

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

Authors: Lena Wang¹, Sharon A. Billings², Li Li³, Daniel R. Hirmas⁴, Keira Johnson¹, Devon Kerins³, Julio Pachon⁵, Curtis Beutler⁶, Karla M. Jarecke¹, Vaishnavi Varikuti⁴, Micah Unruh², Hoori Ajami⁷, Holly Barnard⁸, Alejandro N. Flores⁹, Kenneth Williams⁶, Pamela L. Sullivan¹

¹ College of Earth Ocean and Atmospheric Science, Oregon State University. Address: 101 SW 26th St, Corvallis, OR, 97331, USA

²Department of Ecology and Evolutionary Biology and Kansas Biological Survey & Center for Ecological Research, University of Kansas. Address: 2101 Constant Ave., Lawrence, KS, 66047, USA

³Department of Civil and Environmental Engineering, Pennsylvania State University, Address: Sackett, #212, University Park, PA 16802, USA.

⁴Department of Plant and Soil Science, Texas Tech University. Address: 2500 Broadway Lubbock, Texas 7940 USA.

⁵Sydney Institute of Agriculture, School of Life and Environmental Sciences, University of Sydney, New South Wales, Australia. Address: The University of Sydney, NSW 2006, Australia.

⁶Lawrence Berkeley National Laboratory, Berkeley, CA USA Rocky Mountain Biological Laboratory, Gothic, CO USA. Address: 1 Cyclotron Road, Berkeley, CA 94720, USA.

⁷Department of Environmental Sciences, University of California Riverside. Address: 2460B Geology Building, Riverside, CA 92521USA.

⁸Department of Geography, Institute of Arctic and Alpine Research, University of Colorado – Boulder. Address: Guggenheim 110, 260 UCB Boulder, Colorado 80309-0260, USA.

⁹Department of Geosciences, Boise State University, Boise Address: 1295 University Drive, Boise, ID 83706 USA.

Correspondence to: Pamela L. Sullivan(Sullipam@oregonstate.edu)

Highlights:

1. Soil organic carbon concentrations 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 concentrations
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 concentrations under aspen compared to spruce. Growing season soil moisture, temperature, and CO₂ and O₂ 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 likely access more organically-bound resources; consistent with this, soil organic N exhibited higher $\delta^{15}\text{N}$ values, hinting at a greater degree of organic matter processing. Finally, aspen soils 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, which may have implications for 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 forest cover can directly impact soil organic carbon (SOC) stability. Given that SOC influences 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 Langanieri et al., 2017). Studies consistently show that C under conifers is more readily destabilized than under aspen (Woldeselassie et al., 2012; Langanieri et al., 2013; Boča 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 C (MAOC), which is a relatively stable SOC fraction, than those under conifers (66% compared to 48% MAOC to SOC, respectively; Román Dobarco and Van Miegroet, 2014; 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 C (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 C (DOC) (Cincotta et al., 2019), some of which can undergo microbial uptake and mineralization to CO₂. 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 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 (Amezketta, 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 CO₂ 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 (Mikutta 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 water movement and solute transport—traditionally studied by hydrologists and soil biogeochemists—along with biological and soil formation processes, is key to explaining 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 (Boča 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 (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 at the same time. 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 —integrating physical, chemical, and biological processes from the vegetation canopy to bedrock (Chorover et al., 2007)—drawing on data from biology, hydrology, pedology, and other disciplines 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 higher soil organic carbon (SOC) stocks commonly observed under aspen stands—relative to conifer-dominated soils—are driven by enhanced microbial activity in aspen soils. We further hypothesize that aspen-dominated soils contain more stable microaggregates than spruce soils, driven by higher microbial activity and associated increases in necromass production. Differences in rooting strategies and ecohydrologic factors (e.g., evapotranspiration, soil moisture) between aspen and spruce likely exert secondary controls on C stability. Finally, we hypothesize that the proliferation of fine roots in aspen soils is associated with smaller water-stable aggregates, whereas the deeper, coarser roots in spruce soils promote vertical movement of water and dissolved C down through the soil profile, potentially leading to greater DOC export to streams compared to aspen systems.

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 potential DOC transport into surface water, illuminating the possible trajectories of SOC and DOC in rapidly changing, montane forest watersheds.

2 Study Area

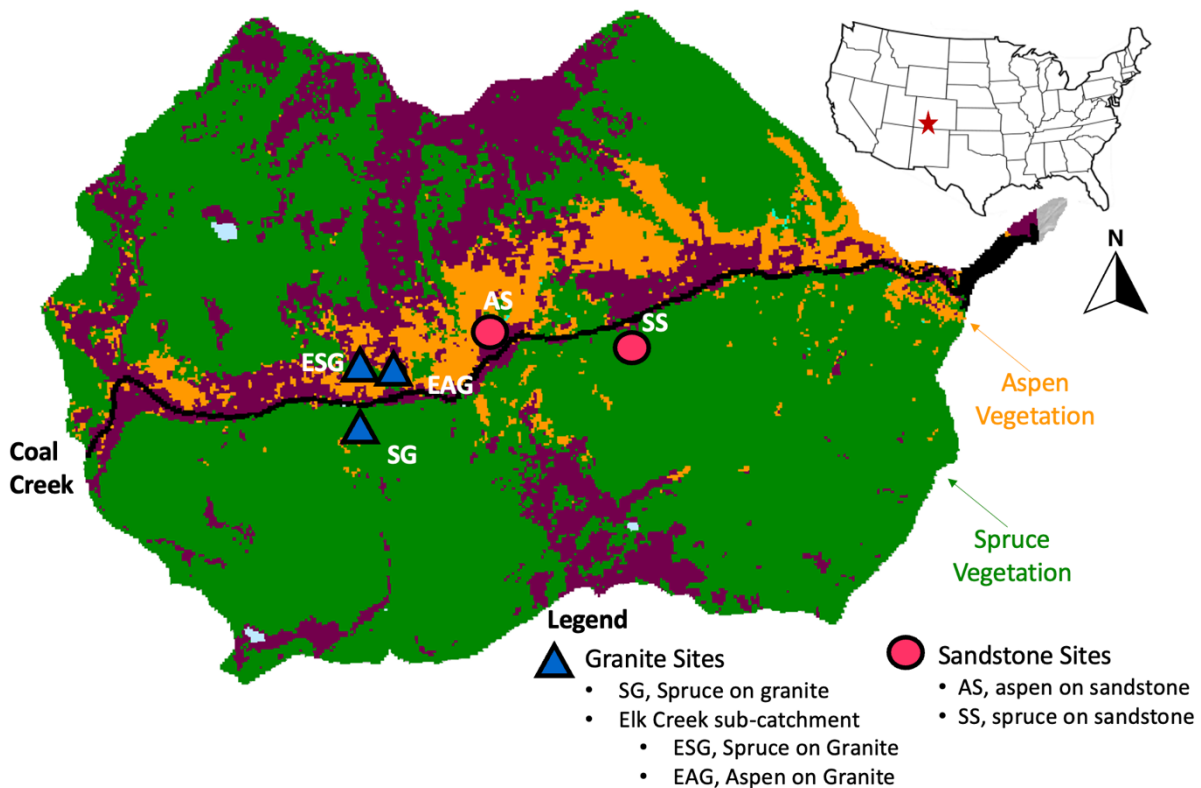


Figure 1: A map of the Coal Creek catchment. Colors represent land cover types, where aspen (orange) are dominantly at lower south-facing slopes while conifer (green) are on both north and south facing slopes. Shapes represent lithology type where granite sites (blue triangles) are in the western part 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 Coal Creek. 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 km²) 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 km²) 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 is 0.9 °C and the mean annual precipitation is 670 mm (Carroll et al., 2018), 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).

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 carbonate free 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. We focused on five sites during this study. Three of our sites lie within the main drainage of Coal Creek including two spruce sites (spruce sandstone, SS; spruce granite, SG) and one aspen (aspen sandstone (AS). The last two sites are located in Elk Creek, a sub-catchment of Coal Creek, which includes one spruce site and one aspen site, both underlain by granite (Elk spruce granite (ESG) and Elk aspen granite (EAG). While ESG is on a dominantly south facing slope, it is north facing within the Elk Creek catchment.

3 Methods

To quantify the impact of aspen vs. conifer land cover on soil organic C 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 spruce was 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 effects (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 (DOC, microbial biomass C, exo-enzyme assays, nitrate) 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 from 3 auger sampling locations within ~100 meters of each pit to characterize soil chemistry (i.e., SOC, DOC, pH). Soils were augured at 10 cm intervals to 110 cm (or deepest possible depth), and samples were stored in coolers with ice packs in the field and transported back to the lab and stored at 4 °C (most analyses) or frozen (SOC, DOC).

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

	Soil Pits	Soil Pits	Auger Samples
Timing	2020-2021 (July and September)	2022 July	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)		
Root Distributions	X	X	
%C and %N	X	X	X
Extractable nitrate concentrations		X	
$\delta^{15}\text{N}$		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 C and Nitrogen Dynamics

We assessed SOC and SON concentrations and stocks and the likelihood of SOC and SON degradation by microbes by analyzing bulk soil samples at 10-cm intervals. We determined SOC and SON on subsamples (~75 mg) via an elemental analyzer (Vario Macro Cube, Elementar, Ronkonkoma, NY). We used SOC and SON concentration measurements to calculate each subsample's C:N ratio. To determine stocks of SOC in each horizon, we multiplied SOC concentrations by soil bulk density obtained in 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 extractable, dissolved organic C (DOC) to estimate organic C that can be relatively easily mobilized and transported out of the soil profiles; note that this differs from DOC measured in soil porewater using lysimeters, and instead represents a salt-extractable pool. We analyzed soil samples at 10-cm intervals to auger refusal 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 moisture was extracted with 30 ml of simulated rainwater (Laegdsmand et al., 1999). The extracted soil solutions were comprised of 47.9 μM NaNO_3 , 4.69 μM KCl , 23.81 μM $\text{CaCl}_2 \times 2\text{H}_2\text{O}$, 12.09 μM $\text{MgSO}_4 \times 7\text{H}_2\text{O}$, and 18.24 μM $(\text{NH}_4)_2\text{SO}_4$ and adjusted to a pH of 4.2 ± 0.5 using HCl . Samples were placed on a shaker table for 30 minutes and centrifuged at 80 Hz (s^{-1}) for 15 minutes. Samples were filtered through 0.45 μm nylon 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 C by horizon from pits dug in the summer of 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 polyethersulfone (PES) filter and their DOC concentration was determined via colorimetry (Bartlett and Ross 1988) on a Synergy HT microplate reader (Agilent, USA). To assess the degree to which soil microbial communities were generating exo-enzymes that catalyze soil organic matter decay and thus can provide assimilable C- and N-rich compounds, we quantified potential activity rates of two such enzymes. We measured activity of β -glucosidase and N-acetyl- β -D-glucosaminidase, herein referred to as BGase and NAGase, which are linked to microbial C (BGase) and N and C (NAGase) acquisition (Sinsabaugh and Moorhead, 1994; Allison et al., 2011, Stone et al., 2014), using 4-methylumbelliferyl β -D-glucopyranoside (for BGase) and 4-methylumbelliferyl N-acetyl-

β -D-glucosaminide (for NAGase) fluorescent tags. These tags were added to slurries made from approximately 1 gram of soil and pH-adjusted 50 mM sodium acetate. We pipetted the blended sample into the desired substrate and incubated all plates 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, and provides a valuable point of comparison to DOC values. 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 $\delta^{15}\text{N}$, 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 $\delta^{15}\text{N}$ 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 $\delta^{15}\text{N}$, 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 C (MAOC) (Kleber et al., 2015). The soil pH was determined in a 1:1 H_2O 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., 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 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).

