Depth and topographic controls on microbial activity in a recently burned sub-alpine catchment

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ABSTRACT

Microbial communities influence and are influenced by environmental conditions that, together with the extracellular enzymes produced by soil microorganisms, control the rate of decomposition of organic matter in soil. Here, we aim to characterize the interaction of landscape position and depth on potential enzyme activities in a recently burned forest catchment. To accomplish this, we first characterized the heterogeneity of environmental properties, including topography, depth, and soil geochemistry, in order to delineate landscape position and depth controls on potential enzyme activities. To account for the impact of recent wildfire on extracellular enzyme activities (EEA), we delineated surface (0–5 cm) and deeper (5–40 cm) soils to understand how fire (which disproportionally impacts the surface) alters the relationship between EEA and the environmental covariates. We excavated 22 soil pits to 40 cm and measured potential activities of seven hydrolytic enzymes involved in carbon (C) (α-glucosidase [AG], β-1,4-glucosidase [BG], β-D-cellobiohydrolase, [CB] and β-xylosidase [XYL]), nitrogen (N) (β-1,4,N-acetylglucosaminidase, [NAG] and leucine-aminopeptidase [LAP]) and phosphorus (P) acquisition (acid phosphatase [PHOS]) across a subalpine catchment. Fire resulted in decreased BG, CB and NAG activity in surface (0–2 cm) soils. Fire altered N and P acquisition strategies with depth suggesting potential nutrient scavenging or increased internal microbial cycling with depth as a response to fire. Digital soil mapping demonstrated consistently higher potential enzyme activities in the convergent zones of the catchment, which were primarily correlated with higher soil moisture, clay content, and vegetative cover as quantified through normalized difference vegetation index (NDVI). Integrating remotely sensed measures of topography with the identification of drivers of microbial C, N, and P cycling can help inform how millimeter-scale processes influence and feedback to patterns at a catchment scale.

1. Introduction

Recent work has highlighted the need to integrate microbial ecology into ecosystem-scale models, such that non-linear variation in microbe-mediated decomposition rates (e.g., across temperature or moisture gradients) might be used to improve model predictions (Allison et al., 2010; Li et al., 2014; Martiny et al., 2017; Shao et al., 2013; Wieder et al., 2013). However, this integration has been hampered by the challenges of scaling (Snajdr et al., 2008) and adequate representation of the complexity of microbial processes (Schimel, 2016). Extracellular enzyme activities (EEA) of soil microorganisms can act as important proxies for nutrient limitation and turnover in soil and provide insight into the biochemical requirements of microbes in terrestrial ecosystems (Burns et al., 2013). Across a landscape, areas with greater water and substrate availability correlate with increased biogeochemical cycling (e.g., Bernhardt et al., 2017; Lohse et al., 2009; McClain et al., 2003). Thus, understanding the environmental controls on microbial activities and identifying relevant proxies that are widely available through...
open-source remotely-sensed data and standard soil measurements are important steps toward accurately incorporating microbial carbon and nitrogen dynamics into ecosystem-scale terrestrial biogeochemical cycling models. Recent work has examined the integration of topographically-derived variables to understand how disturbance alters drivers of enzyme activity across a landscape (Lybrand et al., 2018). In this study, we measured EEA in a high-elevation mixed conifer forest in the Southwestern U.S. to explore the interactive controls of topography, vegetation, and soil chemical and physical factors on microbial dynamics in a recently burned landscape.

Topographic variation in soil morphology and geochemistry exerts first-order control on hydrologic processes and associated biogeochemical and ecological dynamics across spatial and temporal scales. Topography regulates vertical and lateral redistributions of water and solutes leading to variation in vegetation type and cover, rates of biogeochemical processing (reviewed in McClain et al., 2003; Bernhardt et al., 2017), soil morphology (Lybrand and Rasmussen, 2015), and soil physical and chemical properties (Hollera et al., 2015). In water-limited systems, redistribution of water and nutrients from planar landscape positions to convergent landscape positions corresponds with observed intensified rates of microbial C and N cycling (Austin et al., 2004; Dochterl et al., 2016; Lobhe et al., 2013). Areas of increased water and nutrient availability have been recognized as ‘hot spots’ of intensified biogeochemical cycling relative to the surrounding landscape where landscape position controls size, duration, and timing of hot spot activity (Bergstrom et al., 1998; Bernhardt et al., 2017; Hook and Burke, 2000; McClain et al., 2003; Ohraii et al., 1999). More recently, the discussion of ‘ecosystem control points’ has expanded on the hot-spot concept to identify areas of distinct and intensified biogeochemical cycling relative to the surrounding matrix (Bernhardt et al., 2017).

Previous work suggests that topography exerts strong spatial and temporal controls on landscape-scale hot spots (McClain et al., 2003; Lobhe et al., 2009; Lobhe and Dietrich, 2005), but may be less important than geochemical controls in disturbed ecosystems (Lybrand et al., 2018). Scaling microbial activities and identifying drivers of ecosystem controls is important to understanding where correlations between landscape position and microbial activities are sustained, or break down, in response to disturbances such as wildfires.

Changes in soil organic matter with depth through the soil profile dictate the abundance and diversity of microbes and their activities and are also influenced by topography. In forest soils, strong vertical differentiation of microbial community composition and function is evident from the greater phylogenetic richness and microbial biomass in surface soil horizons compared to soil horizons at 30 cm depth (Eilers et al., 2012; Fiermer et al., 2003; Huang et al., 2014; Stone et al., 2014, Brewer et al., 2019). Extracellular enzyme activities are sensitive to changes in nutrient availability and composition, temperature, moisture, pH, redox status, texture and mineral composition or mineral assemblage (Allison et al., 2007; Burns, 1982), all of which can vary significantly with depth in the soil profile and landscape position (Bergstrom et al., 1998; McClain et al., 2003; Gabor et al., 2014; Lybrand and Rasmussen, 2015; Bernhardt et al., 2017). Therefore, the predominant explanatory variables of microbial activities could be expected to differ between surface and subsurface soils and may be influenced by disturbance regimes.

