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Soils signal key mechanisms driving greater protection of organic carbon under aspen compared to spruce forests in a North American montane ecosystem

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Highlights:

1. Soil organic carbon stocks are consistently greater under aspen compared to spruce
2. Microbial Efficiency - Matrix Stabilization model helps explain SOC differences
3. Smaller aggregate sizes under aspen further help explain SOC stocks
4. A lower probability of SOC destabilization likely persists under aspen stands

Abstract

Soil organic carbon (SOC) is often retained more effectively in aspen-dominated forests compared to coniferous forests in North America, yet the reasons why are unclear. A potential driver could be differences in SOC protection mechanisms. Over decades to centuries, chemical (e.g., mineral association) and physical (e.g., aggregation) processes can work to preserve SOC stocks, which can vary across cover types. To investigate this hypothesis, we evaluate controls on SOC concentrations in the Coal Creek watershed (CO, USA), a montane ecosystem dominated by quaking aspen and Engelmann spruce and underlain by granite and sandstone. We examined a combination of biological, chemical, physical, and environmental conditions to evaluate potential abiotic and biotic mechanisms of SOC preservation at multiple depths. As expected, we observed greater SOC under aspen compared to spruce. Growing season soil moisture, temperature, and CO_2 and O_2 varied with slope position and aspect, and thus forest cover type. Dissolved organic carbon (DOC) was lower under aspen compared to spruce. Exo-enzyme data indicate that aspen soil microbes exhibited greater effort to seek organically-bound resources; consistent with this, soil organic N exhibited higher $\delta^{15}N$ values, hinting at a greater degree of organic matter processing. Finally, aspen roots exhibited greater root abundance, and aspen mineral soils revealed smaller mean aggregate diameters compared to conifer sites. Our data suggest enhanced biotic activities in aspen-dominated forest soils that promote both chemical and physical protection of SOC in aspen- relative to spruce-dominated forests, and associated limitations on DOC export.

Keywords (1-7 words): Critical Zone, Ecohydrology, Montane Ecosystems, Soil Organic Carbon, Climate Change

1 Introduction

The distribution and composition of temperate montane forests are changing (Alexander et al.,1987, Anderegg et al., 2013), driven by increasing air temperature, earlier snowmelt, earlier onset and extent of the growing season (Godsey et al., 2014; Mote et al., 2018; Rhoades et al., 2018), and increasing frequency and intensity of disturbance (e.g., drought, fire, logging, and insect infestation; Canelles et al., 2021). For example, aspen stands have lost substantial live density and basal area to Englemann spruce, sub-alpine fir, and Douglas Fir since 1964 with an increasing rate of decline since 1994 (Alexander, 1987; Coop et al., 2014). Changes in montane

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forest cover can directly impact soil organic carbon (SOC) stability. Given that SOC regulates the availability of nutrients, soil stability, ecosystem water fluxes, and biosphere-atmosphere exchange of greenhouse gases (Jackson et al., 2017), and that global SOC reservoirs represent far more C than plant biomass and the atmosphere (Scharlemann et al., 2014), unraveling drivers of SOC stability remains an important research goal (Billings et al., 2021). Between paired aspen and conifer stands at numerous sites throughout North America, SOC pools differ substantially (review in Langaniere et al., 2017). Studies consistently show that carbon under conifers is more readily destabilized than under aspen (Woldeselassie et al., 2012; Laganiere et al., 2013; Boca et al., 2020; Román Dobarco et al., 2021). Further, SOC pools in aspen-dominated environments tend to be composed of larger stocks of mineral-associated organic carbon (MAOC), which is a relatively stable SOC fraction, than those under conifers (Román Dobarco et al., 2021). Yet, the mechanisms driving such differences in SOC stability under aspen and conifer remain elusive.

Examining soil physical attributes and how they can differ with plant cover type may help us understand differences in MAOC fate in aspen vs. conifer forests. For example, soil aggregation is a key process promoting SOC protection in many soil types (Blanco-Canqui and Lal, 2004). Soil aggregation refers to the clustering or binding of soil particles into larger units. This process is promoted by interactions among colloidal material and binding compounds (microaggregates; Six et al., 2004; Blanco-Canqui and Lal, 2005; Weil and Brady, 2017; Araya and Ghezzehei, 2019) and among particulate organic carbon (POC; Cotrufo et al., 2019), and clay minerals or clay-sized particles (Six et al., 2000). The collapse and formation of aggregates influence the protection of SOC. For example, the breakdown of macroaggregates into microaggregates often leads to the release of dissolved organic carbon (DOC) (Cincotta et al., 2019), some of which can undergo microbial uptake and mineralization to CO_2. In contrast, aggregate formation can limit soil microbial access to SOC on aggregates' interiors, helping to shield it from exo-enzymatic attack (Jastrow 1996; Six et al., 2000; Woolf et al., 2019).

Multiple mechanisms may drive differences in soil aggregation across aspen and conifer soils. First, soils beneath conifers are often more acidic (Poponoe et al., 1992; Buck and St. Clair, 2012) and thus may promote a greater abundance of relatively small aggregates, given that increases in soil solution [H^+] can weaken soil aggregation processes (Stătescu et al., 2013). Second, differences in rooting abundance among aspen and conifers may drive differences in aggregate formation across these cover types. Aspen tends to produce shallow roots that generally extend to ~ 30 cm deep (Sheppard et al., 2006), while conifers tend to develop both lateral and tap roots, the latter of which can extend relatively deep into the soil and bedrock (Mauer et al., 2012). Spruce tends to exhibit lower fine root biomass compared to aspen (Mekontchou et al., 2020). Fine roots may promote aggregate formation through enmeshment processes, while coarse roots may promote aggregate collapse because of roots perforating

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aggregates (Bronick and Lal, 2005). Differences in soil moisture between aspen and conifers driven by differences in aspect, foliar cover, and transpiration rates (Buck and St. Clair, 2012) may also influence aggregate stability, as rapid changes in soil moisture can cause aggregates to burst while a gradual increase in moisture can stabilize aggregates (Amezketa, 1999). Combined, these concurrent and competing processes may drive differences in soil aggregation between aspen- vs. conifer-dominated soils in ways that are difficult to predict due to complex and non-linear interactions, and require the synthesis of findings across biological and pedological disciplines to understand.

Soil moisture and temperature not only influence physical aggregation processes, and thus the protection and preservation of SOC, but also the degree to which microbes transform SOC into CO_2 or alter the transport of organic C pools to depth. Where soil moisture is higher, greater transport of organic C pools into the subsurface may be feasible, potentially increasing the amount of organic matter sorbed to minerals at greater depths (Mittuka et al., 2019). Conversely, DOC leaching may increase, and subsequent DOC export could reduce SOC concentrations (Roulet and Moore, 2006; Monteith et al., 2007). Soil temperature also may drive differences in SOC transformations across aspen and conifer sites, given that aspect exerts strong control on aspen distribution. Soil temperatures tend to be warmer under the sunnier, aspen-dominated stands compared to conifer stands (Buck and St. Clair, 2012). In a temperature-limited montane system, warmer temperatures under aspen stands may increase microbial metabolic activity and turnover, and thus accelerate microbial necromass formation, a process linked to greater stocks of relatively persistent SOC (Liang et al., 2019), perhaps due to necromass-promoting aggregate formation and stabilization (Sae-Tun et al., 2022). Thus, understanding soil hydrologic behaviors as well as solute transport down-profile, traditionally the realms of hydrologists and soil biogeochemists, in addition to biological and pedological processes, is important for understanding patterns of SOC transformations.

Finally, differences in the chemical composition of aspen and conifer biomass and their root exudates may explain differences in MAOC stocks between the two stand types (Boca et al., 2020). For example, aspen litter tends to exhibit lower lignin concentrations than coniferous litterfall (Moore et al., 2006). The Microbial Efficiency - Matrix Stabilization (MEMS) framework (Cutrofo et al., 2013) would suggest this more labile plant material may be easier for soil microbes to assimilate and transform into microbial necromass, which can become more physically or chemically protected through aggregation and chemical bonding (Kleber et al., 2007; von Lützow et al., 2008; Cutrofo et al., 2013) and lead to relatively more persistent stocks of SOC (Liang et al., 2019; Buckridge et al., 2022). Differences in microbial activities between aspen and conifer may further be exacerbated by differences in root exudation between these species. For example, Norway spruce can exhibit lower exudation rates than silver birch (Sadnes et al., 2005), and deciduous trees appear to experience greater exudation rates than pines

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(Wang et al., 2021). Though many studies explore the biotic, chemical, physical, and hydrologic processes that can influence SOC transformations and preservation, these processes are rarely examined in tandem. Thus, it remains unclear why conifer-dominated forests consistently harbor smaller amounts of SOC, and why aspen-dominated forests exhibit greater SOC stabilization.