We quantified aggregate size distributions as one key metric of soil structure. 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 C to form aggregates.

3.3 Measuring Rooting Distributions

To determine the relationship between roots, and C 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). We used ImageJ (Schneider et al., 2012) to overlay each image with a 1 cm x 1 cm grid. We then manually checked each 1 cm x 1 cm grid cell for the presence of a fine root (diameter < 1 mm) or coarse root (diameter > 1mm) and noted these presence/absence scores 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; Table 1) 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), O₂ concentration (%) (IB201806, Apogee Instruments, Logan, UT) and CO₂ concentration (ppm) (F0275476, Eosense, Dartmouth, Canada). Data were collected every 30 minutes for moisture, matric potential, and temperature and hourly for O₂ and CO₂ given the power requirements. We focus on CO₂ and O₂ 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 C dynamics. We converted O₂ from millivolt readings to % by adding calibrated values to the millivolt value of O₂. Each calibrated value was specific to the sensor installed and determined using atmospheric concentrations 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 O₂ and CO₂ 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 Wilcoxon Rank sum tests to determine if differences between aspen and spruce concentrations of SOC, DOC, total soil nitrogen and nitrate, and of ratios of DOC to SOC were significant. We used linear mixed effects (LME) methods via the R package *lme4* (Bates et al., 2014) to assess the influence of vegetation type, depth, and their interaction (N=5) on soil abiotic conditions, various forms of soil nitrogen and C and $\delta^{15}\text{N}$, 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 the 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 include vegetation*depth interactions in those models.

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) exhibited little variation with depth (average 33.1% clay and 18.8% sand), while the two other conifer sites had a greater sand and lower silt and clay content, particularly at depths greater than 25 cm (SS and SG; Fig. S1). Cation exchange capacity 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 that declined with depth (Fig S2).

We were able to access and describe soil profiles 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 ferriargillans indicate illuviation. Lithologic discontinuities were identified in SS, ESG, and EAG indicating colluvial inputs into these footslope pedons.

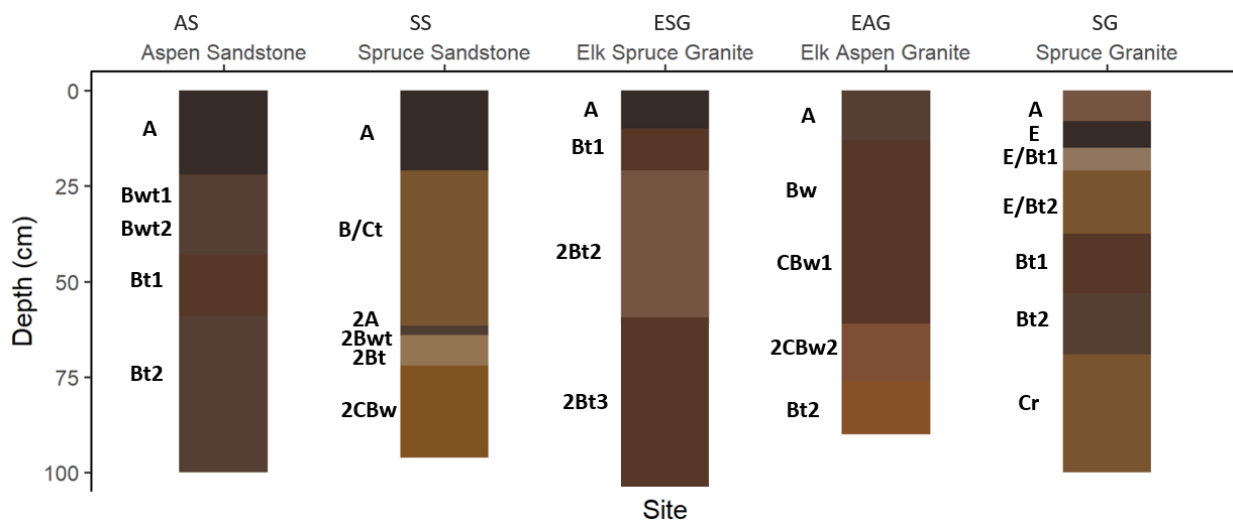


Figure 2: Soil profiles described at each site. Horizon colors represent the moist color of the soils as matched to the soil-color or Munsell chart.

Soils at both aspen sites (AS and EAG) are 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 are Typic Haplocrypts (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 cm³ cm⁻³.

We also examined soil pH. Across the entire soil profile, pH 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 at approximately 60 cm, where the aspen soils became slightly more acidic compared to the conifer soils.

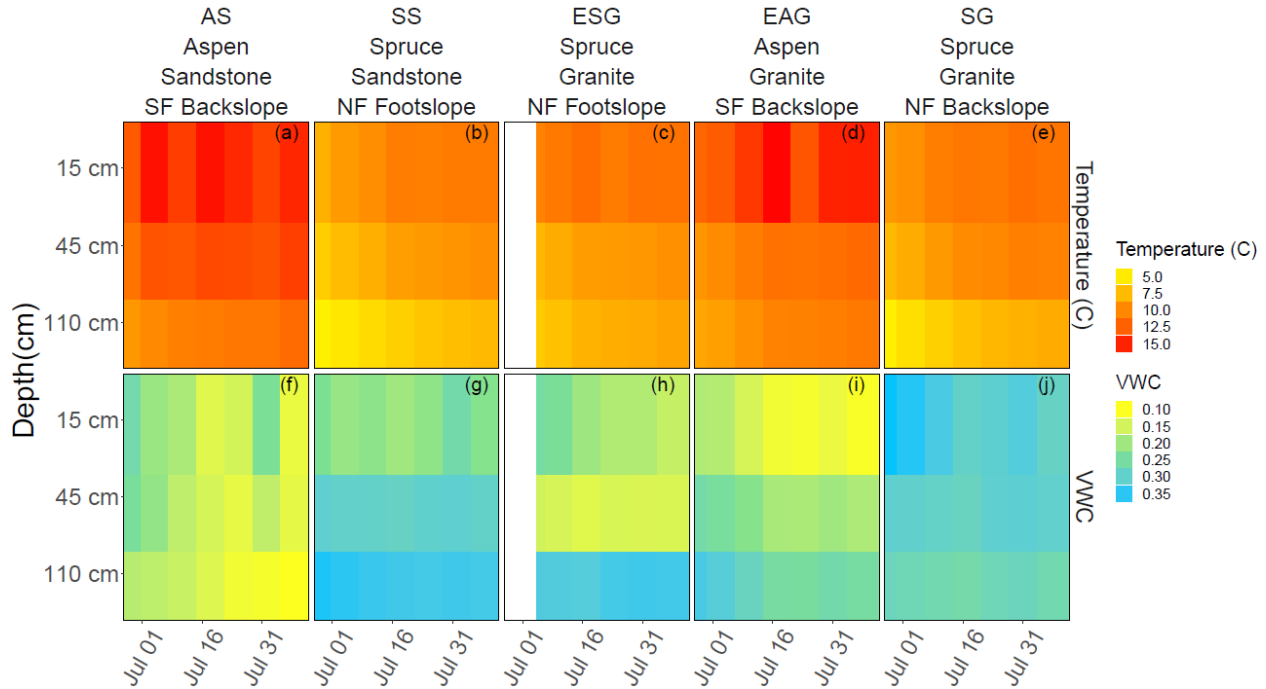


Figure 3: Temperature (a-e; °C) and volumetric water content (VWC (cm³ cm⁻³); f-j) data for aspen sandstone (AS; a, f), spruce sandstone (SS; b, g), spruce granite (ESG; c, h), aspen granite (EAG, d, i), and spruce granite (SG; e, j). AS reflects 2021 data, SS reflects averaged 2021 and 2022, ESG, EAG, and SG reflects 2022 data.

4.3 Soil Organic C 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 (Fig. 4a). SOC concentrations were generally higher under aspen compared to spruce sites ($p < 0.0001$; Fig. 4a), but LME models also suggest that the best fit model included a significant interaction between vegetation and depth ($p < 0.001$), suggesting that SOC declines with depth for both vegetation types but to a greater extent under spruce compared to aspen. Stocks of SOC for all depth intervals ranged between 0.01 and 1.31 kg m⁻² (Fig. 4b); these values did not exhibit consistent declines with depth or clear differences across cover type.

In contrast to SOC concentrations, DOC was generally higher under the spruce stands compared to aspen. Similar to SOC, a model including a significant interaction between vegetation and depth was the best predictor of DOC values ($p < 0.001$), likely reflecting variable DOC values at different depths in both vegetation types (Fig. 4c). The DOC:SOC ratio also exhibited a significant interaction between vegetation type and depth (Fig. 4d; $p = 0.0007$). As with DOC, this significant interaction likely reflects variable ratio values for each cover type across depths.