Wildfires shape the biogeochemistry of a landscape, and burn history is prevalent in US Southwestern mixed-conifer forests (Swetnam and Betancourt, 1987). Novel, high-severity wildfires can have lasting, decadal impacts on regional soil biogeochemistry in mixed-conifer forests (Dove et al., 2020). Differences in fire severity often create a mosaic landscape with variations in vegetation survival, substrate type, and C and N availability that influence microbial community structure and function (Barros et al., 2012). Wildfire is shaped by topography, tending to move upslope leading to higher-severity burn in elevated areas (Barros et al., 2012; Debano, 2006; Lim et al., 2007). This can amplify topographic patterns of microbial activities by exacerbating soil biogeochemical differences in convergent versus planar areas (Dillon et al., 2011). Fire also shows differential vertical effects throughout the soil profile through removal of surface organic matter, deterioration of soil structure and porosity, loss of carbon, nitrogen and other nutrients through volatilization, leaching, erosion, and marked alteration of microbial communities that result from direct (surface-burning) and indirect fire impacts (alterations to soil physicochemical environment and vegetation cover). (Bento-Goncalves et al., 2012; Ferrenberg et al., 2013; Jimenez Esquilln et al., 2007; Weber et al., 2014). These soil fire effects are often most significant in the 0–5 cm layer that generally contains high OM content, but the impacts of fire extend into the soil profile in a manner dependent on the site and fire characteristics, i.e. soil type, topographic position, vegetation cover. (Dooley and Treseder, 2012; Holden and Treseder, 2013; Jimenez Esquilln et al., 2007). Further, the magnitude of fire effects on soil properties correlate directly with burn severity (Certi, 2005; Knelman et al., 2015; Murphy et al., 2006; Lybrand et al., 2018), and can dampen the typical surface–depth trends in microbial abundance and richness (Jimenez Esquilln et al., 2007; Dooley and Treseder, 2012; Holden and Treseder, 2013). Fire studies in the southwestern U.S. typically tend to focus on the dynamics of the surface 15 cm soil (e.g. Jimenez Esquilln et al., 2007; Weber et al., 2014; Knelman et al., 2015), omitting immediate post-burn effects in deeper soils.

In this study, we examined potential EEA in relation to landscape position and depth after a wildfire to investigate the relative importance of vegetative, topographic, and geochemical controls on microbial-driven soil nutrient cycling. The need for spatial relationships of EEA based on independently-derived environmental factors has been highlighted in the literature (Forman and Godron, 1981; Risser et al., 1983). Past attempts to spatially quantify enzyme activities have focused primarily on N-mineralizing enzymes, were limited in spatial scale, or did not account for catchment-scale drivers such as topographic controls on hydrologic flowpaths or ecosystem control locations (e.g. Du et al., 2015; Florinsky et al., 2004). Our study site is located in a sub-alpine mixed conifer forest in the Southwestern United States. Such ecosystems are important to regional C cycling and are currently threatened by disturbances such as climate extremes, insect outbreaks, and changes in fire regime (Allen et al., 2010; Bentz et al., 2010; Westerling, 2006). We investigated the following environmental controls: topography, vegetation, depth in the soil profile, and solute geochemistry on EEA to explain variability in C, N, and P mineralization in a burned forested catchment. We predicted that convergent areas of the catchment would correlate with higher vegetation cover, soil moisture, and soluble ions that would increase potential enzyme activities. We predicted higher EEA in surface soils to correspond with greater substrate availability and for the fire effect to be most pronounced in the surficial soils.

2. Methods

2.1. Study site

This study was conducted in a mixed conifer catchment located in the Jemez River Basin watershed in north-central New Mexico (106°33′23″W, 35°52′19″N) in the Valles Caldera National Preserve, part of the Santa Catalina Mountains - Jemez River Basin Critical Zone Observatory (CJCZO, Chorover et al., 2011). The catchment is located on Redondo Dome, a resurgent lava dome that sits at the southernmost extent of the Rocky Mountains (Fig. 1). The parent material is dominated by rhyolitic volcanioclastics (Golf et al., 2006). The 30-year average mean annual temperature is 4 °C, with average winter (October–April) and summer (May–September) temperatures of approximately +1 °C and 11 °C, respectively (Brotz et al., 2009). The soils are classified as Vitric Andisols. Mean annual precipitation in the catchment is 777 mm yr−1 and is characterized by a bimodal precipitation pattern, with approximately half of annual precipitation falling as snow between late October and April, and the other half falling as rain during the
summer monsoon between July and September. Vegetation cover consists of mixed conifer forest stands of Douglas fir (*Pseudotsuga menziesii*), white fir (*Abies concolor*), blue spruce (*Picea pungens*), corkbark fir (*Abies lasiocarpa var. arizonica*) and Englemann’s spruce (*Picea englemannii*; Muldavin and Tonne, 2003; Muldavin et al., 2006; Coop and Givnish, 2007; Table 1).}