Here, we use a holistic, critical-zone approach (Chorover et al., 2007) to understand SOC dynamics and drivers. We explore a suite of abiotic and biotic factors as they relate to SOC pool sizes across two forest cover types at Coal Creek, a watershed in central Colorado, USA, dominated by Englemann spruce (*Picea engelmanni*) on the north-facing hillslopes, and aspen (*Populus tremuloides*) on the south-facing hillslopes. Coal Creek has experienced relatively high variability in stream water DOC concentrations in recent years (2005-2019; Leonard et al., 2022). The mysterious, almost tripling of stream DOC concentrations in some years (2018-2019) may indicate recent shifts in upslope biogeochemical processes such as greater forest stress associated with climate change (Leonard et al., 2022) and subsequent changes in hydrologic flow paths (Zhi et al., 2020; Kerins et al., 2023) that influence C transport from soil profiles to stream water. We test the hypothesis that oft-observed greater stocks of SOC in soils under aspen stands compared to conifer-dominated soils are linked to greater soil microbial activities in aspen stand soils. We further hypothesize that relatively stable microaggregates are more abundant in aspen-dominated soils than spruce-dominated soils, resulting from higher microbial activities, and thus higher necromass production rates. Differences in rooting strategies and ecohydrology (e.g., evapotranspiration, soil moisture) between aspen and spruce stands will likely exert a secondary control on carbon stability. We finally hypothesize that the proliferation of fine roots in aspen-dominated soils are linked to smaller water-stable aggregates, and the generally coarser and deeper roots under spruce facilitate the transport of moisture and dissolved carbon down through the soil profile to a greater extent than under aspens, a process directly linked to DOC export to streams.

To test these hypotheses, we quantified multiple metrics describing basic abiotic conditions, SOC pools, soil microbial activities, soil aggregate-size distributions, and rooting distributions on five hillslopes dominated by either spruce or aspen, underlain by two contrasting lithologies and located at two hillslope positions (i.e., backslope and footslope). We aim to clarify some of the mechanisms governing aspen- and conifer-dominated forest soil microbial activity, soil aggregation, and soil moisture dynamics and their impact on SOC protection and DOC transport into surface water, illuminating the possible trajectories of SOC and DOC in rapidly changing, montane forest watersheds.

2 Study Area

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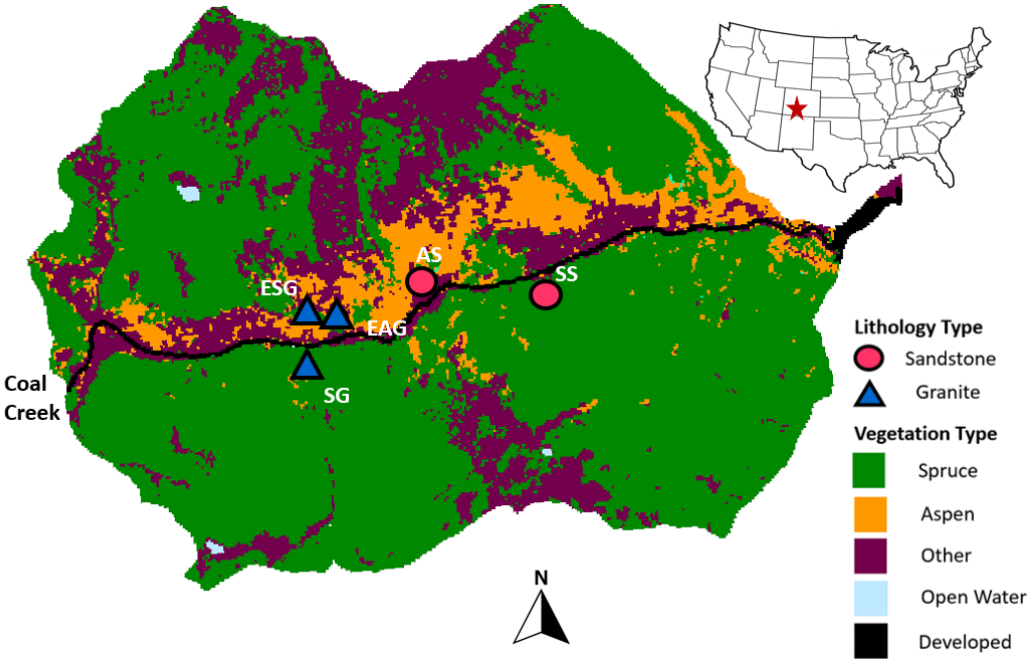

Figure 1: A map of the Coal Creek catchment. Colors represent land cover types, where aspen (orange) are dominantly at lower south-facing slopes while conifer (green) are on both north and south facing slopes. Shape represents lithology type where granite sites (blue triangles) are in the western part of the catchment and sandstone sites (pink circles) are in the eastern part of the catchment. AS is aspen sandstone, and SS is spruce sandstone. ESG and EAG are spruce granite and aspen granite, respectively. They are in Elk Creek, a sub catchment of the Coal Creek catchment. While ESG is on a dominantly south facing slope, it is north facing within the Elk Creek catchment. SG is also a spruce granite site. Note that all sites reside at contrasting hillslope positions: backslope = AS and SG, and footslopes = SS, ESG, and EAG.

Coal Creek (53 km^2) is a high-elevation (2715 m), headwater tributary of the Upper Colorado River Basin located in the Colorado Rocky Mountains near the town of Crested Butte (Fig. 1). Coal Creek is a sub-catchment of the larger East River watershed (300 km^2) and falls within the research domains of the U.S. Department of Energy funded Watershed Function Science Focus Area and Rocky Mountain Biological Laboratory (RMBL). The watershed is seasonally snow-covered from November through June. The area has a continental, subarctic climate with long, cold winters and short, cool summers. The mean annual temperature (1981-2019) is ~9 °C, with an average yearly minimum and maximum of –1.5 °C and 9 °C, respectively (Kerins et al., 2024). Average annual precipitation is 850 mm (Jiang et al., 2023), with approximately 60% falling as snow between October and May. This area has been warming since the 1980s and the fraction of snow has been decreasing roughly at 1% per year (Zhi et al., 2020). Due to these warming temperatures, the growing season in Crested Butte appears to be extending (Wadgymar et al., 2018).

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The geology of Coal Creek is underlain by sandstone, siltstone, shale, and coal units from the Mesa Verde Formation, variegated claystone and shale from the Wasatch Formation, and some intrusive granite diorite, granite, quartz, and monzonite that are Middle Tertiary aged (Gaskill et al., 1991). Soils are predominantly mapped as Alfisols, Mollisols, and Inceptisols (Soil Survey Staff, 2023).

Spruce, aspens, and alpine meadows can be found in the Coal Creek watershed. North-facing slopes are dominated by Engelmann Spruce, while aspen and Engelmann spruce can be found on south-facing slopes.

3 Methods

To quantify the impact of aspen vs. conifer land cover on soil organic carbon dynamics at Coal Creek, we dug two pits roughly one meter deep at all five sites. The first series of pits were dug in the summer 2020 and 2021 (Table 1). The second series of pits were dug in the summer of 2022. Aspen was dominant at two sites (AS and EAG), while spruces were dominant at three sites (SS, ESG, and SG). Because aspen- and conifer-dominated forests in this region tend to occur on hillslopes of contrasting aspects, it was not possible to isolate land cover from aspect affects (e.g., temperature, radiation). While the sites were selected based on their land cover, other key ecosystem features underlying lithology (either granite or sandstone), and hillslope position (either backslopes or footslopes) (Fig. 1) also differed across the sites. We address these site features as potential sources of variation in our response variables in the discussion.

Soil pits were described following Schoeneberger et al. (2012), then each pit face was photographed with a high-resolution, digital single-lens reflex camera (D5600, Nikon, Minato City, Tokyo, Japan) to quantify rooting depth distributions following Billings et al. (2018). Bulk soil samples were collected by depth every 10 cm for the first set of pits (2020-2021), and by horizon for the second set of pits (2022). Samples were then immediately stored in a refrigerator or freezer until they could be ground, sieved to 2 mm and analyzed. Twice in the summer of 2022 (late June and mid-August), soil was collected by auger within ~100 meters of each pit to characterize heterogeneity in soil chemistry. Soils were augured at 10 cm intervals to 110 cm (or deepest depth), and samples were stored in coolers with ice packs in the field and then transported back to the lab and stored at 4 °C (most analyses) or frozen (DOC and microbial biomass C, exo-enzyme assays, nitrate).

Table 1. Sampling design and analysis for the soil pits and augers samples.