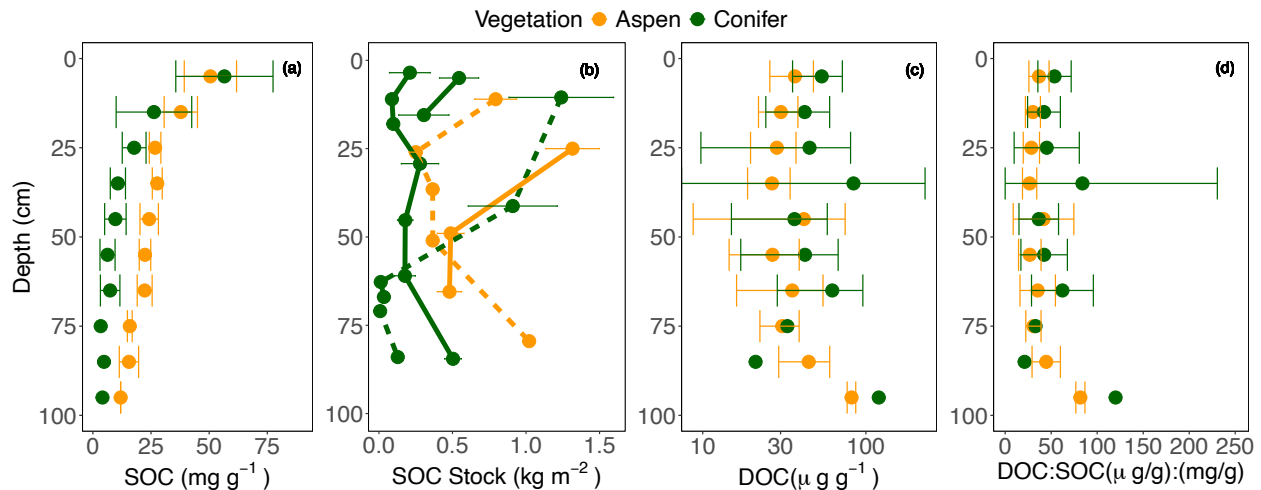


Figure 4: a) Soil organic carbon (SOC) concentrations, (b) SOC stock [by horizon per pit; solid lines indicate sites underlain by granite and dotted lines aspen], (c) dissolved organic carbon (DOC), and (d) the ratio of dissolved organic carbon to soil organic carbon (DOC:SOC) with depth under two different vegetation types, aspen (orange) and spruce (green) at the Coal Creek catchment, Colorado, USA. Values represent mean $\pm$ standard deviation.

Total soil nitrogen ranged from 0.2 mg g^{-1} at depth to 4.63 mg g^{-1} near the surface. A model including an interaction between vegetation type and depth was the best fit ($p = 0.003$; Fig. 5a). Aspen values were greater than those in spruce-dominated soils at all depths; the significant interaction implies that the decline with depth was greater in spruce soils. Nitrate concentrations averaged $214 \pm 323 \text{ ng g}^{-1}$ near the surface and $2.3 \pm 3.8 \text{ ng g}^{-1}$ at depth. Nitrate was elevated under the aspen compared to the spruce sites (Fig. 5b), and values under both vegetation types varied with depth. A model that included both depth and vegetation type with no interaction was a meaningfully better predictor of nitrate concentrations than either depth or vegetation alone ($p = 0.035$), and including a depth-vegetation interaction did not improve model fit. Aspen soil C:N averaged 10.9 ± 1.1 and remained fairly constant with depth (Fig. 5c). The spruce sites showed greater variation 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). Including the interaction between vegetation type and soil depth improved model fit ($p = 0.0008$), indicating that C:N varied more with depth in spruce soils than in aspen soils, where values stayed fairly constant. The lowest C:N value, found at depth in one of the spruce forest, suggests that the soil organic matter there has been heavily processed by microbes (Ziegler et al. 2017).

$\delta^{15}\text{N}$ signatures showed less distinct depth trends compared to the total nitrogen and nitrate, mirroring the relative lack of clear depth trends in C:N. Though variation across sites limited our ability to find statistically-significant differences across vegetation types or a significant influence of depth, $\delta^{15}\text{N}$ of soil organic matter in spruce plots tended to be lower than that of aspen (Fig. 5d), hinting that soil N has undergone more microbial processing (Nadelhoffer and Fry 1988; Billings and Richter 2006) under aspens compared to under conifers. This

interpretation is consistent with the mean spruce C:N values being greater than those in aspen forests (Fig. 5c).

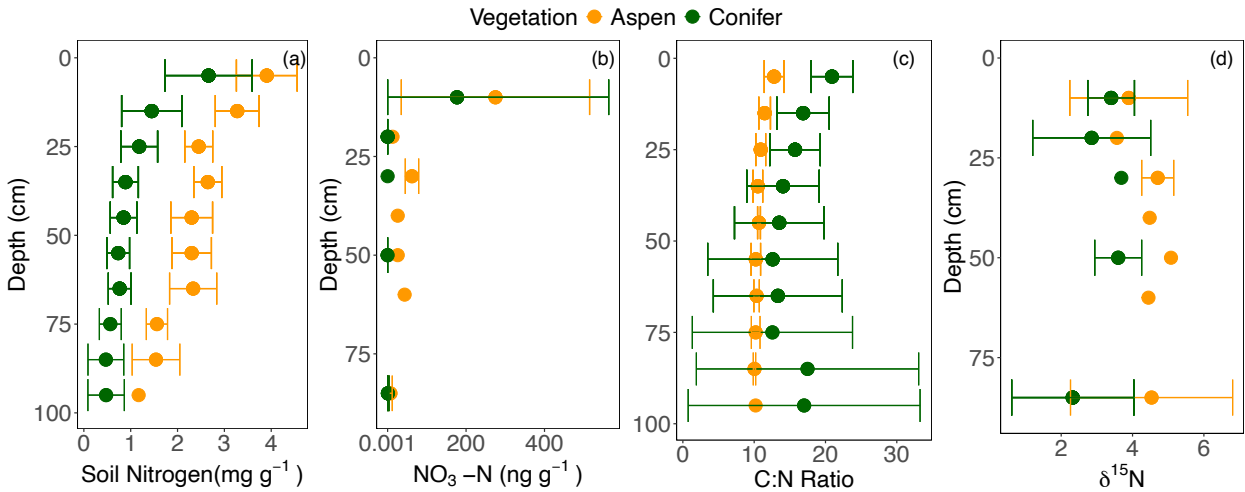


Figure 5: (a) Soil nitrogen, (b) soil nitrate, (c) carbon to nitrogen ratio (C:N), and (d) δ¹⁵N with depth under two different vegetation types, aspen (orange) and spruce (green) at the Coal Creek catchment, Colorado, USA. Values represent mean +/- standard deviation. For each mean and standard deviation, 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 models including vegetation-depth interactions were the most effective at describing total and coarse root fractions ($p < 0.001$), 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 ($p > 0.05$; Fig. 6b), suggesting that the greater total root abundance under aspen was driven more by the coarse root fraction. 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 standardized DOC with 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).

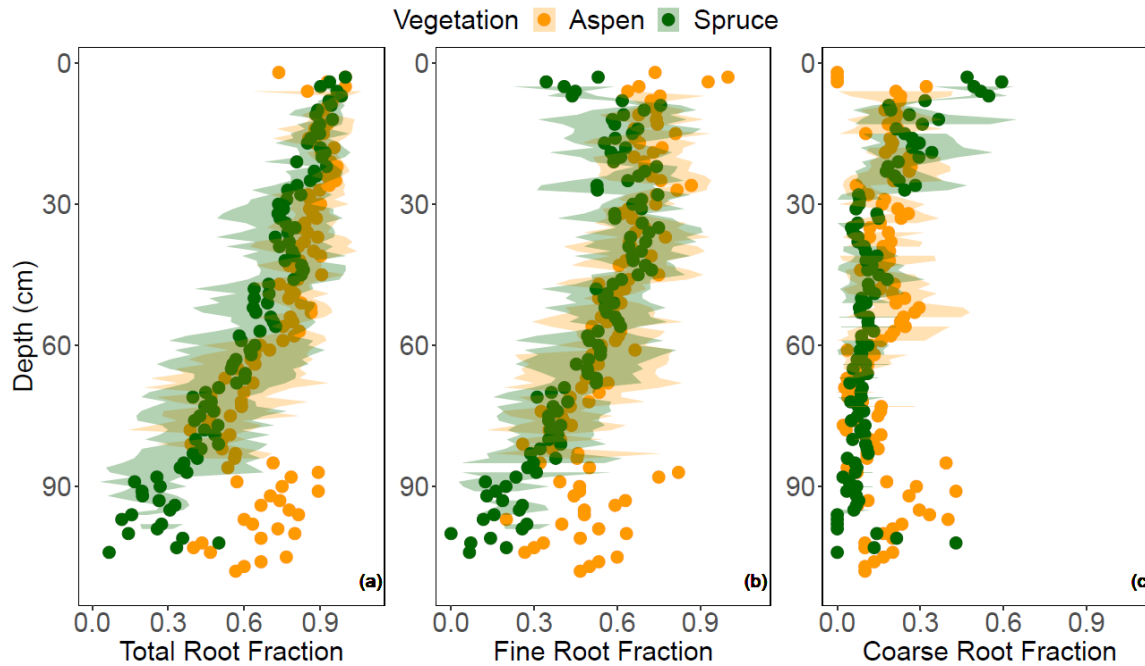


Figure 6: (a) Total, (b) fine, and (c) coarse root fractions quantified at 1-cm depth interval under two different vegetation types, aspen (orange) and spruce (green) at the Coal Creek catchment, Colorado, USA. Values represent mean (points) +/- standard deviation (shading).

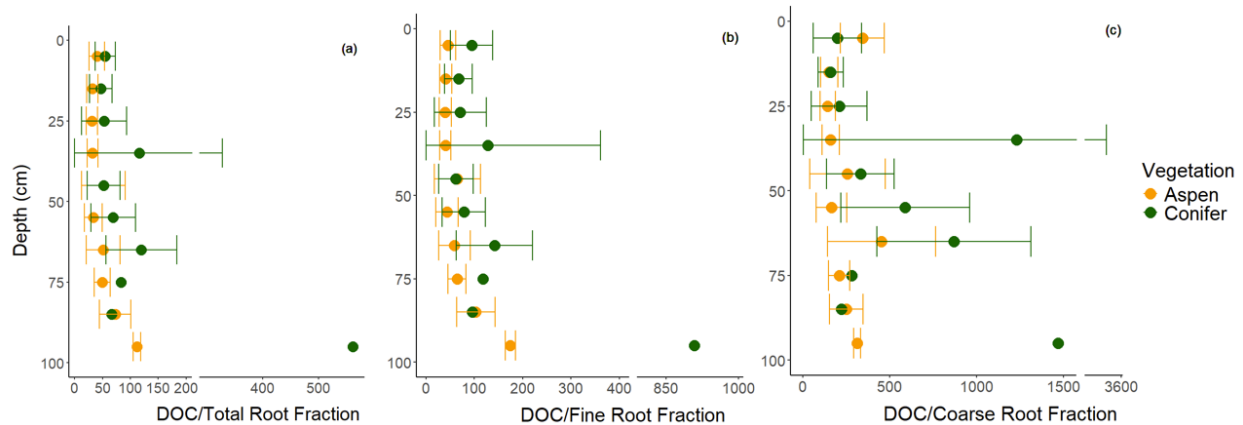


Figure 7: DOC divided by mean (a) total, (b) fine, and (c) coarse root fractions every 10 cm under two different vegetation types, aspen (orange) and spruce (green) at the Coal Creek catchment, Colorado, USA. Values represent mean (points) +/- standard deviation (bars). Root fractions represent the count of fine (<1 mm) or coarse (≥ 1 mm) roots 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

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.