### 2.2. Sample collection

Soil samples were collected 18 days after containment of the

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**Table 1**

<table>
<thead>
<tr>
<th>Site Name</th>
<th>Area (km²)</th>
<th>Location (°)</th>
<th>Elevation (m)</th>
<th>Aspect</th>
<th>Slope (°)</th>
<th>MAT °C</th>
<th>MAP (mm yr⁻¹)</th>
<th>Parent Material</th>
<th>Fractional contribution</th>
<th>Soil Texture</th>
<th>LAI</th>
<th>Vegetation Characteristics</th>
</tr>
</thead>
<tbody>
<tr>
<td>Jemez River Basin ZOB</td>
<td>0.15</td>
<td>106°33'23&quot;W, 35°52'19&quot;N</td>
<td>3027</td>
<td>15.46</td>
<td>9.0 (0.0-35.1)</td>
<td>4.69</td>
<td>650-940</td>
<td>Rhyodacite</td>
<td>Bandelier Tuff</td>
<td>41, 25, 34</td>
<td>1.2 + 0.01</td>
<td>Mixed Conifer</td>
</tr>
</tbody>
</table>

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aVázquez-Ortega et al., 2015

bStielstra (2012).

cMuldavin and Tonne (2003).

dAverage values are followed by range values in parenthesis.
Thompson Ridge Fire (which began May 31, 2013 and was contained July 1, 2013, burning 1906 acres) on July 19, 2013, to capture post-fire microbial activity across the landscape. Three control unburned samples were taken from a nearby ridge in July 15, 2015 in an identical manner to the burned samples (106°33‘23”W, 35°52‘19”N). We expect that the fire signal trumps the inter-annual variation that occurred between sample points. Gutknecht et al. (2010) found that the fire signal on extracellular enzyme activity persisted for 3 years following wildfire. Given the similar vegetation, site and soil characteristics these sites provide analogous unburned comparisons to our burned samples. The overall burn severity of the catchment ranged from moderate to severe (USDA Forest Service, https://fsapps.nwcg.gov/afm/baer/download.php).

Twenty-two soil pits were excavated and soil samples collected to a depth of 40 cm using a spade, sampling at depth intervals of 0–2, 2–5, 5–10, 10–20, 20–30, and 30–40 cm (Table 1). Samples were collected from the up-slope wall of each soil pit. Collected samples were placed in coolers with ice, transferred to refrigerators, then transported on ice to the University of Arizona, where they were maintained at 4 °C. They were sieved to 2 mm within two weeks of collection, with care taken to remove any residual visible plant material, sealed in plastic bags, and stored at 4 °C. Assays for potential enzyme activity and chemical analyses were performed within four months of sample collection per the standard accepted timeframe (Saiya-Cork et al., 2002).

### 2.3. Soil properties

Select soil physical and chemical properties that relate to soil enzymatic activities were characterized. Soil gravimetric water content was determined by drying a subsample at 105 °C for 24 h. Soil pH was measured in distilled water with a 1:2 soil-to-solution mass ratio using a VWR SympHony multimeter with Ross semi-micro combination pH probe and VWR electrical conductivity probe. To measure SOC and total N content, samples were dried at 60 °C, finely ground, and organic C and total N content were determined using a Shimadzu total organic C analyzer with total N module equipped (Shimadzu Scientific Instruments, Inc., Columbia, MD, U.S.A.). Anion data were collected on a water extract using a 1:5 solid:liquid ratio for organic horizons and 1:1 for mineral horizons on a Dionex ICS-1000 ion chromatography system with AG22 + AS 22 anion exchange columns and carbonate eluent (EPA Method 300.0). Cations, trace metals, metalloids and rare earth elements were measured on a water extract via inductively-coupled plasma mass spectrometer on an Agilent 7700x with a collision cell using He as the buffer gas. They were treated to remove organics using NaOCl adjusted to pH 9.5, and carbonate using Na acetate buffer was adjusted to approximate that of the specific sample. Twenty-two soil pits were excavated and soil samples collected to a depth of 40 cm using a spade, sampling at depth intervals of 0–2, 2–5, 5–10, 10–20, 20–30, and 30–40 cm (Table 1). Samples were collected from the up-slope wall of each soil pit. Collected samples were placed in coolers with ice, transferred to refrigerators, then transported on ice to the University of Arizona, where they were maintained at 4 °C. They were sieved to 2 mm within two weeks of collection, with care taken to remove any residual visible plant material, sealed in plastic bags, and stored at 4 °C. Assays for potential enzyme activity and chemical analyses were performed within four months of sample collection per the standard accepted timeframe (Saiya-Cork et al., 2002).

### 2.4. Extracellular enzyme activity analysis

The potential activities of seven hydrolytic enzymes involved in C, N and P acquisition were assayed according to a modified protocol using a fluorometric deep-well microplate technique (Saiya-Cork et al., 2002; Gebhardt et al., 2017; described briefly below). Carbon acquisition was assayed by β-glucosidase (AG), β-1,4-glucosidase (BG), β-D-celllobiohydrolase, (CB) and β-xylanase (XYL); N acquisition was assayed by β-1,4-N-acetylglucosaminidase, (NAG) and leucine-aminopeptidase (LAP); and P acquisition was assayed by acid phosphatase (PHOS). The specific functions of these enzymes are listed in Supplemental Table S1. Briefly, 2.75 g of field-moist, refrigerated soil were homogenized in 91 ml of sodium acetate buffer using a Waring Laboratory blender with stainless steel blade for 1 min. The pH of the sodium acetate buffer was adjusted to approximate that of the specific soils being assayed, ranging from 5.3 to 7.2.200 mL of 200 μM fluorometric substrate proxies specific to each enzyme was added to 800 μL of each soil slurry. Assays were run with two internal standards: dilution series (0–100 μM) of 4-methylumbelliferone (MUB) or 7-amino-4-methylcoumarin (MUC), each mixed with soil homogenate. Plates were incubated at 15 °C for 4 h in the dark, based on optimized durations determined in pilot studies for these soils. After the incubation period, plates were centrifuged for 3 min at 2900 g, after which 250 μL of soil slurry were transferred from each well into a black Greiner flat-bottomed 96-well plate and then fluorescence was measured using a fluorometer (Biotek Synergy 4, Winooski, VT, USA) set at 360 nm excitation and 450 nm emission. Incubation time was adjusted for samples with activity higher than the detection limit. Total enzyme activity was calculated from fluorescence values as the rate of substrate converted in nmol h⁻¹ g⁻¹ soil (Gorman et al., 2011).