	Soil Pits	**Soil Pits**	**Auger Samples**
Timing	2020-2021	2022	2022 (June and August)
Total Depth (cm)	~110	~110	~110
Soil Sampling Intervals	10 cm	Horizon	10 cm
Soil moisture and gas sensors	3 depths (15, 45, 110 cm)		

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Root Distributions	X	X	
%C and %N	X	X	X
Extractable nitrate concentrations		X	
$\delta^{15}N$		X	
pH	X	X	X
Effective cation exchange capacity (ECEC)	X		
Texture	X		
Wet aggregate size distribution (ASD)		X	
Dissolved organic carbon (DOC)		X	X
Microbial biomass carbon		X	
β-glucosidase and N-acetyl-β-D-glucosaminidase		X	

3.1 Measuring Soil Organic Carbon and Nitrogen Dynamics

We assessed SOC concentrations and stocks, and the likelihood of SOC degradation by microbes by analyzing bulk soil samples at 10-cm intervals for %C, %N, and carbon to nitrogen ratio (C:N). The %C and %N were determined by completing dry combustion on 70-100 mg of soil sample. After combustion, the sample was analyzed on an elemental analyzer (Vario Macro Cube, Elementar, Ronkonkoma, NY). To determine the overall stock of SOC per horizon (Zeng et al., 2021), we used %C and the soil bulk density from each horizon. Bulk density was measured using a three-dimensional laser scanner (3D Scanner Ultra HD, NextEngine, Inc., Santa Monica, CA) following Rossi et al. (2008).

We measured dissolved organic carbon (DOC) to estimate organic carbon that can be easily mobilized and transported out of the soil profiles. We analyzed soil samples at 10-cm intervals that were collected at each site during the growing season. Soil samples were extracted within three months of collection date. A total of 7.5 g of soil at field capacity was extracted with 30 ml of simulated rainwater (Laegdsmand et al., 1999). Samples were placed on a shaker table for 30 minutes and then centrifuged at 4800 RPM for 15 minutes. Samples were filtered through 0.45 µm syringe filters and 50 ml acid washed syringes. Filtered samples were stored in 10 ml centrifuge tubes, frozen and shipped overnight in a cooler with dry ice to the University of Kansas. DOC was analyzed from the thawed samples using a Violet-pink Mn (III)-pyrophosphate solution and a microplate reader (Biotek, UT).

To better understand the potential for microbial activity in these soils, we quantified microbial biomass carbon by horizon from pits dug in summer 2022 (Brooks et al. 1985). We exposed 5 g of each soil sample to chloroform for 24 h. To these fumigated sub-samples and to 5 g of unfumigated sub-samples, we added 20 ml of 0.5 M K_2SO_4 and shook for 30-40 minutes at 220 rpm. These samples were filtered through a 0.45 µm filter and their DOC concentration was

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determined via colorimetry (Bartlett and Ross 1988) on a Synergy HT microplate reader (Agilent, USA). We further measured the activity of two extracellular enzymes linked to microbial C and N acquisition (β-glucosidase and N-acetyl-β-D-glucosaminidase, herein referred to as BGase and NAGase, respectively) to develop some metrics of how actively and efficiently soil microbes in these soils can induce the decay of soil organic matter (Sinsabaugh and Moorhead, 1994; Allison et al., 2011, Stone et al., 2014). Measurements of 4-methylumbelliferyl β-D-glucopyranoside were used to quantify BGase activity and measurements of 4-methylumbelliferyl N-acetyl- β-D-glucosaminide were used to quantify NAGase activity on samples collected by horizon. To obtain these measurements approximately 1 gram of soil was blended by hand for 30 seconds with 125 mL of pH-adjusted 50 mM sodium acetate. The blended sample was pipetted into the desired substrate and incubated at 25 °C for 18 hours. Fluorescence from a Synergy HT plate reader (Agilent, USA) was used as a proxy for each enzyme's capacity to cleave monomers from the respective molecules undergoing decay (DeForest, 2009; German et al., 2011).

We quantified salt-extractable NO_3^- because of its importance as a biotically-available form of N, and also because of its status as a readily leachable ion. As such, it can serve as an indicator of each soil's capacity to undergo elemental loss in surface soil with hydrologic fluxes. We extracted ~10 g (fresh weight) of each soil sample with 0.5M K_2SO_4 and repeated the shaking and filtering steps described above for MBC. Extracts were analyzed for NO_3^- (Synergy HT, Agilent, USA) using Shand et al. (2008), a microplate-based approach that relies on hydrazine sulphate and sulphanilamide to generate a color intensity directly related to NO_3^- concentration.

We also quantified soil organic matter $\delta^{15}N$, given these signatures' value as an indicator of the degree to which soil microbes have processed soil organic matter (Nadelhoffer and Fry 1988; Billings and Richter 2006). Sub-samples of each soil were dried, ground to fine powder, and weighed into a tin capsule for analysis. Values of $\delta^{15}N$ were obtained at the Kansas State University Stable Isotope Lab, where an Elementar EA Vario Pyrocube linked to an Elementar GeovisION Isotope Ratio Mass Spectrometer determine N concentration and $\delta^{15}N$, respectively.

3.2 Measuring Soil Chemical and Physical Properties

To better assess possible differences in the chemical and physical controls on SOC stability we also measured pH, effective cation exchange capacity (ECEC), soil texture, and wet aggregate size distribution (ASD). We focused on pH as it is known to strongly control microbial communities and mineral associated organic carbon (MAOC) (Kleber et al., 2015). The soil pH was determined in a 1:1 soil slurry (Soil Survey Staff, 2022). We focused on ECEC because ECEC has a high positive correlation with SOC, clay content, and aluminum and iron oxides (Solly et al., 2020), which are highly correlated with the formation of MAOC (Kleber et al., 2015). ECEC was determined by summing Ca, Mg, and K extracted using a Mehlich-3 solution (Culman et al.,

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2019). Mehlich-3 extraction was used instead of an ammonium acetate extraction, because the soils samples had a pH of <7.5 and there is very little to no calcium carbonate. In these conditions Mehlich-3 and ammonium acetate extractions yield similar ECEC values (Rutter et al., 2021).

We examined soil texture at each pit for several reasons. First, the total amount of clay is important to MAOC, and second, texture is known to impact the distribution and connectivity of pores. This connectivity influences how easily oxygen can diffuse into a soil profile and thus processes such as microbial respiration (Schjønning et al., 1999; Moldrup et al., 2001), and further regulates water and solute transport down-profile. Soil texture was analyzed on pit samples collected from 2020-2021 using a laser diffraction (LD) unit (Bettersizer S3, Bettersize Instruments, Dandong, Liaoning, China). Five grams of soil was ground and sieved to 2 mm, and organic matter was removed by treating samples with 30% hydrogen peroxide. Ten ml of 10% sodium hexametaphosphate (HMP) was added to the solution to prevent flocculation. The soil solution was pipetted into the Bettersizer until obscuration levels were between 14-20. We set clay- silt and silt-sand boundaries to be 6.6 and 60.33 µm, respectively (Makó et al., 2017).

Aggregate-size distributions were measured on each soil horizon following Nimmo and Perkins (2002). Briefly, around 25 g of the largest air-dried aggregates were fully saturated with a Dickson apparatus (Dickson et al., 1991), and placed on a Yoder device where sieves (#4, 10, 17, 70) and soil samples were raised and lowered in the water 2.8 cm per stroke at a rate of 36 strokes per a minute for 10 minutes. Following this agitation in water, the sieves with their respective aggregates were placed in a drying oven at 105 °C for 12 hours. The soil material remaining on each sieve was dispersed with 200 ml of 2 g L^{-1} HMP, mixed for 10 minutes, passed through the sieve again, and oven dried at 105 °C for 2 hours. Weights were recorded and mass fractions of water-stable aggregates were then calculated. Sieves divided aggregates into 5 classes: aggregates > 4.76 mm, aggregates between 2-4.76 mm, aggregates between 0.21-1 mm, and aggregates less than 0.21 mm. To simplify our analysis, we agglomerated these into 3 classes following Souza et al. (2023): fine aggregates (< 0.21 mm), intermediate aggregates (0.21-4.76 mm), and coarse aggregates (> 4.76 mm). A weighted geometric mean aggregate diameter (GMD) was calculated for each triplicate using the mass fractions of each aggregate-size class; the mean and standard deviation were calculated from these triplicate values to represent the aggregate diameter of each sample. The GMD values were divided by SOC content and the resulting values were used to characterize the propensity of carbon to form aggregates.

3.3 Measuring Rooting Distributions

To determine the relationship between roots, and carbon stability and transport, we measured the fraction of soil volume containing fine and coarse roots throughout the soil profiles using images collected from all 10 pits (e.g., 2020/2021 and 2022). Each image was overlain with a

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1x1 cm grid and analyzed using ImageJ (Schneider et al., 2012). The presence of a fine root (diameter < 1 mm) or coarse root (diameter > 1mm) was noted for each grid cell. Our focus is the soil volume containing roots and thus directly influenced by roots. As such, only presence/absence and not count data were recorded, and in any cell containing both fine and coarse roots the presence of only the coarse root(s) was recorded given their greater volume (Billings et al., 2018). These measures are thus a conservative measure of direct root influence on soil volumes, derived at the cm scale for soil pedons. Centimeter-scale cell presence/absence data were transformed into the fraction of each 1-cm thick layer containing roots.