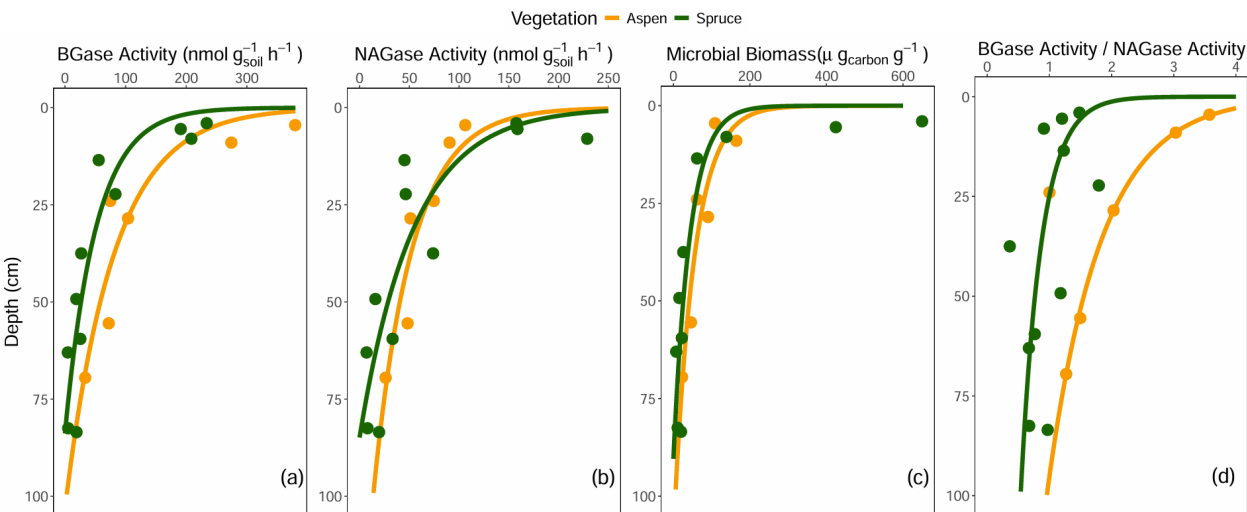


Figure 8: Soil (a) β -glucosidase (BGase) (b) β -N-acetyl glucosaminidase (NAGase) (c) microbial biomass and (d) the ratio of BGase to NAGase at the Coal Creek catchment, Colorado, USA. Each point represents one site and one depth, and curves represent exponential fit of the data, with each curve defined by multiple spruce and aspen sites.

4.4.3 Soil O₂ and CO₂

We examined soil O₂ and CO₂ concentrations during the growing season to better understand patterns of respiration (Fig. 9). Soil CO₂ concentrations increased with depth across all sites, while O₂ concentrations were more variable. Soil O₂ concentrations remained relatively stable at aspen sites and at spruce granite sites (AS, EAG, and SG). However, O₂ concentrations decreased with depth at the remaining two spruce sites—one sandstone and one granite (SS and ESG).

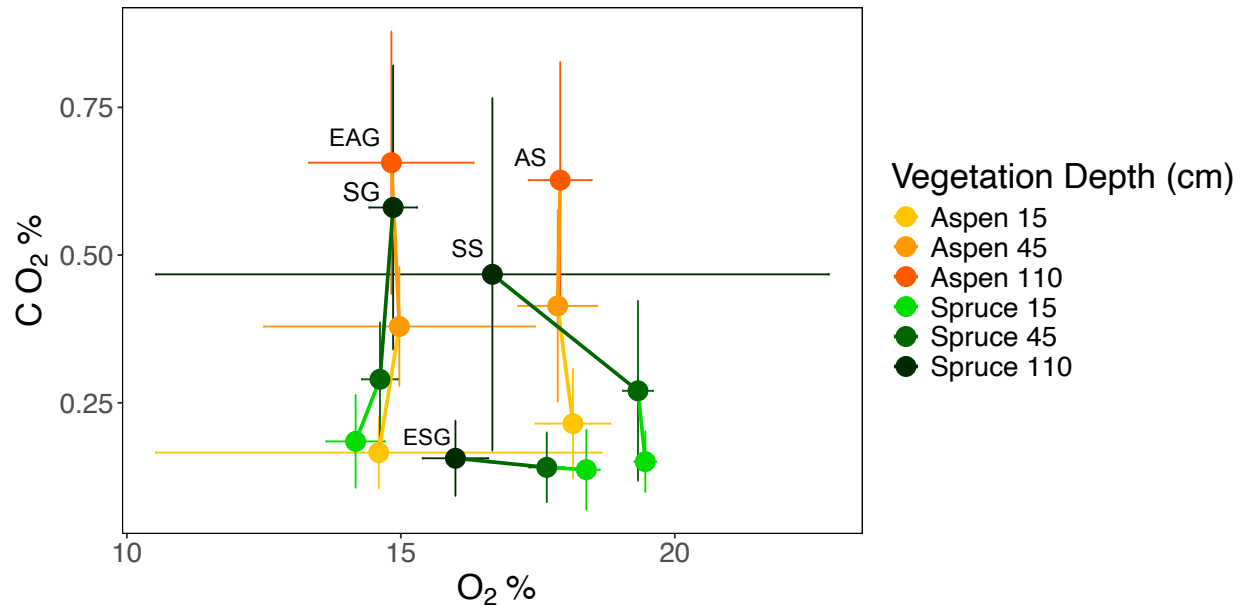


Figure 9: Soil gas concentrations of O_2 (%) and CO_2 (%) at aspen (orange) and spruce (green) sites during the growing season at depths 15 cm (light), 45 cm (medium), and 110 cm (dark) at the Coal Creek catchment, Colorado. Values represent mean (points) $\pm$ standard deviation (bars) with lines connecting depths within each profile. The shallowest depth of each site is labeled: AS, Aspen Sandstone; 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). Aspen aggregates tended to be finer, with fewer intermediate and coarse aggregates compared to the spruce soil (Fig. 10b-d). LME models indicated that vegetation-depth interactions were the most meaningful in driving all three aggregate size classes ($p < 0.001$). To explore the propensity of SOC to promote and stabilize aggregation in these soils, we standardized aggregates by SOC concentrations (Fig. 11; Souza et al. 2023). LME models indicate that an interaction between vegetation type and depth contributes to variation in the fine aggregate:SOC data (Fig. 11a; $p < 0.0001$), suggesting that in the bottom third of the profile, SOC in spruce soils also contributes to fine aggregate formation. Adding an interaction between vegetation and depth to the model improved model fit for coarse aggregate:SOC values ($p < 0.0001$), highlighting a higher coarse aggregate:SOC ratio in the spruce sites that varied little with depth compared to aspen soils (Fig. 11b) and suggesting that SOC in spruce-dominated soils exhibits a higher propensity to form coarse aggregates throughout the soil profile.

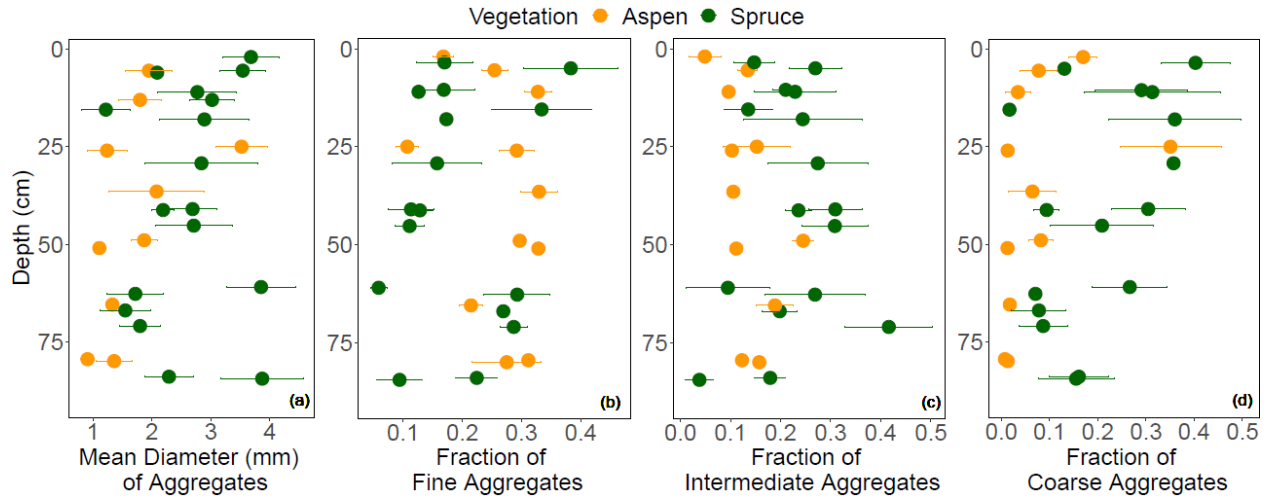


Figure 10: (a) Diameter of soil aggregates, and fraction of (b) fine aggregates (< 0.21 mm), (c) intermediate aggregates (0.21-4.76 mm), and (d) coarse aggregates (> 4.76 mm) that contribute to the overall soil aggregate diameter at the Coal Creek catchment, Colorado, USA. Values represent (a) geometric mean or (b-d) mean (points) +/- standard deviation (bars). Colors are associated with vegetation, aspen (orange) and spruce (green).