#### 2.5. Environmental covariates

Potential enzyme activities were compared with topographic variables derived from a digital elevation model (DEM), and aerial imagery from the National Agriculture Imagery Program (NAIP) collected 2014-06-09, approximately 1-year post-burn. All data were projected to a common coordinate system, NAD 83 UTM Zone 13N, prior to analyses. We used a 1 m resolution LiDAR-derived DEM generated in 2010 (snow-off conditions; Guo et al., 2010) to calculate topographic variables including plan and profile curvature, wetness index, and catchment slope and area, using the System for Geoscientific Analyses (SAGA, v. 2.0.8, 2011). We used a parallel processing algorithm (v. 2.0.8) with multiple flow paths to calculate catchment aspect, slope and area (Freeman, 1991). The calculated catchment slope and area were used to calculate the SAGA Wetness Index (SAGAWI; Boehner et al., 2002), and the modified catchment area from the SAGAWI calculation was used to calculate the slope length factor (Moore et al., 1991). Additionally, we included normalized difference vegetation index (NDVI, Tucker, 1979), calculated from the NAIP imagery (rgis.unm.edu/getdata, USDA-FSA-APFO Aerial Photography Field Office, 2015) using ArcGIS 10.1 (ESRI, Redlands, CA).

We resampled the 1 m DEM to 2, 5, and 10 m pixel resolution in order to identify the most appropriate scale for comparison with enzyme activity. The same topographic variables were calculated at each spatial resolution, and a correlation matrix between EEA at each sampled depth and the topographic variables at each sample resolution was calculated. From the correlation matrix, the spatial resolution with the highest number of correlations > +0.4 or < -0.4 between EEA and the topographic variable was determined to be 10 m (Table S4), and this data was used to model enzyme activity.

Interpolated maps of select depth-weighted EEA and geochemical variables were generated using optimized inverse distance weighting (IDWopt) in ArcGIS 10.1. We analyzed EEA surface (0–5 cm) and deep (5–40 cm) values and calculated a single depth-weighted mean across the total sampled depth of each soil profile. Due to missing values, depth-weighted EEA and geochemical variables were calculated using only the available data, e.g., if the 20–30 cm layer BG value was missing, a depth-weighted mean was calculated using the data from the 0–2, 2–5, 5–10, 10–20, and 30–40 cm layers only and applying a total depth of 30 cm. To generate the interpolated maps, we followed the IDWopt procedure of Molotch et al. (2005). We could not perform kriging due to the limited number of sites sampled. Using IDWopt, we adjusted the power of the IDW function, search radius, search sectors, and number of neighbors to minimize the root mean square error (RMSE) and the mean error of prediction of the interpolated maps. We adjusted the search radius from 75 to 250 m, in 25 m increments, and we aimed for interpolated...
maps where the RMSE approached one, and the mean error of prediction approached zero.

### 2.6. Statistical analysis

All statistics were performed using R (v. 3.1.1, [www.r-project.org](http://www.r-project.org)). The Shapiro-Wilk test of normality and Levene’s test of equal variances was performed in R using R ‘stats’ and ‘car’ packages, respectively (Fox and Weisberg, 2018), to assess whether any univariate parameter distributions among enzyme groups deviated significantly from normal. Following Box-Cox transformations using the R: MASS package, we selected log data transformations to improve the assumption of normality for subsequent statistical analyses and log transformed data are presented in the figures. Two-way analysis of variance (ANOVA) was used to test for the effects of burn status (i.e. control vs. burned) and depth on enzyme activity treated as fixed factors and site location was used as a random effect to account for differences in horizons among treatments (Figs. 2 and 3, see supplement for ANOVA model output). When ANOVA models indicated a significant treatment effect, a post-hoc Tukey’s honestly significant difference (HSD) test was conducted using the ‘car’ package to determine differences between treatment means. Due to the uneven sample sizes among treatments a non-parametric Kruskal-Wallis test was used to confirm ANOVA results. A significance level of p < 0.05 was used as a random effect to account for differences in horizons between depth increments (Figs. 2 and 3, see supplement for ANOVA model output). When ANOVA models indicated a significant treatment effect, a post-hoc Tukey’s honestly significant difference (HSD) test was conducted using the ‘car’ package to determine differences between treatment means. A significance level of p < 0.05 was used as a random effect to account for differences in horizons between depth increments (Figs. 2 and 3, see supplement for ANOVA model output).

The results of the two-way ANOVA examining the effects of burn status (B), depth (D) and their interaction (B:D) are also presented in the figure. The symbols * * * represent the significant levels of p < 0.001, p < 0.01 and p < 0.05, respectively. Full ANOVA results can be found in Supplementary Table 7. Data points represent log-transformed activity data across burn (n = 22) vs unburned (n = 3). Error bars represent mean ± the standard error.