3.4 Sensor Data

Soil sensor arrays were installed in the first set of pits (2020/2021) at the completion of sampling. Sensors were installed at depths of 15 cm, 45 cm, and 110 cm (or deepest depth) to monitor soil temperature (°C) and volumetric water content (VWC ; EC-5, Meter Group, Pullman, WA), matric potential (kPa) (Teros 21, Meter Group, Pullman, WA), O_2 concentration (%) (IB201806, Apogee Instruments, Logan, UT) and CO_2 concentration (ppm) (F0275476, Eosense, Dartmouth, Canada). Data were collected every 30 mins for moisture, matric potential, and temperature and hourly for O_2 and CO_2 given the power requirements. We focus on CO_2 and O_2 as they are indicators of soil microbial and root biotic activities including heterotrophic respiration. Microbial activity directly and indirectly affects the formation of MAOC, SOC stabilization, and microaggregation (Dohnalkova et al., 2022). We used sensor data to investigate additional environmental controls on carbon dynamics. We converted O_2 from ppm to % by adding calibrated values to the ppm value of O_2. Each calibrated value was specific to the sensor installed and determined prior to installation. To focus on the growing season, we selected data from June 15-August 29, which was 14 days before the first sample was collected (June 29th) and ending 14 days after the last sample was collected (August 15th). AS reflects 2021 data, SS reflects average daily 2021 and 2022, and ESG, EAG, and SG reflects 2022 data. These differences were because pits were installed with sensors in different years and some of the instrumentation had power outages and other unforeseen issues. We averaged daily temperature and VWC by week and examined average and standard deviation of the O_2 and CO_2 over the growing season.

3.5 Data Analysis

Spatial replicates controlling for all ecosystem-scale factors were not feasible in this study. Instead, we advance our understanding of SOC stability by examining a more diverse suite of biotic and abiotic ecosystem characteristics than is often the case in SOC-focused work. Our work begins to unravel the complex interactions among cover type characteristics, soil properties, and hydrologic settings in SOC dynamics. We used linear mixed effects (LME) methods via the R package *lme4* (Bates et al., 2014) to assess the influence of vegetation type,

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depth, and their interaction on soil abiotic conditions, various forms of soil nitrogen and carbon, ASD, and root abundances. We tested if variables were normally distributed using the Shapiro-Wilks test, and transformed the data to achieve a normal distribution if they were non-normal. The soil chemical properties of SOC, EOC, EOC:SOC, ECEC were log transformed, while C:N data were transformed with the function $x^{1/3}$. Root fractions and soil solution pH did not require transformation to meet model assumptions. We assessed if vegetation type exerted a meaningful influence on the previously mentioned variables by constructing four models. The two simplest models included only vegetation type or depth, both as fixed effects. A third model included those fixed effects additively (e.g., Vegetation + Depth), and a fourth model included their interaction. We resolved the lack of independence of soil depth within each pedon by incorporating site identifiers as a random effect term in the model. We then tested the normality of the model residuals using Shapiro-Wilk test. For all models that passed this test, we compared the model fits using analysis of variance (ANOVA) and visually examined model residual errors for homogeneity of variance; the best model fit was selected based on the lowest Akaike information criterion (AIC) following Hauser et al. (2020). We interpret the results of these LME models conservatively, given the low number of replicate sites for each land cover type. We could not perform a LME model on microbial biomass and enzyme data due to the relatively limited number of samples. This limited our ability to run LME models on depth interactions with vegetation.

4 Results

4.1 Soil Properties and Development

Clay, silt, and sand content at the aspen sites (AS and EAG; Fig. S1) and one of the conifer sites (ESG) remained constant with depth (average 33.1% clay and 18.8% sand), while texture was more variable in the other conifer sites (SS and SG; Fig. S1). Soil ECEC was similar among the aspen and conifer sites with averages of 7.2 ± 4.9 and 8.2 ± 6.8 (meq/100 g soil), respectively, with elevated values at the surface which followed an exponential decline with depth (Fig S2).

Soil profiles were described to approximately 100 cm (Fig. 2, Table. S1). All sites had weak to moderately strong subangular blocky structure throughout the soil profile, and most sites had weak to moderately strong granular structure in A and upper B horizons. Dendritic tubular pores, interpreted to be abandoned root channels, were present throughout the soil profile of aspen sites, while they were less common in the conifer soil profiles. Aspen sites exhibited faint organic stains and organoargillans (i.e., dark, organic stained clay films) throughout the soil profile, while conifer sites had clay bridges and krotovina throughout the soil profile. The krotovina suggest greater bioturbation under conifer than aspen. Both vegetation types exhibited ferriargillans (i.e., clay coats that include Fe oxides), clay films, and charcoal, although ferriargillans and clay films were more prominent under conifer. Clay bridges, organoargillans, and ferriagllians indicate illuviation. Lithologic discontinuities were identified in SS, ESG, and EAG indicating colluvial inputs into these footslope pedons.

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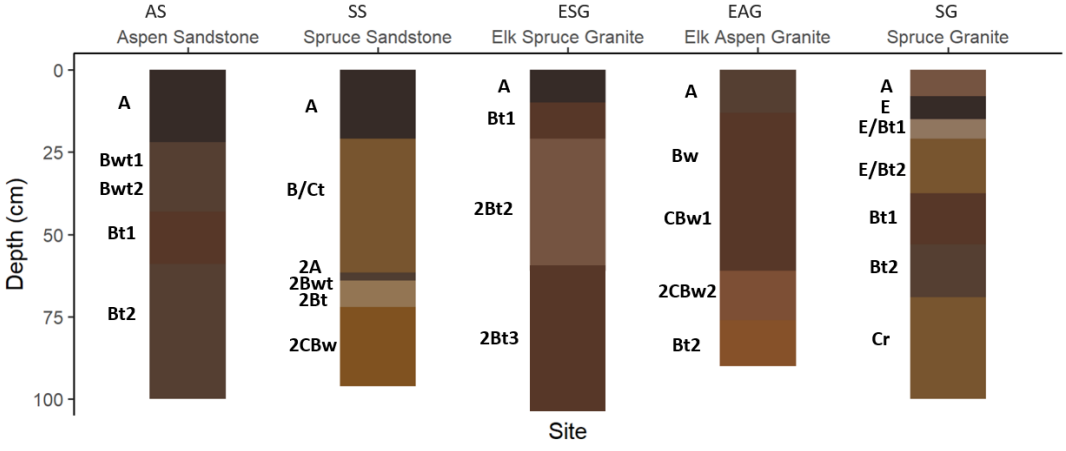

Figure 2: Soil profiles described at each site showing which depths were aggregated into A, upper B, and lower B horizons. Horizon colors represent the moist color of the soils as matched to the soil-color or Munsell chart.

Soils at both aspen sites (AS and EAG) were classified as Ustic Haplocryolls with thick SOC-enriched surface horizons (mollic epipedons) and showing evidence of incipient subsoil development in the form of moderately thick cambic horizons. Soils under conifer sites were classified as Typic Haplocryepts (SS and SG) and Eutric Haplocryalfs (ESG). Although surface horizons under conifer were not as well-developed (ochric epipedons), the subsurface showed similar incipient pedogenesis in the form of cambic horizons for SS and SG and greater development in the case of ESG where an argillic horizon was identified between 19-90 cm below the mineral surface.

4.2 Soil abiotic conditions

To understand how soil abiotic conditions are linked to SOC forms and processing pathways, we focused our analysis of soil temperature and moisture during the growing season (June – August; Fig. 3). As expected, soil temperature increased at all sites as the growing season progressed peaking in mid to late July, with the warmest temperatures observed near the surface and lower variability observed at depth. We also observed that the aspen sites (AS & EAG), which are on south-facing slopes, are warmer than conifer sites with an average surface soil (15 cm deep) temperature of 14.3 ± 1.2 and 10.4 ± 1.0 °C, respectively, during the growing season. Aspen sites were generally drier than conifer. The average volumetric water content in the surface soils (15 cm deep) at aspen sites was 0.15 ± 0.05 and the average volumetric water content at spruce sites was 0.24 ± 0.05 $cm^3\,cm^{-3}$.

We also examined soil pH and found the average pH across the entire soil profile was similar at the aspen and spruce sites, 5.6 ± 0.3 and 5.3 ± 0.4, respectively, but their depth trends differed with spruce soils having slightly more acidic pH near the surface compared to the aspen (Fig. S2). This trend reversed after approximately 60 cm where the aspen soils became slightly more acidic compared to the conifer soils.