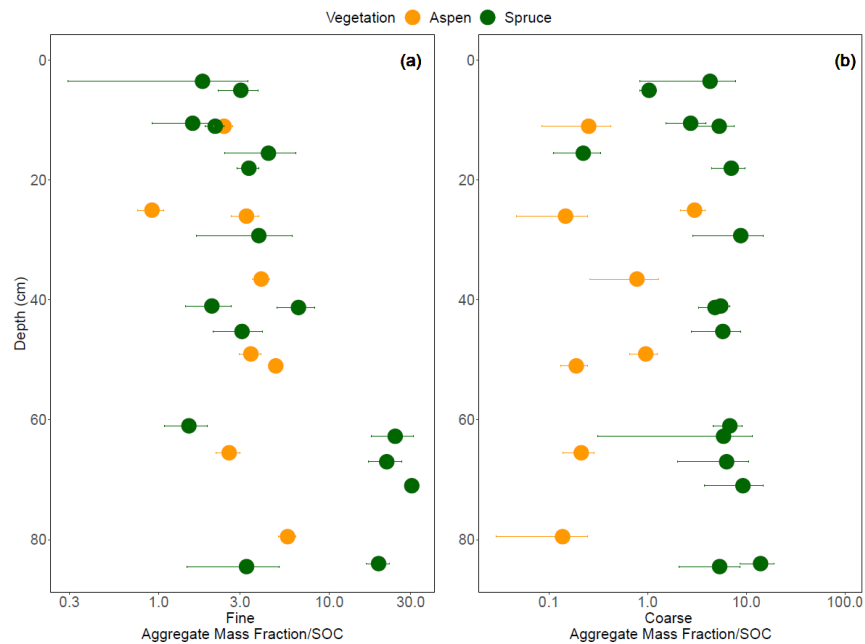


Figure 11: The fraction of (a) fine aggregates (< 0.21 mm) and (b) coarse aggregates (> 4.76 mm) divided by the fraction of SOC at the Coal Creek catchment, Colorado, USA. Values represent mean (points) +/- standard deviation (bars). Colors are associated with vegetation, aspen (orange) and spruce (green). Please note each aggregate size class is divided by the total SOC, not the C associated with each size class.

5 Discussion

By integrating knowledge from biology, pedology, hydrology, and soil chemistry we were better able to understand how multiple factors interact to drive observed SOC patterns in aspen and conifer montane forests. Our data indicate that differences in SOC protection contribute to the commonly observed patterns of elevated SOC storage in soils beneath aspen compared to conifer stands (Woldeselassie et al., 2012, Laganieri et al., 2013, Boča et al., 2020, Román Dobarco et al., 2021). Furthermore, our study 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 C 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 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.

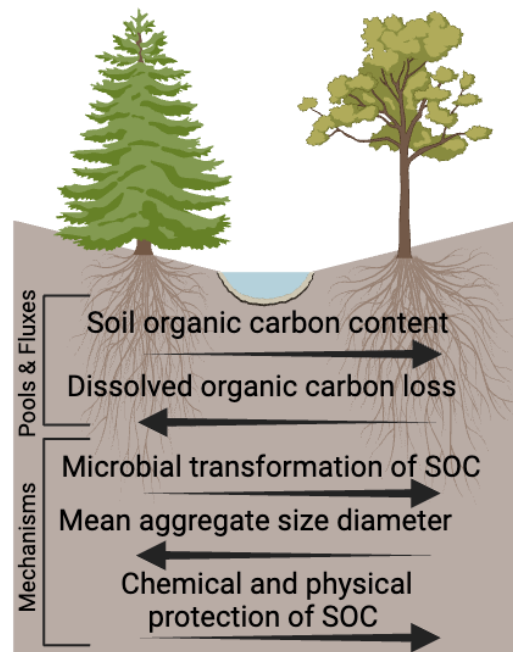


Figure 12. Summary of observations across aspen and spruce sites at Coal Creek, CO (USA) that are interpreted to indicate a greater amount of chemical and physical protection of SOC under aspen sites.

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 C fate, in these montane forests is largely controlled by biotic processes linked to soil mineral material. Here greater values of total N, nitrate, BGase and $\delta^{15}\text{N}$ 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 have been widely reported, with generally lower lignin and higher nitrogen content in aspen litter (Moore et al., 2006). Our inference about litterfall differences promoting microbial byproduct stabilization is 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, $\delta^{15}\text{N}$, 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 due to a greater abundance of particulate organic matter (POM) in spruce compared to aspen forest soils (Cotrufo et al., 2015; Cotrufo et al., 2019); this may be the case since spruce litterfall is more difficult to decompose. 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 — especially at depth, where MAOC tends to dominate SOC pools (Jackson et al. 2017).

Our soil data also indicate that SOC pools in aspen soils are more strongly dominated by MAOC compared to those in spruce soils. 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 in deeper soil layers (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 (Figure 7). This pattern—especially evident in total and fine root abundance—suggests that DOC moves more readily through spruce soil profiles, potentially leading to greater DOC losses 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; Boča 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. In our study aspen cover occurs where soil temperatures are warmer (Fig. 2). As such, 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. We note that the volumetric fraction of soil moisture was also lower in the aspen, particularly at the shallowest soils, but that aspen soils appear to stay sufficiently moist (0.10-0.20 under aspen vs. 0.20-0.30 under the spruce) to support microbial activity responses to the higher temperatures. Consistent with this idea, soil CO₂ and O₂ 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 the soil 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 $\delta^{15}\text{N}$ 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 C 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 harm global water quality by altering light and thermal regimes, nutrient cycling (e.g., Morris et al., 1995; Cory et al., 2015), the transport and bioavailability of heavy metals (e.g., Dupré et al., 1999; Trostle et al., 2016), and creating 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 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 C 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 C 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 C demand (Belay-Tedla et al., 2009, Hu et al., 2017), and recalcitrant C 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 C 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 to be associated with larger aggregates (Fig. 10), a potential for greater DOC loss per unit SOC (Fig. 4c), greater sand content (depth >25 cm; Fig. S1) and thus likely greater values of hydraulic conductivity, and generally higher soil moisture content (Fig. 3) compared to aspen-dominated soils. 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 ongoing efforts to investigate suites of biotic and abiotic features across whole ecosystems — the critical zone (Richter and Billings, 2015)—to better understand SOC dynamics (e.g., Keller, 2019; Mainka et al., 2022; Wasner et al., 2024). It also provides a foundation for future studies that could incorporate more spatially replicated sites across key environmental gradients. Specifically, our data suggest that organic matter from aspen supports higher microbial transformation rates and greater stabilization of SOC, reducing the likelihood that labile SOC is transported down the soil profile. Consequently, aspen-dominated stands may be less likely to promote the movement of DOC across the landscape and 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) can be important for projecting not just CO₂ release to the atmosphere and SOC stabilization, but down-profile and downstream C 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 C from hillslopes to streams.

Data statement

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

766
 767 **Author Contributions (CRediT):**
 768 Wang, L: *Conceptualization, Data curation, Formal analysis, Investigation, Methodology,*
 769 *Visualization Writing – original draft, Writing – review and editing*
 770 Billings, S.: *Conceptualization, Funding acquisition, Investigation, Methodology, Writing –*
 771 *original draft, Writing – review and editing*
 772 Li, L.: *Conceptualization, Investigation, Funding acquisition, Writing – review and editing*
 773 Hirmas, D.R.: *Data Curation, Funding acquisition, Methodology, Investigation, Writing – review*
 774 *and editing*
 775 Johnson, K.: *Data Curation, Investigation, Writing – review and editing*
 776 Kerins, D. : *Investigation, Writing – review and editing*
 777 Pachon, J: *Data Curation, Investigation, Writing – review and editing*
 778 Curtis Beutler: *Investigation, Writing – review and editing*
 779 Jarecke, K.M.: *Data Curation, Investigation, Writing – review and editing*
 780 Varikuti, V: *Data Curation, Investigation, Writing – review and editing*
 781 Unruh, Micah,: *Writing – review and editing*
 782 Ajami, H: *Data Curation, Investigation, Funding acquisition, Methodology, Writing – review and*
 783 *editing*
 784 Barnard, H.R.: *Investigation, Funding acquisition, Writing – review and editing*
 785 Flores, A.N: *Funding acquisition, Writing – review and editing*
 786 Williams, K. H.: *Funding acquisition, Investigation, Writing – review and editing*
 787 Sullivan, P.L.: *Conceptualization, Funding acquisition, Methodology, Project administration,*
 788 *Supervision, Visualization, Writing – original draft, Writing – review and editing*

789

790 **Competing Interests**

791 The authors declare that they have no conflict of interest

792

793 **Acknowledgements**

794 We would like to thank Reece Gregory, Nicole Hornslein, Ariel Mollhagen, and Michael
 795 Mackenzie. This material is based upon work supported by the National Science Foundation
 796 under Grants NSF 2121694 (P. L. Sullivan) and 2012796 (P. L. Sullivan); NSF 2012669 (H. R.
 797 Barnard), the Department of Energy under Grant DE-SC0020146 (L. Li; P. L. Sullivan), NSF
 798 2121639 (S.A. Billings), and NSF 2121760 (H. Ajami; D. Hirmas). This material is partially based
 799 upon work supported as part of the Watershed Function Scientific Focus Area funded by the
 800 U.S. Department of Energy, Office of Science, Office of Biological and Environmental Research
 801 under Contract No. DE-AC02-05CH11231. Finally, our understanding of these sites benefited
 802 from data provided for project doi.org/10.46936/mone.proj.2023.60933/60008945 awarded to

803 SAB and PLS by the Molecular Observation Network (MONet) at the Environmental Molecular
804 Sciences Laboratory (<https://ror.org/04rc0xn13>), a DOE Office of Science user facility sponsored
805 by the Biological and Environmental Research program under Contract No. DE-AC05-
806 76RL01830.

807

808 References

809 Alaghmand, S., Beecham, S. and Hassanli, A., 2014. Impacts of vegetation cover on surface-
810 groundwater flows and solute interactions in a semi-arid saline floodplain: a case study of the
811 Lower Murray River, Australia. *Environmental Processes*, 1, pp.59-71.
812 <https://doi.org/10.1007/s40710-014-0003-0>

813 Alban, D.H., 1982. Effects of nutrient accumulation by aspen, spruce, and pine on soil
814 properties. *Soil Science Society of America Journal*, 46(4), pp.853-861
815 <https://doi.org/10.2136/sssaj1982.03615995004600040037x>

816 Alexander, R.R., 1987. *Ecology, silviculture, and management of the Engelmann spruce--*
817 *subalpine fir type in the central and southern Rocky Mountains* (No. 659). US Department of
818 Agriculture, Forest Service.

