutrient requirements. Care should therefore be taken to interpret these EEA rates as microbial investment in nutrient acquisition rather than as nutrient limitation itself.

If subsurface EEA reductions persist after fire, then SOC is more likely to accumulate, mitigating reduced inputs of C from litter and root secretions. Our observation of similar PMC across burn severities, despite differences in EEAs, suggests that fire may not be as destabilizing for SOC stores as expected, at least in this Pacific Northwest coniferous ecosystem. This has important implications for global change models that include anticipated soil C losses after fire. As previous authors have pointed out in other ecosystems (Holden et al., 2015; Pellegrini et al., 2022; Taş et al., 2014), predictions that fire will result in heightened decomposition of SOC overlook aspects of the system that could function as balancing, rather than exacerbating, feedback loops.

AUTHOR CONTRIBUTIONS

Regina O'Kelley: Conceptualization; data curation; formal analysis; investigation; methodology; resources; supervision; visualization; writing—original draft; writing—review and editing. **Abigail Evered**: Data curation; investigation; methodology; visualization; writing—original draft; writing—review and editing. **Hayley Peter-Contesse**: Conceptualization; data curation; funding acquisition; investigation; methodology; supervision; visualization; writing—review and editing. **Jennifer Moore**: Investigation; methodology; resources; supervision; validation; writing—review and editing. **Kate Lajtha**: Conceptualization; funding acquisition; investigation; methodology; resources; supervision; writing—original draft; writing—review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

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SUPPORTING INFORMATION

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

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