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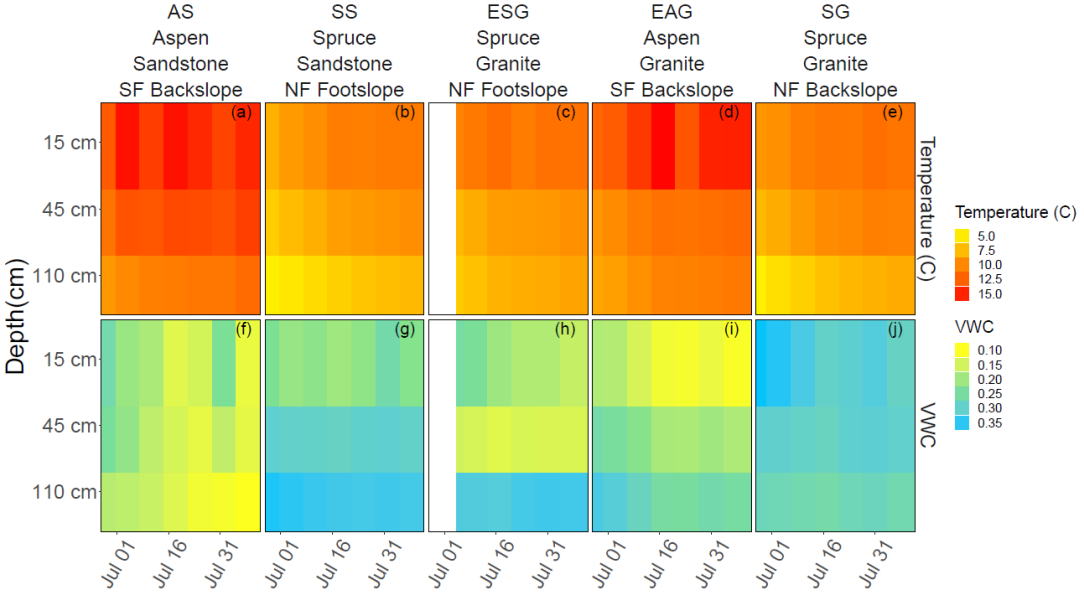

Figure 3: Temperature (a-d; °C) and volumetric water content (VWC (cm^3 cm^{-3}); e-i) data for aspen sandstone (AS; a, f), spruce sandstone (SS; b, g), spruce granite (ESG; c, h), aspen granite (EAG, d, i), and spruce granite (SG; e, j). AS reflects 2021 data, SS reflects averaged 2021 and 2022, ESG, EAG, and SG reflects 2022 data.

4.3 Soil Organic Carbon and Nitrogen

Across all sites, SOC concentrations ranged from 46.0-62.6 mg g^{-1} near the surface (5 cm deep) to 4.8 to 29.0 mg g^{-1} at depth (65 cm deep), while SOC stocks had a similar range across depth with value observed between 0.005-1.31 kg m^{-2}. SOC concentrations and stocks were generally higher under aspen compared to spruce sites (Fig. 4a-b). The LME models suggested vegetation interacts with depth to exert a meaningful effect on SOC (p-value < 0.001), whereby both SOC declines with depth for both vegetation types but to a greater extent under spruce compared to aspen. In contrast to SOC, DOC was higher under the spruce stands compared to the aspen (Fig. 4c). The DOC concentrations also declined with depth but this decline was more muted than that of SOC concentrations. The additive effect of vegetation and depth appeared to have a more meaningful effect on DOC than a vegetation-depth interaction. The ratio of DOC (µg g^{-1}) to SOC (mg g^{-1}) appeared higher at the spruce sites compared to the aspen (Fig. 4d). The ratio under both vegetation types increased with depth, ranging from 0.24 to 10. The LME model suggests vegetation-depth interactions have the most meaningful effect on DOC:SOC. Both greater SOC and lower DOC:SOC under aspen, in comparison to spruce, suggest that different processes drive SOC dynamics under these two vegetation types.

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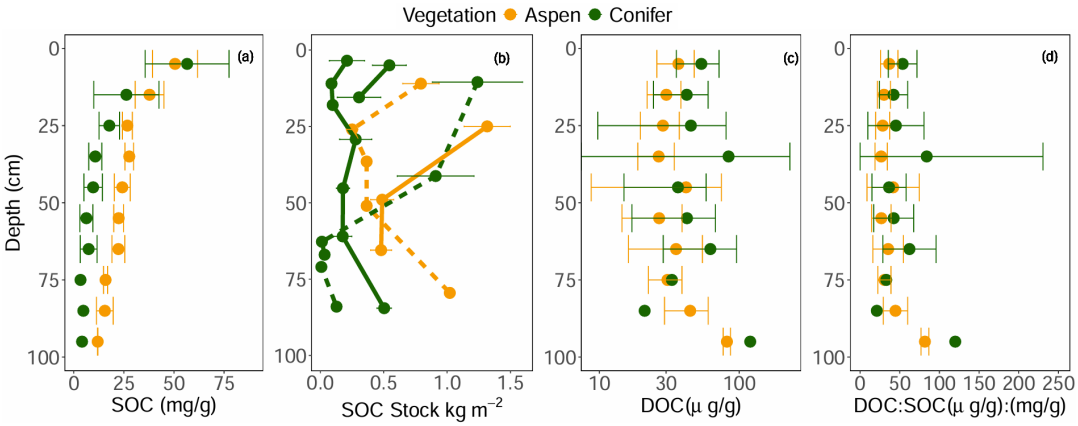

Figure 4: The mean and standard deviation of (a) soil organic carbon (SOC) concentrations, (b) SOC stock [by horizon per pit], (c) dissolved organic carbon (DOC), and (d) the ratio of dissolved organic carbon to soil organic carbon (DOC:SOC) with depth under two different vegetation types, aspen (orange) and spruce (green).

Total soil nitrogen and nitrate concentrations were elevated under the aspen compared to the spruce sites (Fig. 5a & b). Under both vegetation types, soil nitrogen and nitrate declined with depth, with values of total nitrogen reaching as high as 4.63 mg g^{-1} near the surface and as low as 0.2 mg g^{-1} at depth, while nitrate concentrations averaged 214 $\pm$ 323 mg g^{-1} near the surface and 2.3 $\pm$ 3.8 mg g^{-1} at depth. The LME models suggest that the vegetation-depth interaction model was most effective at explaining soil nitrogen, and that vegetation type was an influence on soil nitrogen depending on the depth at which the comparison across cover types was made. The LME models also indicate that vegetation exerts a strong control on nitrate concentrations.

The ratio of organic C to N showed no consistent trend with depth in either vegetation type. Instead, aspen soil C:N averaged 10.9 ± 1.1 and remained fairly constant with depth (Fig. 5c). The spruce sites showed a large range in behavior with depth with a similar mean value of 19.3 in the top 20 cm but widely variable values at the deepest points, ranging from 4.6 to 28.7 (Fig. 5c). The $\delta^{15}N$ showed less distinct depth trends compared to the total nitrogen and nitrate, mirroring the lack of depth trends in C:N. Values of $\delta^{15}N$ of soil organic matter in spruce plots tended to be lower than that of the aspen(Fig. 5d), suggesting that soil N has undergone more microbial processing (Nadelhoffer and Fry 1988; Billings and Richter 2006) under aspens compared to under conifers. Here the LME models suggested vegetation interacts with depth to exert a meaningful effect on $\delta^{15}N$ values.

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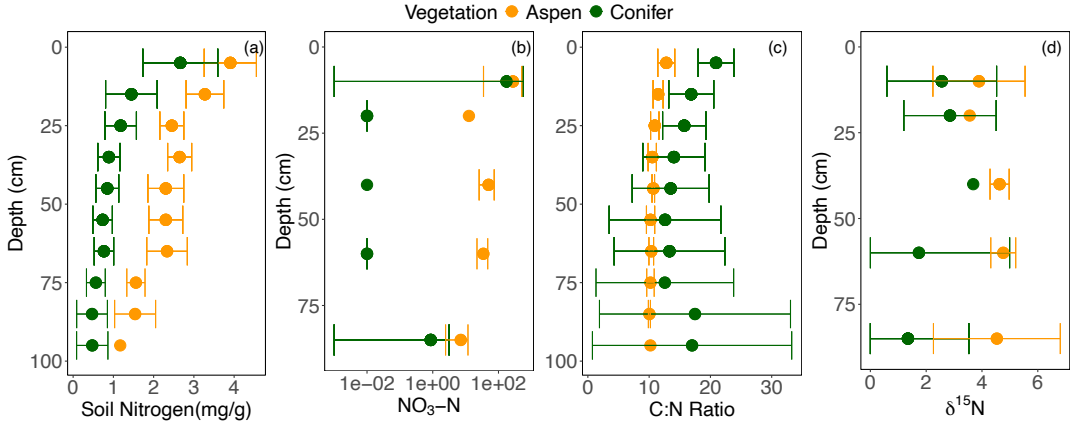

Figure 5: The mean and standard deviation of (a) soil nitrogen, (b) soil nitrate, (c) carbon nitrogen ratio (C:N), and $\delta^{15}N$ with depth under two different vegetation types, aspen (orange) and spruce (green). For each mean and standard deviation, where error bars are not visible the deviation is smaller than the point.

4.4 Biotic activity

4.4.1 Roots

The LME models indicate that vegetation-depth interactions were meaningful in driving total and coarse root fractions (p-values <0.001), with generally greater root abundances in the aspen compared to the spruce (Fig. 6a &c). In contrast, vegetation type offered no additional explanatory power to the depth-dependent fine root abundance (Fig. 6b). The difference between aspen and spruce root abundances were continuous with depth for the total root fraction but more punctuated with coarse root fraction. For example, higher coarse root fractions were observed from 30-60 cm and greater than 90 cm for the aspen as compared to the spruce. Interestingly, overall spruce root fractions decreased faster with depth than aspen root fractions. When we compared the DOC to rooting abundance, we found generally greater concentrations of DOC per unit root abundance under spruce soils, particularly with respect to total and fine roots (Fig. 7).