819 Allison, S.D., 2014. Modeling adaptation of carbon use efficiency in microbial communities.
820 *Frontiers in Microbiology*, 5, p.571. <https://doi.org/10.3389/fmicb.2014.00571>.

821 Alvarez-Cobelas, M., Angeler, D. G., Sánchez-Carrillo, S., Almendros, G., 2012. A worldwide view
822 of organic carbon export from catchments. *Biogeochemistry*, 107, 275-293.
823 <https://doi.org/10.1007/s10533-010-9553-z>

824 Amézketa, E., 1999. Soil aggregate stability: a review. *Journal of sustainable agriculture*, 14(2-3),
825 pp.83-151. https://doi.org/10.1300/J064v14n02_08.

826 Anderegg, L.D., Anderegg, W.R., Abatzoglou, J., Hausladen, A.M. and Berry, J.A., 2013. Drought
827 characteristics' role in widespread aspen forest mortality across Colorado, USA. *Global Change*
828 *Biology*, 19(5), pp.1526-1537. <https://doi.org/10.1111/gcb.12146>.

829 Anderson, M.A., Graham, R.C., Alyanakian, G.J. and Martynn, D.Z., 1995. Late summer water
830 status of soils and weathered bedrock in a giant sequoia grove. *Soil Science*, 160(6), pp.415-
831 422. <https://doi.org/10.1097/00010694-199512000-00007>.

832 Anderson, S.P., Hinckley, E.L., Kelly, P. and Langston, A., 2014. Variation in critical zone
833 processes and architecture across slope aspects. *Procedia Earth and Planetary Science*, 10,
834 pp.28-33. <https://doi.org/10.1016/j.proeps.2014.08.006>

835 Andrus, R.A., Hart, S.J., Tutland, N. and Veblen, T.T., 2021. Future dominance by quaking aspen
836 expected following short-interval, compounded disturbance interaction. *Ecosphere*, 12(1),
837 p.e03345. <https://doi.org/10.1002/ecs2.3345>.

838 Angers, D.A. and Caron, J., 1998. Plant-induced changes in soil structure: processes and
839 feedbacks. *Biogeochemistry*, 42, pp.55-72. <https://doi.org/10.1023/A:1005944025343>

840 Araya, S.N. and Ghezzehei, T.A., 2019. Using machine learning for prediction of saturated
841 hydraulic conductivity and its sensitivity to soil structural perturbations. *Water Resources*
842 *Research*, 55(7), pp.5715-5737. <https://doi.org/10.1029/2018WR024357>

843 Attou, F., Bruand, A. and Le Bissonnais, Y., 1998. Effect of clay content and silt—clay fabric on
844 stability of artificial aggregates. *European Journal of Soil Science*, 49(4), pp.569-577.
845 <https://doi.org/10.1046/j.1365-2389.1998.4940569.x>

846 Averill, C., Turner, B.L. and Finzi, A.C., 2014. Mycorrhiza-mediated competition between plants
847 and decomposers drives soil carbon storage. *Nature*, 505(7484), pp.543-545.
848 <https://doi.org/10.1038/nature12901>

849 Banwart, S., Bernasconi, S.M., Bloem, J., Blum, W., Brandao, M., Brantley, S., Chabaux, F., Duffy,
850 C., Kram, P., Lair, G. and Lundin, L., 2011. Soil processes and functions in critical zone
851 observatories: hypotheses and experimental design. *Vadose Zone Journal*, 10(3), pp.974-987.
852 <https://doi.org/10.2136/vzj2010.0136>

853 Belay-Tedla, A., Zhou, X., Su, B., Wan, S. and Luo, Y., 2009. Labile, recalcitrant, and microbial
854 carbon and nitrogen pools of a tallgrass prairie soil in the US Great Plains subjected to
855 experimental warming and clipping. *Soil Biology and Biochemistry*, 41(1), pp.110-116.
856 <https://doi.org/10.1016/j.soilbio.2008.10.003>

857 Bergstrom, A., Jencso, K. and McGlynn, B., 2016. Spatiotemporal processes that contribute to
858 hydrologic exchange between hillslopes, valley bottoms, and streams. *Water Resources*
859 *Research*, 52(6), pp.4628-4645. <https://doi.org/10.1002/2015WR017972>

860 Berner, R.A., 1992. Weathering, plants, and the long-term carbon cycle. *Geochimica et*
861 *Cosmochimica Acta*, 56(8), pp.3225-3231. [https://doi.org/10.1016/0016-7037\(92\)90300-8](https://doi.org/10.1016/0016-7037(92)90300-8)

862 Besnard, E., Chenu, C., Balesdent, J., Puget, P. and Arrouays, D., 1996. Fate of particulate
863 organic matter in soil aggregates during cultivation. *European Journal of Soil Science*, 47(4),
864 pp.495-503. <https://doi.org/10.1111/j.1365-2389.1996.tb01849.x>

865 Billings, S.A., and Richter, D.D., 2006. Changes in stable isotopic signatures of soil nitrogen and
866 carbon during forty years of forest development. *Oecologia* 148: 325–333; 10.1007/s00442-
867 006-0366-7. <https://doi.org/10.1007/s00442-006-0366-7>

868 Billings, S.A., Hirmas, D., Sullivan, P.L., Lehmeier, C.A., Bagchi, S., Min, K., Brecheisen, Z., Hauser,
869 E., Stair, R., Flournoy, R. and deB. Richter, D., 2018. Loss of deep roots limits biogenic agents of
870 soil development that are only partially restored by decades of forest regeneration. *Elem Sci*
871 *Anth*, 6, p.34. <https://doi.org/10.1525/elementa.287>.

872 Billings, S.A., Lajtha, K., Malhotra, A., Berhe, A.A., de Graaff, M.-A., Earl, S., Fraterrigo, J.,
873 Georgiou, K., Grandy, S., Hobbie, S.E., Moore, J.A.M., Nadelhoffer, K., Pierson, D., Rasmussen,
874 C., Silver, W.L., Sulman, B.N., Weintraub, S., and Wieder, W., 2021. Soil organic carbon is not

875 just for soil scientists: Measurement recommendations for diverse practitioners. *Ecological*
876 *Applications* 31 doi: 10.1002/eap.2290

877 Boča, A., Jacobson, A.R. and Van Miegroet, H., 2020. Aspen soils retain more dissolved organic
878 carbon than conifer soils in a sorption experiment. *Frontiers in Forests and Global Change*, 3,
879 p.594473. <https://doi.org/10.3389/ffgc.2020.594473>.

880 Bogner, C., Gaul, D., Kolb, A., Schmiedinger, I. and Huwe, B., 2010. Investigating flow
881 mechanisms in a forest soil by mixed-effects modelling. *European Journal of Soil Science*, 61(6),
882 pp.1079-1090. <https://doi.org/10.1111/j.1365-2389.2010.01300.x>

883 Bornyasz, M.A., Graham, R.C. and Allen, M.F., 2005. Ectomycorrhizae in a soil-weathered
884 granitic bedrock regolith: linking matrix resources to plants. *Geoderma*, 126(1-2), pp.141-160.
885 <https://doi.org/10.1016/j.geoderma.2004.11.023>

886 Brewen, C.J., Berrill, J.P., Ritchie, M.W., Boston, K., Dagley, C.M., Jones, B., Coppoletta, M. and
887 Burnett, C.L., 2021. 76-year decline and recovery of aspen mediated by contrasting fire regimes:
888 Long-unburned, infrequent and frequent mixed-severity wildfire. *Plos one*, 16(2),
889 p.e0232995. <https://doi.org/10.1371/journal.pone.0232995>.

890 Brzostek, E.R., Greco, A., Drake, J.E. and Finzi, A.C., 2013. Root carbon inputs to the rhizosphere
891 stimulate extracellular enzyme activity and increase nitrogen availability in temperate forest
892 soils. *Biogeochemistry*, 115, pp.65-76. <https://doi.org/10.1007/s10533-012-9818-9>

893 Bronick, C.J. and Lal, R., 2005. Soil structure and management: a review. *Geoderma*, 124(1-2),
894 pp.3-22. <https://doi.org/10.1016/j.geoderma.2004.03.005>

895 Brusseau, M.L. and Rao, P.S.C., 1990. Modeling solute transport in structured soils: A
896 review. *Geoderma*, 46(1-3), pp.169-192. [https://doi.org/10.1016/0016-7061\(90\)90014-Z](https://doi.org/10.1016/0016-7061(90)90014-Z)

897 Buck, J.R. and St. Clair, S.B., 2012. Aspen increase soil moisture, nutrients, organic matter and
898 respiration in Rocky Mountain forest communities. *PLoS One*, 7(12),
899 p.e52369. <https://doi.org/10.1371/journal.pone.0052369>.

900 Buckeridge, K.M., Creamer, C. and Whitaker, J., 2022. Deconstructing the microbial necromass
901 continuum to inform soil carbon sequestration. *Functional Ecology*, 36(6), pp.1396-1410.
902 <https://doi.org/10.1111/1365-2435.14014>

903 Burnett, B.N., Meyer, G.A. and McFadden, L.D., 2008. 'Aspect-related microclimatic influences
904 on slope forms and processes, northeastern Arizona', *Journal of Geophysical Research*, 113(F3),
905 p. F03002. Available at: <https://doi.org/10.1029/2007JF000789>.