We performed separate principal component analyses (PCA) on the geochemical and EEA variables. PCAs were calculated using the function “prcomp” from the “stats” package in R (v. 3.1.1). PCA was used to determine the differences among the observed EEA and geochemistry variables among all sites and all sampled depths. Only complete observations were used to calculate the PCAs. Extracellular enzyme activity values were natural log transformed and all values were z-scored prior to performing the PCA. We used the covariance matrix to calculate the principal components and loadings, and the PCA loadings were used to generate biplots.

We performed partial least squares regression (PLSR) to determine the relative contributions of the geochemical and topographic variables to variability in the EEA variables. All PLSRs were calculated in R (v. 3.1.1) using the “pls” package (Mevik and Wehrens, 2007). PLSRs were calculated using natural log-transformed and z-scored EEA values as response variables. Only complete sets of enzyme, geochemical, and topographic variables were used to calculate the PLSRs. We performed separate PLSRs using all enzyme variables, and only N-mineralizing enzymes, C-mineralizing enzymes, and P-mineralizing enzymes as response variables. We used midpoint depth, TIC, TOC, TN, clay%, electrical conductivity (EC), pH, and total solid phase concentrations of Na, Mg, Ca, K, P, NO₃, SO₄, Cr, Mn, Fe, Co, Ni, Cu, Zn as geochemical explanatory variables, and used elevation, NDVI, catchment aspect, profile curvature, plan curvature, SAGA wetness index, catchment slope, and slope length factor as topographic explanatory variables. Only explanatory variables were z-scored prior to calculating the PLSRs. All PLSRs were performed using leave-one-out-cross-validation (LOOCV) and the kernel partial least squares algorithm (kernelPLS), which is analogous to the nonlinear iterative partial least squares algorithm (NIPALS). We allowed a maximum of 10 components, and used the minimum root mean square error of prediction (RMSEP) and maximum coefficient of multiple determination (R²) to determine the optimum number of components.

**Fig. 2.** Enzymatic activity with depth for enzymes assayed at 15°C involved in carbon (α-glucosidase [AG], β-1,4-glucosidase [BG], β-D-cellobiohydrolase, [CB] and β-xylanase [XYL]), nitrogen (β-1,4,N-acetylglucosaminidase, [NAG] and leucine-aminopeptidase [LAP]) and phosphorus acquisition (acid phosphatase [PHOS]). The results of the two-way ANOVA examining the effects of burn status (B), depth (D) and their interaction (B:D) are also presented in the figure. The symbols “***,” “**,” and “*” represent the significant levels of p < 0.05, p < 0.05 and p < 0.001, respectively. Full ANOVA results can be found in Supplementary Table 7. Data points represent log-transformed activity data across burn (n = 22) vs unburned (n = 3). Error bars represent mean ± the standard error.
number of components to include in each PLSR. We used both the explanatory and response variables loadings to determine the relative interaction between the geochemical and topographic variables.

We separated surface (0–5 cm; n = 20) and deep (5–40 cm; n = 76) EEA measurements to account for the well-established biological and physical differences between organic horizon and mineral soil samples. We performed separate PLSRs between the EEA variables and environmental covariates to isolate the potential impact of fire disturbance on EEA and to understand how fire potentially alters the relationships between EEA and the environmental covariates. We hypothesized that surface horizons were more impacted immediately by fire disturbance, and that fire disturbance minimally impacted deeper soil horizons at the time samples were taken (i.e. before significant soil wetting occurred post-fire). Deeper soil horizons are protected from extreme increases in temperature, and due to the timing of sampling would not have experienced significant infiltration of fire byproducts. PLSRs for the surface and deep measurements were performed similarly as the full EEA and C-, N- and P-mineralizing enzyme PLSRs, as described above.

3. Results

3.1. Interactive effects of fire disturbance and depth on extracellular enzyme activity

Fire resulted in decreased enzymatic activity in the surface (0–2 cm) soils for BG, CB, and NAG involved in C and N cycling (Fig. 2; p < 0.05). Enzyme activities decreased with depth in unburned sites for all enzymes assayed (Fig. 2; p < 0.05). Declines in enzyme activity with depth were observed for all enzymes in the burned soils with the exception of NAG and PHOS that showed no significant variance between the means in surface vs. subsoils (Fig. 2; p < 0.05). Significant interaction effects were observed between burn status and depth for enzymes BG, CB, NAG, and PHOS (Fig. 2, Table S7; p < 0.01). Higher LAP activity was observed in the burned soils relative to the unburned soils across all depths with no interactive effects between burn status and depth (Fig. 2, Table S7, p < 0.001).

Fire altered nutrient acquisition strategies with depth. Ratios of enzymatic C:P and N:P activities showed significant decreases with depth in burned soils and were lower in the burned soils (Fig. 3, Table S8, p < 0.05). Higher enzyme C:N ratios were observed in unburned vs. burned soils (Table 2, Table S9, p < 0.05). Higher enzyme C:N ratios were observed in the burned soils relative to the unburned control with no interactive effects observed between burn status and depth (Fig. 3).

Fire effects were most pronounced in surface (0–2 cm) soils (Fig. 2, Table 3). Statistically significant declines in soil TOC, TN, P, pH, GWC, EC were observed in both burned and unburned soils (Table 2, Table S9, p < 0.05). Fire resulted in decreased surface (0–2 cm) concentrations of soil TOC, TN, and extractable P (Table 2, Table S9, p < 0.05). Interactive effects between burn status and depth were observed in TOC, TN, P, and pH. Soil C:N, C:P, and N:P ratios increased with depth and in burned and unburned soils. Significantly higher soil C:P and N:P ratios were observed in unburned vs. burned soils (Table 2, Table S9, p < 0.01).