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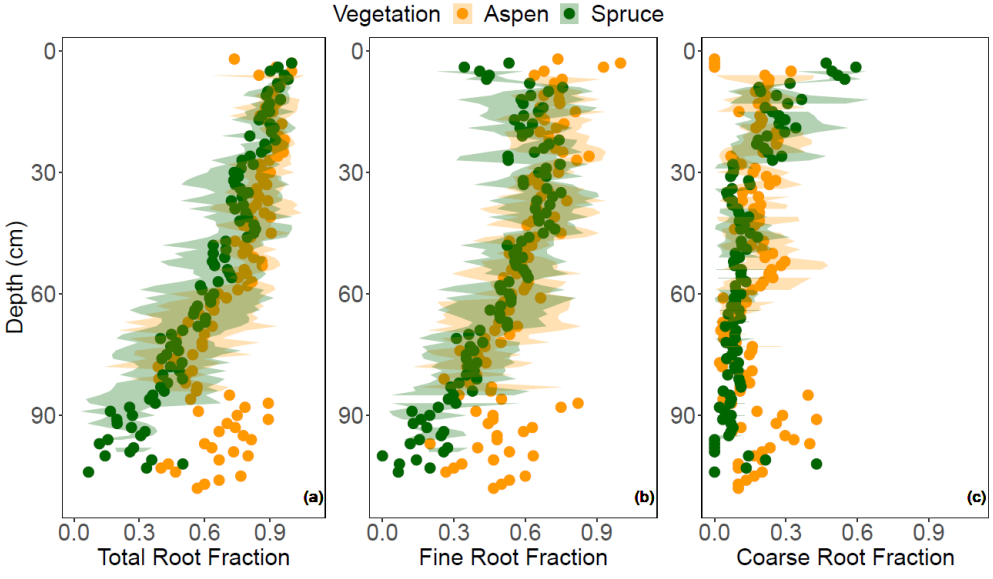

Figure 6: The mean (points) and standard deviation(shading) of (a) total, (b) fine, and (c) coarse root fractions quantified at 1-cm depth interval under two different vegetation types, aspen (orange) and spruce (green).

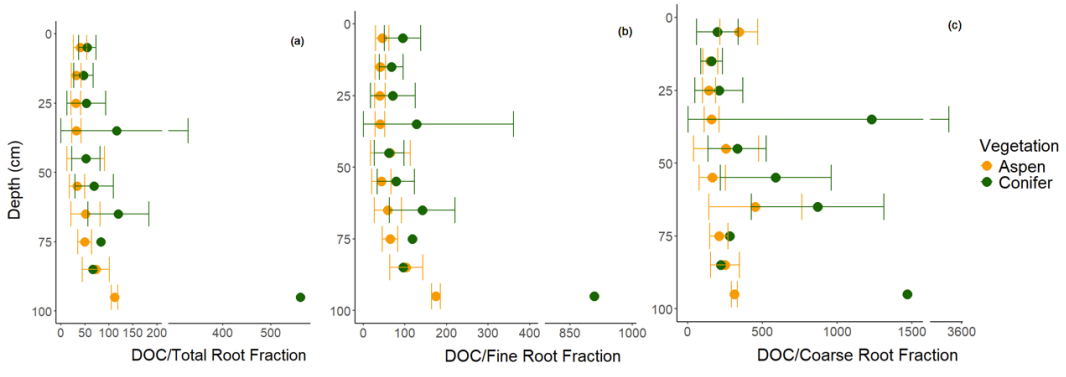

Figure 7: The mean (points) and standard deviation (bars) of DOC divided by mean (a) total, (b) fine, and (c) coarse root fractions every 10 cm under two different vegetation types, aspen (orange) and spruce (green). Root fractions represent the count of fine (<1 mm) or coarse (≥1 mm) in 10 cm depth increments.

4.4.2 Enzyme activity and microbial biomass

Exo-enzyme activity, their ratios, and microbial biomass C decreased from the surface with depth (Fig. 8a.-d.). Exo-enzyme activity standardized by microbial biomass lacked distinct depth trends (data not shown). Beta values of exponential decay curves fit to these

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data, merged for each cover type, were larger (more negative) for the spruce sites compared to aspen, indicating steeper declines in exo-enzymatic activities, microbial biomass C, and BGase activity relative to NAGase activity in spruce-dominated forest soils.

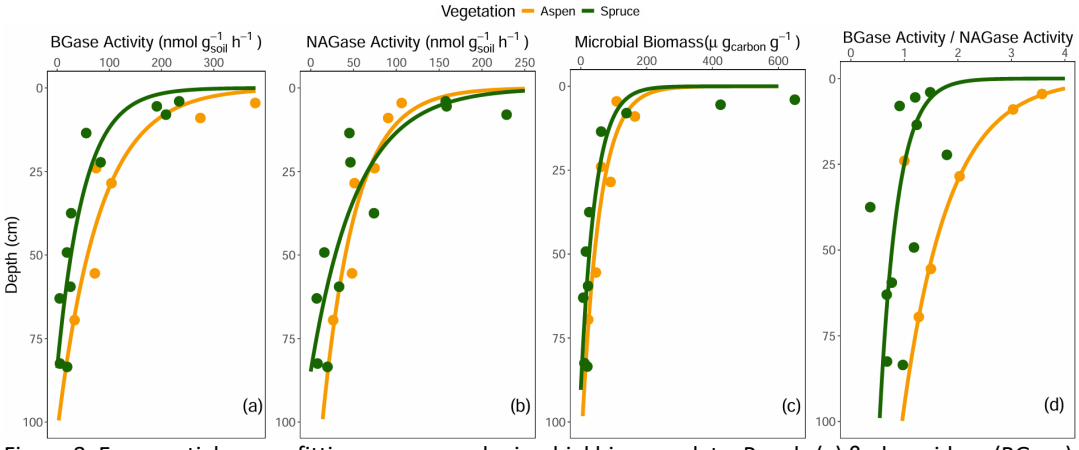

Figure 8: Exponential curves fitting enzyme and microbial biomass data. Panels (a) β-glucosidase (BGase) (b) β-N-acetyl glucosaminidase (NAGase) (c) microbial biomass and (d) the ratio of BGase to NAGase. Each point represents one site and one depth, with each curve thus defined by multiple spruce and aspen sites.

4.4.3 Soil O_2 and CO_2

We examined soil O_2 and CO_2 concentrations during the growing season to better understand patterns of respiration (Fig. 9). Soil CO_2 concentrations increased with depth across all sites, while O_2 concentrations were more variable. Soil O_2 concentrations remained relatively stable at aspen sites and at spruce granite sites (AS, EAG, and SG). However, O_2 concentrations decreased with depth at the remaining two spruce sites—one sandstone and one granite (SS and ESG).

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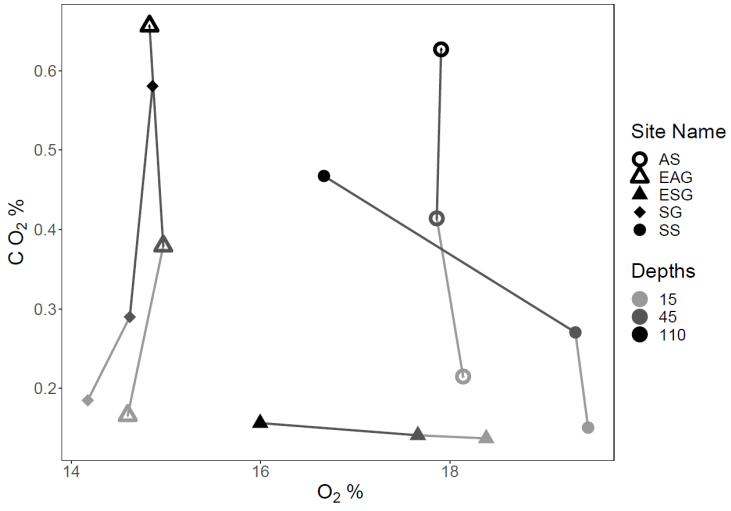

Figure 9: Average and standard error (obscured by symbols) of the soil O_2 (%) and CO_2 (%) concentrations during the growing season at depths 15 cm (light gray), 45 cm (dark gray), and 110 cm (black), with lines connecting depths within each profile. Open shapes are aspen sites, closed shapes are spruce sites, circles are sandstone sites, and other shapes are granite sites. AS, Aspen Sandtone; EAG, Elk Aspen Granite; ESG, Elk Spruce Granite; SG, Spruce Granit; SS, Spruce Sandstone.

4.4 Soil Aggregates

The mean geometric diameter of soil aggregates was generally smaller under aspen compared to spruce (Fig. 10a), and aspen aggregates tended to be finer, with fewer intermediate and coarse aggregates compared to granite (Fig. 10b-d). LME indicated that vegetation-depth were the most meaningful in driving fine, intermediate, and coarse aggregate fractions (p-values <0.001). Of the three aggregate size fractions, the fine aggregate fraction was most characterized by vegetation and depth interactions.