906 Brzostek, E.R., Greco, A., Drake, J.E. and Finzi, A.C., 2013. Root carbon inputs to the rhizosphere
907 stimulate extracellular enzyme activity and increase nitrogen availability in temperate forest
908 soils. *Biogeochemistry*, 115, pp.65-76. <https://doi.org/10.1007/s10533-012-9818-9>

909 Canelles, Q., Aquilué, N., James, P. M., Lawler, J., & Brotons, L. (2021). Global review on
910 interactions between insect pests and other forest disturbances. *Landscape Ecology*, 36, 945-
911 972. <https://doi.org/10.1007/s10980-021-01209-7>

- Carbone, M.S., Still, C.J., Ambrose, A.R., Dawson, T.E., Williams, A.P., Boot, C.M., Schaeffer, S.M. and Schimel, J.P., 2011. Seasonal and episodic moisture controls on plant and microbial contributions to soil respiration. *Oecologia*, 167, pp.265-278. <https://doi.org/10.1007/s00442-011-1975-3>
- Chen, S., Franklin, R.E. and Johnson, A.D., 1997. Clay film effects on ion transport in soil. *Soil science*, 162(2), pp.91-96.
- Chorover, J., Kretzschmar, R., Garcia-Pichel, F., and Sparks, D. L, 2007. Soil biogeochemical processes within the critical zone. *Elements*, 3(5), 321-326. <https://doi.org/10.2113/gselements.3.5.321>
- Cincotta, M. M., Perdrial, J.N., Shavitz, A., Libenson, A., Landsman-Gerjoi, M., Perdrial, N., Armfield, J., Adler, T., and Shanley, J.B., 2019. Soil aggregates as a source of dissolved organic carbon to streams: an experimental study on the effect of solution chemistry on water extractable carbon." *Frontiers in Environmental Science*: 172. <https://doi.org/10.3389/fenvs.2019.00172>.
- Clark, A.L. and Clair, S.B.S., 2011. Mycorrhizas and secondary succession in aspen–conifer forests: Light limitation differentially affects a dominant early and late successional species. *Forest Ecology and Management*, 262(2), pp.203 207. <https://doi.org/10.1016/j.foreco.2011.03.024>.
- Coop, J.D., Barker, K.J., Knight, A.D. and Pecharich, J.S., 2014. Aspen (*Populus tremuloides*) stand dynamics and understory plant community changes over 46 years near Crested Butte, Colorado, USA. *Forest Ecology and Management*, 318, pp.1 12. <https://doi.org/10.1016/j.foreco.2014.01.019>.
- Cory, R. M., Harrold, K. H., Neilson, B. T., and Kling, G. W., 2015. Controls on dissolved organic matter (DOM) degradation in a headwater stream: the influence of photochemical and hydrological conditions in determining light-limitation or substrate-limitation of photo-degradation. *Biogeosciences*, 12(22), 6669-6685. <https://doi.org/10.5194/bg-12-6669-2015>
- Cotrufo, M.F., Wallenstein, M.D., Boot, C.M., Denef, K. and Paul, E., 2013. The Microbial Efficiency-Matrix Stabilization (MEMS) framework integrates plant litter decomposition with soil organic matter stabilization: Do labile plant inputs form stable soil organic matter?. *Global change biology*, 19(4), pp.988-995. <https://doi.org/10.1111/gcb.12113>
- Cotrufo, M.F., Soong, J.L., Horton, A.J., Campbell, E.E., Haddix, M.L., Wall, D.H. and Parton, W.J., 2015. Formation of soil organic matter via biochemical and physical pathways of litter mass loss. *Nature Geoscience*, 8(10), pp.776-779. <https://doi.org/10.1038/ngeo2520>.
- Cotrufo, M.F., Ranalli, M.G., Haddix, M.L., Six, J. and Lugato, E., 2019. Soil carbon storage informed by particulate and mineral-associated organic matter. *Nature Geoscience*, 12(12), pp.989-994. <https://doi.org/10.1038/s41561-019-0484-6>.

950 Cruz-Paredes, C., Tájmel, D. and Rousk, J., 2021. Can moisture affect temperature dependences
 951 of microbial growth and respiration?. *Soil Biology and Biochemistry*, 156, p.108223.
 952 <https://doi.org/10.1016/j.soilbio.2021.108223>

953 Cryer, D.H. and Murray, J.E., 1992. Aspen regeneration and soils. *Rangelands Archives*, 14(4),
 954 pp.223-226.

955 Culman, S., 2019. Calculating Cation Exchange Capacity, Base Saturation, and Calcium
 956 Saturation. Ohioline, 22 Aug., ohioline.osu.edu/factsheet/anr-81.

957 Dapples, E.C., 1947. Sandstone types and their associated depositional environments. *Journal of*
 958 *Sedimentary Research*, 17(3), pp.91-100. [https://doi.org/10.1306/D42692BA-2B26-11D7-](https://doi.org/10.1306/D42692BA-2B26-11D7-8648000102C1865D)
 959 [8648000102C1865D](https://doi.org/10.1306/D42692BA-2B26-11D7-8648000102C1865D)

960

961 DeForest, J.L., 2009. The influence of time, storage temperature, and substrate age on potential
 962 soil enzyme activity in acidic forest soils using MUB-linked substrates and L-DOPA. *Soil Biology*
 963 *and Biochemistry*, 41(6), pp.1180-1186. <https://doi.org/10.1016/j.soilbio.2009.02.029>
 964 [Get rights and content](https://doi.org/10.1016/j.soilbio.2009.02.029)

965 de Wit, H.A., Bryn, A., Hofgaard, A., Karstensen, J., Kvilevåg, M.M. and Peters, G.P., 2014.
 966 Climate warming feedback from mountain birch forest expansion: reduced albedo dominates
 967 carbon uptake. *Global Change Biology*, 20(7), pp.2344-2355.
 968 <https://doi.org/10.1111/gcb.12483>

969 Dickson, E.L., Rasiah, V. and Groenevelt, P.H., 1991. Comparison of four prewetting techniques
 970 in wet aggregate stability determination. *Canadian journal of soil science*, 71(1), pp.67-72.
 971 <https://doi.org/10.4141/cjss91-006>

972 Dohnalkova, A.C., Tfaily, M.M., Chu, R.K., Smith, A.P., Brislawn, C.J., Varga, T., Crump, A.R.,
 973 Kovarik, L., Thomashow, L.S., Harsh, J.B. and Keller, C.K., 2022. Effects of Microbial-Mineral
 974 Interactions on Organic Carbon Stabilization in a Ponderosa Pine Root Zone: A Micro-Scale
 975 Approach. *Frontiers in Earth Science*, 10, p.799694. <https://doi.org/10.3389/feart.2022.799694>

976 Dupré, B., Viers, J., Dandurand, J. L., Polve, M., Bénézech, P., Vervier, P., & Braun, J. J. (1999).
 977 Major and trace elements associated with colloids in organic-rich river waters: ultrafiltration of
 978 natural and spiked solutions. *Chemical Geology*, 160(1-2), 63-80.
 979 [https://doi.org/10.1016/S0009-2541\(99\)00060-1](https://doi.org/10.1016/S0009-2541(99)00060-1)

980 Eusterhues, K., Rumpel, C. and Kögel-Knabner, I., 2005. Organo-mineral associations in sandy
 981 acid forest soils: Importance of specific surface area, iron oxides and micropores. *European*
 982 *Journal of Soil Science*, 56(6), pp.753-763. <https://doi.org/10.1111/j.1365-2389.2005.00710.x>

983 Evans, C. D., Monteith, D. T., and Cooper, D. M., 2005. Long-term increases in surface water
 984 dissolved organic carbon: observations, possible causes and environmental
 985 impacts. *Environmental pollution*, 137(1), 55-71. <https://doi.org/10.1016/j.envpol.2004.12.031>

986 Even, R. J., & Cotrufo, M. F., 2024. The ability of soils to aggregate, more than the state of
 987 aggregation, promotes protected soil organic matter formation. *Geoderma*, 442, 116760.

988 Fang, C. and Moncrieff, J.B., 2001. The dependence of soil CO₂ efflux on temperature. *Soil*
 989 *Biology and Biochemistry*, 33(2), pp.155-165. [https://doi.org/10.1016/S0038-0717\(00\)00125-5](https://doi.org/10.1016/S0038-0717(00)00125-5)

990 Fossum, C., Estera-Molina, K.Y., Yuan, M., Herman, D.J., Chu-Jacoby, I., Nico, P.S., Morrison,
 991 K.D., Pett-Ridge, J. and Firestone, M.K., 2022. Belowground allocation and dynamics of recently
 992 fixed plant carbon in a California annual grassland. *Soil Biology and Biochemistry*, 165,
 993 p.108519. <https://doi.org/10.1016/j.soilbio.2021.108519>

994 Geological Survey (US) and Gaskill, D.L., 1991. *Geologic map of the gothic quadrangle, Gunnison*
 995 *County, Colorado*. The Survey. <https://doi.org/10.3133/gq1689>.

996 German, D.P., Weintraub, M.N., Grandy, A.S., Lauber, C.L., Rinkes, Z.L. and Allison, S.D., 2011.
 997 Optimization of hydrolytic and oxidative enzyme methods for ecosystem studies. *Soil Biology*
 998 *and Biochemistry*, 43(7), pp.1387-1397. <https://doi.org/10.1016/j.soilbio.2011.03.017>

999 Ghotsa Mekontchou, C., Houle, D., Bergeron, Y., Roy, M., Gardes, M., Séguin, A. and Drobyshev,
 1000 I., 2022. Contrasting structure of root mycorrhizal communities of black spruce and trembling
 1001 aspen in different layers of the soil profile in the boreal mixedwoods of eastern Canada. *Plant*
 1002 *and Soil*, 479(1-2), pp.85-105. <https://doi.org/10.1007/s11104-022-05410-8>

1003 Gillabel, J., Denef, K., Brenner, J., Merckx, R. and Paustian, K., 2007. Carbon sequestration and
 1004 soil aggregation in center-pivot irrigated and dryland cultivated farming systems. *Soil Science*
 1005 *Society of America Journal*, 71(3), pp.1020-1028. <https://doi.org/10.2136/sssaj2006.0215>

1006 Gislason, S.R., Oelkers, E.H., Eiriksdottir, E.S., Kardjilov, M.I., Gisladottir, G., Sigfusson, B.,
 1007 Snorrason, A., Elefsen, S., Hardardottir, J., Torssander, P. and Oskarsson, N., 2009. Direct
 1008 evidence of the feedback between climate and weathering. *Earth and Planetary Science*
 1009 *Letters*, 277(1-2), pp.213-222. <https://doi.org/10.1016/j.epsl.2008.10.018>

1010 Godsey, S.E., Kirchner, J.W. and Tague, C.L., 2014. Effects of changes in winter snowpacks on
 1011 summer low flows: case studies in the Sierra Nevada, California, USA. *Hydrological Processes*,
 1012 28(19), pp.5048-5064. <https://doi.org/10.1038/s41612-018-0012-1>.

1013 Graham, R., Rossi, A. and Hubbert, R., 2010. Rock to regolith conversion: Producing hospitable
 1014 substrates for terrestrial ecosystems. *GSA today*, 20, pp.4-9.