3.2. Correlations among EEA, geochemistry, and topography in burned samples

Principal component analysis (PCA) of EEA indicated that all enzymes (BG, CB, AG, XYL, NAG, and PHOS) except LAP behaved similarly (Fig. 4a). LAP was ordinated along a different axis compared to the remaining enzymes, with a PC2 eigen vector of 0.922 (Table S1). The PCA of the geochemical variables showed that all geochemical indicators behaved similarly, with all variables ordinated in the same direction in the biplot (Fig. 4b, Table S2).

The partial least squares regression (PLSR), using all enzymes as response variables, indicated BG, CB, XYL, AG, NAG, and PHOS responded positively to NDVI, SAGA WI, and clay content, but responded negatively to elevation. LAP responded differently than all other enzymes: it responded positively to total nitrogen (TN) and negatively to EC were observed in both burned and unburned soils (Table 2, Table S9, p < 0.05). Interactive effects between burn status and depth were observed in TOC, TN, P, and pH. Soil C:N, C:P, and N:P ratios increased with depth and in burned and unburned soils. Significantly higher soil C:P and N:P ratios were observed in unburned vs. burned soils (Table 2, Table S9, p < 0.01).

The separate C-mineralizing enzymes (BG, CB, XYL, AG) and P-mineralizing enzyme (PHOS) PLSRs behaved similarly to the full enzyme PCA. Using 2 components for both C enzymes and PHOS PLSRs, the RMSEP was minimized and the R² was maximized (Table S4). The C enzyme PLSR, using 2 components, accounted for 50.6% of the variance in the explanatory variables, and percent variance explained in the C enzymes ranged from 27.2% to 38.1%. The PHOS PLSR, using 2 components, accounted for 46.1% of the variance in the explanatory variables, and 32.9% of the variance in PHOS enzyme activity. The C enzymes again responded positively to NDVI, SAGA WI, and clay
content, along with Zn and NO3, but negatively to elevation (Fig. 4d). The PHOS PLSR indicated PHOS responded positively to NDVI, SAGA WI, and clay content, and negatively to elevation (Fig. 4e).

The separate N-mineralizing enzyme (NAG and LAP) PLSR indicated that NAG and LAP were each responding to different environmental variables within the catchment (Fig. 4f). NAG behaved similarly to the C- and P-mineralizing enzymes, in responding positively to SAGA WI and NDVI, and negatively to elevation, whereas LAP behaved differently than all other enzymes, responding positively to NO3, TN, and Zn, and negatively to soil depth (as indicated by midpoint horizon depth). The N enzyme PLSR, using four components, accounted for 59.0% of the variance in the explanatory variables, and accounted for 36.2% of the variance in NAG and 58.3% of the variance in LAP. Using four components, the RMSEP and R2 for NAG were 1.11 and 0.011, respectively, and the RMSEP and R2 for LAP were 0.92 and 0.45, respectively.

Surface and deep EEA PLSRs reflected varying relationships between enzyme activities and the environmental covariates. The surface EEA PLSR indicated that all the EEA variables coordinated along the same axis (Fig. 4g); similar to the full EEA PLSR (Fig. 4c), the deep EEA PLSR indicated that all EEA variables, except LAP, coordinated along the same axis, LAP coordinated perpendicular to the other EEA variables (Fig. 4h). The surface EEA PLSR indicated that enzyme activities positively respond to NDVI, clay%, and SAGAWI, and NO3, Zn, and TN concentrations (Fig. 4g). The deep EEA PLSR indicated that enzyme activities positively responded to NDVI, clay%, and SAGAWI, and a large number of geochemical factors (Fig. 4h). Regardless of the shifting relationships between the EEA variables and the geochemical factors, SAGAWI, NDVI, and clay% were consistently and positively related to enzyme activity at both surface and deep soil horizons.

3.3. Spatial distribution of potential EEA

All IDW maps of enzyme activities and geochemical factors used 22 maximum and 10 minimum neighbors, and had powers of 1, except NO3 with a power of 2.45 (Table S3). Mean errors approached zero for all, except BG and NO3, with errors of 1.14 mmol h−1 g−1 and -5.68 μg g−1; RMSE varied for each map, with a minimum of 0.02 μg g−1 for Zn and 111.36 μg g−1 for NO3 concentration. For the IDW maps, we focused on BG and LAP activity, as BG represented the behavior of CB, XYL, AG, NAG, and PHOS, and LAP responded to different environmental variables compared to the other measured enzymes based on the PLSR results. The spatial patterns of EEA as suggested by IDW interpolation showed highest activity in convergent areas (Fig. 5). BG activity was highest in the convergent zone and at the catchment outlet (Fig. 5a), and was greatest throughout the lowest elevations of the catchment. Coincident with BG activity, SAGA WI (Fig. 5c) and NDVI (Fig. 5d) and clay content (Fig. 5e) were all highest throughout the convergent zone. LAP activity was highest in the convergent zone, but the greatest LAP activity was found at mid elevation sites in the convergent zone, and centered on sites Q, O, and H (Fig. 5b). LAP activity was spatially coincident with multiple geochemical factors, including TN (Fig. 5f), NO3 (Fig. 5g) and Zn (Fig. 5h) concentration in the soil. TN and NO3 were highest at sites Q and O, and D; Zn was highest at site O and throughout the western facing side of the catchment.