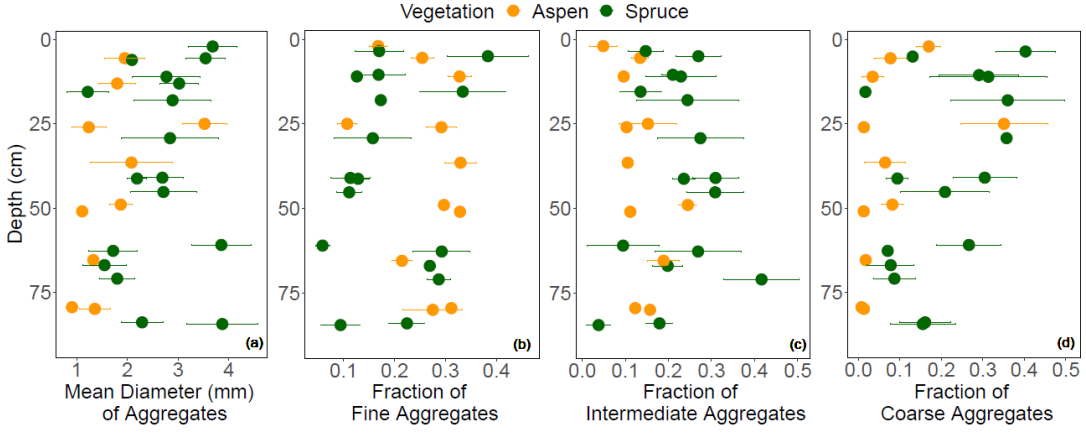

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Figure 10: The geometric mean and standard deviation of (a) all aggregates, and fraction of (b) fine aggregates (< 0.21 mm), (c) intermediate aggregates (0.21-4.76 mm), and (d) coarse aggregates (> 4.76 mm). Colors are associated with vegetation, aspen (orange) and spruce (green).

We standardized aggregates by SOC to investigate the propensity of SOC to form large aggregates (Fig. 11; Souza et al. 2023). We observed a higher coarse aggregate:SOC ratio in the spruce sites, suggesting that SOC in spruce-dominated soils exhibits a higher propensity to form coarse and intermediate aggregates (data not show), while the fine aggregate:SOC ratio tended to be higher in the aspen.

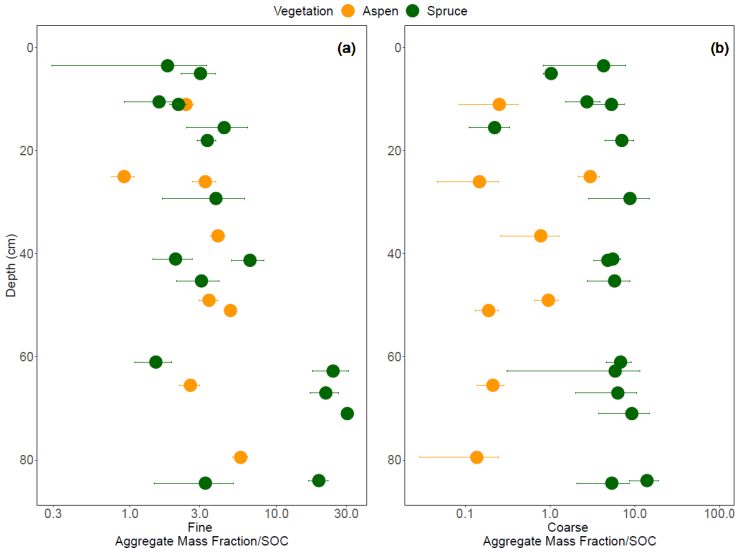

Figure 11: The mean and standard deviation of the fraction of (a) fine aggregates (< 0.21 mm) and (b) coarse aggregates (> 4.76 mm) divided by the fraction of SOC. Colors are associated with vegetation, aspen (orange) and spruce (green).

5 Discussion

Our data indicate that differences in SOC protection give rise to often observed patterns of elevated SOC storage in soils under aspen compared to those in conifer stands (Woldeselassie et al., 2012, Laganiere et al., 2013, Boca et al., 2020, Román Dobarco et al., 2021), and that by integrating knowledge from biology, pedology, hydrology, and soil chemistry we can better understand how factors interact to drive observed SOC patterns in aspen and conifer montane forests. Our study further suggests that aspen-dominated soils may experience enhanced degrees of microbial transformation of SOC, with the products of those transformations exhibiting a greater tendency to reside in relatively small aggregates and thus protect carbon to a greater degree (Fig. 12). Consistent with this idea, we also observed less DOC loss in aspen soils compared to soil under spruce stands and slightly higher concentrations of DOC per unit root abundance under the spruce stands. These differences suggest greater infiltration of DOC

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to deeper horizons in spruce soils compared to those in aspen stands. It is important to highlight that spatial replicates controlling for all factors of interest at an ecosystem scale were not feasible, but that our work moves beyond considerations of vegetation biomass characteristics that often dominate investigations of contrasting SOC dynamics. Instead we begin to unravel the complex interactions among cover type characteristics, soil properties, and hydrologic settings (e.g., hillslope position). Below, we discuss the drivers of SOC form and fate in greater detail and interpret these findings in light of recent increases in stream water DOC concentration in this spruce-dominated watershed.

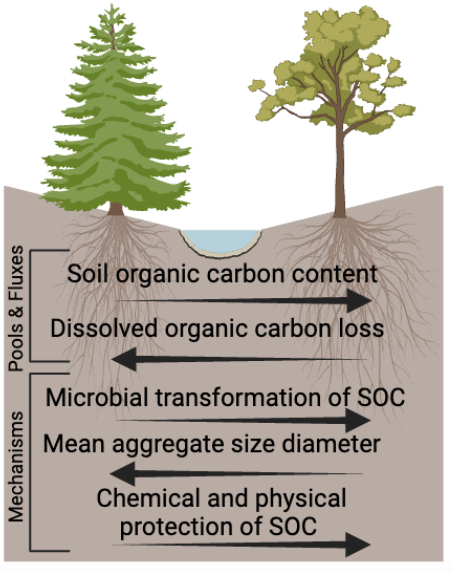

Figure 12. Summary of observations across aspen and spruce sites at Coal Creek, CO (USA) that are interpreted to indicate a greater amount of chemical and physical protection of SOC under aspen sites.

5.1 Microbial data are consistent with the Microbial Efficiency - Matrix Stabilization framework

Our data provide multiple lines of evidence that SOC protection, and thus fate, in these montane forests is largely controlled by biotic action linked to soil mineral material. Here greater values of total N, nitrate, BGase and $\delta^{15}N$ and lower C:N under aspen compared to spruce (Fig. 5, 8), suggest a greater degree of microbially processed organic matter under the aspen stands where greater SOC contents were measured (Fig. 4). These data hint that the microbial community under aspen stands functions in a manner consistent with the Microbial Efficiency - Matrix Stabilization (MEMS) framework (Cotrufo et al., 2012), transforming relatively labile leaf litter (e.g., under aspen) into byproducts more readily stabilized within soil profiles to a greater extent than appears to occur with slower-turnover litterfall (e.g., spruce). Differences in litterfall composition and thus decay rates across aspen and conifer species are typical, with generally lower lignin and higher nitrogen content in aspen litter (Boča et al., 2020). Our inference about litterfall differences promoting microbial byproduct stabilization is

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consistent with findings from across western Canada, where investigators observe relatively more active microbial communities under aspen compared to paired spruce stands throughout a growing season (Norris et al., 2016). Specifically, one interpretation of these C:N, $\delta^{15}N$, exo-enzyme, SOC, and DOC data at our sites is that tree species-specific composition of litterfall appears to have prompted greater microbial activities (Fig. 8), likely promoting greater contributions of microbial necromass to the SOC pool. This, in turn, may promote greater SOC retention in aspen-dominated soils; though Investigation of specific necromass-derived compounds in these soils (e.g., Liang et al., 2019) is beyond the scope of this work, it represents a valuable way forward to testing this inference.

5.2 SOC transformations likely influence aggregate sizes and the probability of destabilization

The smaller aggregate sizes in aspen-dominated soils further support the notion that SOC stability is enhanced by higher microbial activity and increased necromass production rates. SOC is better protected and has generally longer mean residence times in smaller aggregates than larger aggregates (Six and Jastrow, 2002; Six et al., 2004). Literature hints that the larger size aggregates (Fig. 10c) and greater propensity for C to form large aggregates (Fig. 11b) observed in the spruce-dominated soils at our sites may be promoted by relatively higher concentrations of particulate organic matter (POM) under spruce soils compared to aspen (Cotrufo et al., 2015; Cotrufo et al., 2019). Taken together, these lines of evidence are consistent with aspen-dominated forests harboring SOC pools that tend to promote relatively small aggregate formation that can preserve SOC to a greater extent, particularly deeper in the profile where MAOC tends to dominate SOC pools (Jackson et al. 2017).

We also observed patterns in soil data suggesting that aspen soil SOC pools are more dominated by MAOC than those under spruce. The greater abundances of smaller aggregates and total soil nitrogen and nitrate concentrations, and lower C:N ratios (Fig. 5a-c), in aspen compared to conifer soils are consistent with relatively greater MAOC than POC concentrations (Kögel-Knaper et al., 2008; Ye et al., 2018; Sokal et al., 2022). Combined with the lower DOC:SOC ratio in aspen-dominated soils, these data suggest that a greater fraction of SOC in aspen-dominated soils is mineral-bound and relatively difficult to transform into microbially-available pools of DOC. We interpret these data to suggest that microbially-mediated transformations of SOC promote differences in the abundance of MAOC and the physical structure of soil aggregates that leads to differences in the SOC protection.

5.3 Roots may indirectly regulate depth profiles of EOC losses

Roots can influence SOC stability through their promotion of both physical and chemical protection. Specifically, roots can play an important role in the formation and breakdown of soil aggregates (Oades, 1984; Singer et al., 1992; Le Bissonnais 1996; Attou et al., 1998), they can create biopores that can support the transport of DOC to depth (Sigen et al., 1997; Angers and Caron, 1998; Boger et al., 2010; Zhang et al., 2015; Lucas et al., 2019), and root exudates can prime microbial activity, enhance decomposition, and support the formation of MAOC (Jilling et al., 2021; Fossum et al., 2022). Our data revealed little direct correspondence of root abundance with SOC. However, per unit root abundance, spruce soils appear to harbor more DOC compared to aspen. This was particularly evident per unit total and fine roots, and is

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suggestive of greater movement of DOC through spruce soil profiles with potential greater losses of DOC to stream water compared to aspen-dominated soils. A complementary explanation would be that there are differences in the amount of DOC exudation by roots between the two species, and indeed such difference in exudation rates have been hypothesized in the literature (Buck and St. Clair, 2012; Boca et al., 2020). We might expect that greater exudation would lead to a greater increase in the MAOC pool and enhanced C stability (Even and Cotrufo, 2024), which could explain the lower values of DOC relative to SOC observed under aspen.

5.4 Aspect exerts some control on Coal Creek SOC dynamics.

South-facing slopes tend to be warmer and drier than north-facing slopes in the northern hemisphere (Burnett et al., 2008), and thus they can prompt more microbial decomposition of SOC. As such, aspen cover tends to be confounded with warmer soil temperatures; this was the case in our study (Fig. 2). It is possible that the exo-enzymatic signals of generally greater microbial activity in aspen-dominated soils compared to spruce-dominated soils (Fig. 8) is prompted more so by enhanced soil temperatures than by differences in aspen and spruce organic matter characteristics, and that enhanced soil temperatures also contribute to smaller soil aggregates, perhaps also due to greater microbial activities. Consistent with this idea, soil CO_2 and O_2 concentrations generally suggest that microbial activities in the warmer, aspen-dominated soils are greater than in the cooler, spruce-dominated soils. Cooler, wetter conditions of the spruce-dominated soils, particularly following snow melt may prompt a deeper infiltration of moisture and DOC down profile, leading to the elevated DOC/root biomass observed under the spruce stands. While disentangling the impact of elevated soil temperatures from that of the chemical composition of organic inputs from aspen trees within the soil profile is difficult, soil nitrogen and $\delta^{15}N$ data are consistent with the idea that litterfall chemistry, and not just temperatures, promoted greater microbial activities in the aspen-dominated soils. We suggest that investigating the comprehensive, integrated effects of warmer, aspen-dominated sites on SOC dynamics compared to cooler, spruce-dominated sites offer a straightforward approach to assessing landscape-scale transitions in watershed carbon dynamics.

6 Changes in SOC destabilization and release have implications for stream water quality

Widespread increases in stream water DOC concentrations have been reported around the world in recent decades (Evans et al., 2005; Alvarez-Cobelas, 2012; Stanley et al., 2012; Pagano et al., 2014). Increases in stream water DOC concentration can negatively impact global water quality in multiple ways by modifying light and thermal regimes, affecting natural nutrient cycling by absorbing incoming thermal radiation (Morris et al., 1995; Kelly et al., 2001; Larson et al., 2007; Cory et al., 2015), altering the transport and bioavailability of heavy metals (Dupré et al., 1999; Neubauer et al., 2013; Tang and Johannesson, 2003; Pourret et al., 2007; Trostle et al., 2016), and prompting the creation of potentially harmful disinfection byproducts (Leonard et al., 2022). Consistent with these global trends, recent findings at Coal Creek also report increasing DOC concentrations (Leonard et al., 2022; Kerins et al., 2024). As such, our research may help to shed light on drivers of stream water DOC, and thus has implications for changing

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drinking water quality in the region. Specifically, our work hints that differences in aggregate-size distributions may play an underappreciated role in influencing stream water carbon chemistry. Aggregate size can be modulated by vegetation type (i.e., smaller aggregates associated with Aspen) (Fig. 11; Jiménez et al., 2012; Zhao et al., 2017), and aggregation and disaggregation both represent mechanisms that can influence the transport of DOC to streams (Fan et al., 2022). Larger aggregates appear more prone to induce DOC transport into streams due to their relatively greater propensity to undergo fragmentation and associated loss of DOC (Cincotta et al., 2019; Fan et al., 2022).

Understanding how these different types of vegetation affect the chemical and physical properties of soil, and how this influences carbon release, is further complicated by climate change. Increasing temperature, a phenomenon evident in many Rocky Mountain environments including Coal Creek (Zhi et al., 2020), can cause aggregates to become less stable (Lavee et al., 1996, Wang et al., 2016), soil microbes to increase their carbon demand (Belay-Tedla et al., 2009, Hu et al., 2017), and recalcitrant carbon to undergo decay more rapidly (Luo et al., 2009). Dry soil conditions, which are often prompted by warming (Lakshmi et al., 2003), can induce a decrease in microbial biomass, which is often incorporated into stable aggregates (Gillballi et al., 2007). In addition to warming induced changes to subsurface properties and function, changing stand composition prompted by warming and drying can alter carbon dynamics. Some research indicates a high mortality rate among aspen stands and the expansion of conifer stands associated with increases in drought (Anderegg et al., 2013, Brewen et al., 2021), while others indicate the expansion of bark beetles and wildfires may promote the encroachment of aspen into conifer stands (Andrus et al., 2021). Our work suggests that the distribution of spruce and aspen in a watershed may influence soil release of DOC and its subsequent transport into streams, given that spruce vegetation appears associated with larger aggregates than aspen (Fig. 10) and the potential for greater DOC loss per unit SOC (Fig., 4c). Thus, shifts in stand composition associated with perturbations linked to large-scale global changes have the potential to influence DOC transport from the hillslope to the stream.

7 Conclusions

Our work explores the interplay of different forest cover types and abiotic conditions in governing soil microbial activities, which then influence the propensity of SOC pools to form and stabilize soil aggregates of different sizes. In turn, these processes appear to promote varying capacities of a soil to protect SOC from destabilization. Our work contributes to the on-going process of examining suites of biotic and abiotic whole-ecosystem (i.e., the critical zone, Richter and Billings, 2015) features to understand SOC dynamics (e.g., Keller, 2019; Mainka et al., 2022; Wasner et al., 2024) and offers a springboard for subsequent studies in which a greater number of spatially replicated sites across all gradients of interest may be feasible. Specifically, our data suggest that aspen-derived organic matter is linked to greater

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transformation rates by soil microbes and greater stabilization of SOC stocks, prompting a lower probability of relatively labile pools of SOC undergoing transport down-profile. If so, this suggests that aspen-dominated stands may experience a lower probability of promoting DOC transport across landscapes into streams. This phenomenon may be driven by greater rates of microbial necromass formation and generation of relatively smaller aggregates, and highlights how models like MEMS (Cotrufo et al., 2013) have import for projecting not just CO_2 release to the atmosphere and SOC stabilization, but down-profile and downstream carbon transport as well. Though soil temperature differences likely played a role in the greater soil microbial activities in aspen, the generally higher nitrogen in aspen soils lends credence to the idea that litterfall chemistry itself played a key role in the higher rates of soil microbial activities. As such, the patterns that emerge in our data suggest that processes that control landcover ultimately also control SOC dynamics and soil structure in ways that may directly impact the delivery of organic C pools deep within soil profiles and stream water quality, and be sensitive to changing climatic conditions. Here, we demonstrate how the critical zone paradigm offers a valuable approach for examining, interrogating, and understanding watersheds, linking vegetation dynamics to subsurface processes and ultimately to the flux of water and carbon from hillslopes to streams.

Data statement

Soil sensor and soil properties data can be obtained at HydroShare, http://www.hydroshare.org/resource/9948ad04a9a74246ad9bd5f8decb40b9

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Competing Interests

The authors declare that they have no conflict of interest

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