4. Discussion

4.1. What influences EEA?

We found positive correlations between C, N and P extracellular activities and SAGA WI in the burned sites. Topography exerts strong influence over microbial enzyme activities, with the highest C-, P- and N-enzyme activities in convergent areas of the landscape (Fig. 3; Du et al., 2015; Lybrand et al., 2018; Moore et al., 2004). Landscape position has been shown to be a strong driver of microbial biomass and community composition due to its control over variations in water and nutrient flow from planar to convergent zones (Brockett et al., 2012; Du et al., 2015; Liu et al., 2009; Nemergut et al., 2005). We did not see
We found that all enzymes assayed, with the exception of NAG and PHOS (Fig. 2, p < 0.05). The shifts in enzyme C:P and N:P acquisition strategies with depth (Fig. 3) suggest potential nutrient scavenging or increased biological activity in soil. We observed increased enzyme C:N ratios post-wildfire in contrast to reference soils (Fig. 2). These differences in C:N ratios have been used as an indicator for the allocation of resources toward C or N acquisition, demonstrating an overall shift in strategy toward N acquisition in burned soils (Sinsabaugh et al., 2009). We expected that microbes responding to fire disturbance in early succession may be appreciable differences in nutrient loadings or moisture content in convergent, depositional zones (Table 2.), but still found strong correlations between these environmental drivers in the PLSR analysis (Fig. 4). Higher activities could be the result of decreased substrate availability in convergent zones which supports higher microbial biomass and altered community composition, which may explain the higher enzyme activities (Liu et al., 2009; Du et al., 2015).

Table 3
Partial least squares regression (PLSR) result summary table for each of the presented PLSR biplots presented in Fig. 4c-h. The root mean square error of prediction (RMSEP) indicates the relative error in the PLSR for each variable, and the coefficient of determination (R²) indicates the ability of the PLSR to explain the variability for each enzyme. The % variance explained represents the proportion of the variation that the included components, generated from the explanatory variables, explain for each of the included enzymes.

<table>
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<th>R²</th>
<th>% Variance Explained</th>
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a Partial Least Squares Regression.
b Root mean square error of prediction.
c Coefficient of determination.
d Explanatory variables in the partial least squares regression.

4.2. EEA differences from surface to deeper soils

Vertical distribution of C, N, and P enzyme activities has been reported in several forest soils ranging from tropical forests, to Mediterranean evergreen forests and temperate forests, to boreal ecosystems (Andersson et al., 2004; Prietzel, 2001; Stone et al., 2014; Trasar-Cepeda et al., 2000; Wittmann et al., 2004). In this sub-alpine mixed conifer forest, fire altered the nutrient acquisition strategies with depth (Fig. 3).

Many soil properties vary as a function of depth, with a general decrease in substrate availability, changes in substrate stoichiometry, and lower microbial biomass in deeper soils (Fierer et al., 2003; Snajdr et al., 2008). As a result, biological activity in soil is most pronounced and largely concentrated in the topsoil (Ekschmitt et al., 2008a; Rumpel and Kögler-Knabner, 2010; Spielvogel et al., 2008; Stone et al., 2014). In this study, enzyme activities declined with depth in burned sites for all of the enzymes assayed with the exception of NAG and PHOS (Fig. 2, p < 0.05). The variation among specific enzyme activities at different soil depths reflects multiple factors, including the concentration of plant and microbe-derived compounds, the abundance and functional capacity of microorganisms, as well as preferential stabilization of microbial C by soil minerals (Ekschmitt et al., 2008a, 2008b; Snajdr et al., 2008; Stone et al., 2014).

C:P and N:P enzyme activity ratios decreased with depth in the burned soils (Fig. 3). Phosphorus-mineralizing (PHOS) enzymes are produced by bacteria, fungi and plant roots and transform complex organic P into assimilable phosphate by the cleavage of a phosphate group (Burns et al. 1982) and is regulated by the nutrient demand of plants and microbes (Antibus et al., 1999; Sinsabaugh et al., 1993). PHOS activity typically depends on P demand from plants and microbes, organic P substrate availability, and P limitation in soil. Previous work from mixed conifer forests in the Colorado Rocky Mountains, U.S. shows that PHOS in surface soil declines with increasing fire severity and the loss of vegetation (Knelman et al., 2015). Fire effects on P availability vary where some studies show increased P availability (e.g. Dyreness et al., 1989; Hauer and Spencer, 1998; Saa et al., 1993; Romanay et al., 1994), others show decreased P availability (Carreira et al., 1996) or dependence on burn severity (Ketterings and Bigham, 2000). Fire can cause a release in inorganic P due to release of orthophosphates from organic matter. Availability can be decreased by adsorption to newly exposed or created Fe and Al hydrous oxide surfaces or precipitation with Ca. On the other hand, P availability could be increased by increases in pH, causing desorption from Fe and Al hydrous oxide surfaces.

Shifts in enzyme C:P ratios with depth suggest higher potential P acquisition in deeper layers following wildfire (Fig. 3, p < 0.05). NAG (an enzyme involved in mining key nutrients of microbial cell walls) and PHOS did not decrease with soil depth in response to fire (Fig. 2, p < 0.05). The shifts in enzyme C:P and N:P acquisition strategies with depth (Fig. 2, p < 0.05) suggest potential nutrient scavenging or increased internal microbial cycling with depth as a response to fire.

We observed increased enzyme C:N ratios post-wildfire in contrast with reference soils (Fig. 2). These differences in C:N ratios have been used as an indicator for the allocation of resources toward C or N acquisition, demonstrating an overall shift in strategy toward N acquisition in burned soils (Sinsabaugh et al., 2009). We expected that microbes responding to fire disturbance in early succession may be...
Fig. 4. Principal component analysis (PCA) and partial least squares regression (PLSR) biplot results, see Table 3 and Supplemental Tables S2 and S3 for summary results. A) EEA PCA biplot, PC1 explained 70.3% of the variance in the EEA dataset, and PC2 explained 14.5% of the variance. All enzymes aligned along the same axis, except LAP. B) Geochemical PCA biplot, PC1 explained 49.6% of the variance and PC2 explained 13.5% of the variance in the geochemical dataset, all variables aligned along the same axis. C) EEA PLSR, including all measured enzyme activities; the enzymes were positively related to NDVI, SAGA wetness index, clay content, and Zn, except LAP, which was most responsive to total nitrogen (TN). D) C EEA PLSR, included only the C-mineralizing enzymes; the C-mineralizing enzymes exhibited similar responses as in part C. D) N EEA PLSR, included only the N-mineralizing enzymes; NAG behaved similarly to the C-mineralizing enzymes. LAP was most responsive to Zn and total nitrogen (TN). F) PHOS EEA PLSR, included only the P-mineralizing enzymes; PHOS responded to the same variables as the C-mineralizing enzymes. G) EEA Surface (0–5 cm). After fire, all enzyme activity aligned along the same axis, and was positively related to NDVI, SAGA wetness index, and clay. PLSR H) EEA Deep (5–40 cm) PLSR. All C- and P-mineralizing, and NAG enzymes responded positively to NDVI, SAGA wetness index, and clay content, as well as a suite of geochemical variables. LAP aligned along a different axis and was most positively related to suite of geochemical and topographic variables.
Fig. 5. Inverse distance weighting (IDW) maps for A) BG and B) LAP. C) Calculated SAGA Wetness index for the MC ZOB, using the 10m DEM. D) Measured NDVI for the MC ZOB using NAIP imagery. E) IDW map for clay content. F) IDW map for total nitrogen (TN). G) IDW map for nitrate (NO$_3$) concentration. H) IDW map for zinc (Zn) concentration.
co-limited by both C and other macronutrients such as N (e.g., Knelman et al., 2015). Our results indicate that even shortly following fire disturbance, enzyme changes alongside rapid shifts in nutrient availability characteristic of post-fire succession and respond, not just in surface soils, but effects can be seen in deeper (5–40 cm) soils. Previous studies have found that in high-severity forest fire soils that enzyme C:N activity values increased (Knelman et al., 2015). Fire causes selective heat induced mortality to fungal communities, altering the ratio of bacteria:fungi. These trends could reflect a shift in the ratio of fungi to bacteria as a response to fire (DeBano et al., 1998), with potentially higher fungal biomass - in deeper soils (Smithwick et al., 2012). We argue that shifts in the ratios of C, N, and P EEA indicate a shift in microbial nutrient allocation patterns with depth soon after fire, and reflect intensified nutrient recycling in burned, deep soils in response to fire.

At depth, TOC and a large number of geochemical factors including Na, Zn, Ni, Cr, Ca, Fe, Mn and Co become more important in terms of explanatory variables of EEA. This may be due to differential controls on enzyme efficiencies, upregulation of enzymes in response to limited nutrient availability, substrate binding, and enzyme immobilization that may differ from surface to deeper profile (Burns, 1982; Burns et al., 2013). The differential drivers between surface and deep enzyme activities may be coincident with release of N after wildfire, consistent with surface fire effects typically seen in forested soils (Dooley and Treseder, 2012; Holden and Treseder, 2013; Knelman et al., 2015). Indeed, LAP activity coincided most strongly with N availability (Fig. 4e). We expected fire effects to be most apparent in surface soils, and in fact, surface BG activity decreased. Despite shifts in explanatory geochemical variables with depth, at the scale of the burned catchment NDVI, % clay content, and SAGA WI remained the primary explanatory variables describing enzyme activities, indicating that these variables exert fundamental landscape-scale control of biogeochemical cycling, even with widespread and high-severity disturbance.

Inverse distance weighting revealed spatial co-occurrence of these peak activity levels with increased SAGA WI, NDVI, TN and NO3 concentrations (Fig. 5). Landscape position in this watershed was important for shaping the C, N- and P- acquiring activities of microbial communities, where soil wetness stands out as a key factor (Figs. 4 and 5). This is consistent with prior investigations revealing soil moisture controls on microbial biomass and soil respiration (Bowden et al., 1998; Jauhiainen et al., 2008; Wang et al., 2013). Interestingly, Zn was found to spatially co-occur with enzyme activity (Fig. 5a, b and h). While TOC did not have a significant effect on determining the spatial distribution of enzyme activities throughout the watershed (Fig. 3; Fig 5.), TOC was found to be a significant correlate at depth (Fig. 4h). This discrepancy between surface and deep correlates of enzyme activities may be a result of differential and stronger effects of fire at the soil surface.

5. Conclusion

We characterized the activities of seven hydrolytic enzymes involved in key nutrient transformation steps in order to identify spatial heterogeneity and environmental determinants of microbe-mediated biogeochemical cycling in a post-fire sub-alpine forest watershed. The application of spatial interpolation techniques, which enabled integration of point-scale functional measurements of microbial activities with landscape topography, revealed topographic controls on enzyme activities at the landscape scale. Direct fire burn effects were most pronounced for the enzyme BG at the surface and resulted in a shift in nutrient acquisition ratios at depth for C:P and N:P, indicating that fire effects on nutrient allocation strategies and microbial communities are not limited to surface soils. The analysis also indicated superimposed soil chemical influences (e.g., Zn effects) that should be considered in future studies. Further integration of soil science, ecosystem ecology, and microbiology through modeling, which requires this kind of explicit up-scaling from point measurements, is essential for building a predictive framework of terrestrial biogeochemical cycling in the face of ongoing anthropogenic change.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.soilbio.2020.107844.

References


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