1015 Hemingway, J.D., Rothman, D.H., Grant, K.E. et al., 2019. Mineral protection regulates long-
 1016 term global preservation of natural organic carbon. *Nature* 570, 228–231.
 1017 <https://doi.org/10.1038/s41586-019-1280-6>

1018 Hodge, A., Berta, G., Doussan, C., Merchan, F. and Crespi, M., 2009. Plant root growth,
 1019 architecture and function. <https://doi.org/10.1007/s11104-009-9929-9>

1020 Hodges, C., Kim, H., Brantley, S.L. and Kaye, J., 2019. Soil CO₂ and O₂ concentrations illuminate
 1021 the relative importance of weathering and respiration to seasonal soil gas fluctuations. *Soil*

1022 *Science Society of America Journal*, 83(4), pp.1167-
 1023 1180. <https://doi.org/10.2136/sssaj2019.02.0049>.

1024 Hoff, C.C., 1957. A comparison of soil, climate, and biota of conifer and aspen communities in
 1025 the central Rocky Mountains. *The American Midland Naturalist*, 58(1), pp.115-
 1026 140. <https://doi.org/10.2307/2422365>

1027 Homer, C. H., Fry, J. A., and Barnes, C. A., 2012. The National land cover database, US geological
 1028 survey fact sheet 2012–3020. *US Geological Survey: Reston, VA, USA*.

1029 Hu, Y., Wang, Z., Wang, Q., Wang, S., Zhang, Z., Zhang, Z. and Zhao, Y., 2017. Climate change
 1030 affects soil labile organic carbon fractions in a Tibetan alpine meadow. *Journal of Soils and*
 1031 *Sediments*, 17, pp.326-339. <https://doi.org/10.1007/s11368-016-1565-4>

1032 Hubbard, Susan S., Kenneth Hurst Williams, Deb Agarwal, Jillian Banfield, Harry Beller, Nicholas
 1033 Bouskill, Eoin Brodie et al., 2019. The East River, Colorado, Watershed: A mountainous
 1034 community testbed for improving predictive understanding of multiscale hydrological–
 1035 biogeochemical dynamics. *Vadose Zone Journal* 17, no. 1: 1-25.
 1036 <https://doi.org/10.2136/vzj2018.03.0061>.

1037 Jackson, R. B., K. Lajtha, S. E. Crow, G. Hugelius, M. G. Kramer, and G. Pineiro. 2017. The ecology
 1038 of soil carbon: Pools, vulnerabilities, and biotic and abiotic controls. *Annual Review of Ecology,*
 1039 *Evolution, and Systematics* 48:419–445. [https://doi.org/10.1146/annurev-ecolsys-112414-](https://doi.org/10.1146/annurev-ecolsys-112414-054234)
 1040 [054234](https://doi.org/10.1146/annurev-ecolsys-112414-054234)

1041 Jastrow, J.D. 1996. Soil aggregate formation and the accrual of particulate and mineral-
 1042 associated organic matter. *Soil Biology and Biochemistry* 28:665-676.
 1043 [https://doi.org/10.1016/0038-0717\(95\)00159-X](https://doi.org/10.1016/0038-0717(95)00159-X)

1044 Jastrow, J.D., Miller, R.M. and Boutton, T.W., 1996. Carbon dynamics of aggregate-associated
 1045 organic matter estimated by carbon-13 natural abundance. *Soil Science Society of America*
 1046 *Journal*, 60(3), pp.801-807. <https://doi.org/10.2136/sssaj1996.03615995006000030017x>

1047 Jencso, K.G., McGlynn, B.L., Gooseff, M.N., Bencala, K.E. and Wondzell, S.M., 2010. Hillslope
 1048 hydrologic connectivity controls riparian groundwater turnover: Implications of catchment
 1049 structure for riparian buffering and stream water sources. *Water Resources Research*, 46(10).
 1050 <https://doi.org/10.1029/2009WR008818>

1051 Jiang, P., Shuai, P., Sun, A., Mudunuru, M. K., and Chen, X., 2023. Knowledge-informed deep
 1052 learning for hydrological model calibration: an application to Coal Creek Watershed in
 1053 Colorado. *Hydrology and Earth System Sciences*, 27(14), 2621-2644.
 1054 <https://doi.org/10.5194/hess-27-2621-2023>

1055 Jilling, A., Keiluweit, M., Gutknecht, J.L. and Grandy, A.S., 2021. Priming mechanisms providing
 1056 plants and microbes access to mineral-associated organic matter. *Soil Biology and Biochemistry*,
 1057 158, p.108265. <https://doi.org/10.1016/j.soilbio.2021.108265>

1058 Jin, L., Andrews, D. M., Holmes, G. H., Lin, H., and Brantley, S. L., 2011. Opening the “black box”:
 1059 Water chemistry reveals hydrological controls on weathering in the Susquehanna Shale Hills

1060 Critical Zone Observatory. *Vadose Zone Journal*, 10(3), 928– 942.
 1061 <https://doi.org/10.2136/vzj2010.0133>

1062 Johnson, K., Harpold, A., Carroll, R. W., Barnard, H., Raleigh, M. S., Segura, C., ... and Sullivan, P.
 1063 L., 2023. Leveraging Groundwater Dynamics to Improve Predictions of Summer Low-Flow
 1064 Discharges. *Water Resources Research*, 59(8), e2023WR035126.
 1065 <https://doi.org/10.1029/2023WR035126>

1066 Keller, C.K., 2019. Carbon exports from terrestrial ecosystems: A Critical-Zone framework.
 1067 *Ecosystems* 22:1691-1705. <https://doi.org/10.1007/s10021-019-00375-9>

1068 Kerins, D., and Li, L., 2023. High dissolved carbon concentration in arid rocky mountain streams.
 1069 *Environmental Science & Technology*, 57(11), 4656-4667.
 1070 <https://doi.org/10.1021/acs.est.2c06675>

1071 Kerins, D., Sadayappan, K., Zhi, W., Sullivan, P. L., Williams, K. H., Carroll, R. W., Barnard H.,
 1072 Sprenger M., Wenming D., Williams K., Pedrial J., and Li, L., 2024. Hydrology outweighs
 1073 temperature in driving production and export of dissolved carbon in a snowy mountain
 1074 catchment. *Water Resources Research*, 60(7), e2023WR036077.
 1075 <https://doi.org/10.1029/2023WR036077>

1076 Kleber, M., Eusterhues, K., Keiluweit, M., Mikutta, C., Mikutta, R. and Nico, P.S., 2015. Mineral–
 1077 organic associations: formation, properties, and relevance in soil environments. *Advances in*
 1078 *agronomy*, 130, pp.1-140. <https://doi.org/10.1016/bs.agron.2014.10.005>.

1079 Kleber, M., Sollins, P. and Sutton, R., 2007. A conceptual model of organo-mineral interactions
 1080 in soils: self-assembly of organic molecular fragments into zonal structures on mineral surfaces.
 1081 *Biogeochemistry*, 85, pp.9-24. <https://doi.org/10.1007/s10533-007-9103-5>

1082 Kochenderfer, J.N., 1973. Root distribution under some forest types native to West Virginia.
 1083 *Ecology*, 54(2), pp.445-448. <https://doi.org/10.2307/1934355>

1084 Kögel-Knabner, I., Guggenberger, G., Kleber, M., Kandeler, E., Kalbitz, K., Scheu, S., Eusterhues,
 1085 K. and Leinweber, P., 2008. Organo-mineral associations in temperate soils: Integrating biology,
 1086 mineralogy, and organic matter chemistry. *Journal of Plant Nutrition and Soil Science*, 171(1),
 1087 pp.61-82. <https://doi.org/10.1002/jpln.200700048>

1088 Laegdsmand, M., Villholth, K.G., Ullum, M. and Jensen, K.H., 1999. Processes of colloid
 1089 mobilization and transport in macroporous soil monoliths. *Geoderma*, 93(1-2), pp.33-
 1090 59. [https://doi.org/10.1016/S0016-7061\(99\)00041-5](https://doi.org/10.1016/S0016-7061(99)00041-5)

1091 Laganier, J., Paré, D., Bergeron, Y., Chen, H.Y., Brassard, B.W. and Cavard, X., 2013. Stability of
 1092 soil carbon stocks varies with forest composition in the Canadian boreal biome. *Ecosystems*, 16,
 1093 pp.852-865. <https://doi.org/10.1007/s10021-013-9658-z>.

1094 Laganier, J., Boča, A., Van Miegroet, H. and Paré, D., 2017. A tree species effect on soil that is
 1095 consistent across the species' range: the case of aspen and soil carbon in North America.
 1096 *Forests*, 8(4), p.113. <https://doi.org/10.3390/f8040113>.

1097 Lakshmi, V., Jackson, T.J. and Zehrhuhs, D., 2003. Soil moisture–temperature relationships:
 1098 results from two field experiments. *Hydrological processes*, 17(15), pp.3041-3057.
 1099 <https://doi.org/10.1002/hyp.1275>

1100 Lal, R., 2004. Mechanisms of Carbon Sequestration in Soil Aggregates AU-Blanco-Canqui,
 1101 Humberto. *Crit. Rev. Plant Sci*, 23(6), pp.481-504. <https://doi.org/10.1080/07352680490886842>

1102 Langston, A.L. *et al.* (2015) 'Evidence for climatic and hillslope-aspect controls on vadose zone
 1103 hydrology and implications for saprolite weathering: CLIMATIC CONTROL ON VADOSE ZONE
 1104 MOISTURE', *Earth Surface Processes and Landforms*, 40(9), pp. 1254–1269. Available at:
 1105 <https://doi.org/10.1002/esp.3718>.

1106 Larson, J. H., Frost, P. C., Lodge, D. M., & Lamberti, G. A. (2007). Photodegradation of dissolved
 1107 organic matter in forested streams of the northern Great Lakes region. *Journal of the North
 1108 American Benthological Society*, 26(3), 416-425.

1109 Lavelle, P., Spain, A., Fonte, S., Bedano, J. C., Blanchart, E., Galindo, V., ... and Zangerlé, A., 2020.
 1110 Soil aggregation, ecosystem engineers and the C cycle. *Acta Oecologica*, 105, 103561.
 1111 <https://doi.org/10.1016/j.actao.2020.103561>

1112 Leonard, Laura T., Gary F. Vanzin, Vanessa A. Garayburu-Caruso, Stephanie S. Lau, Curtis A.
 1113 Beutler, Alexander W. Newman, William A. Mitch, James C. Stegen, Kenneth H. Williams, and
 1114 Jonathan O. Sharp. Disinfection byproducts formed during drinking water treatment reveal an
 1115 export control point for dissolved organic matter in a subalpine headwater stream." *Water
 1116 Research X* 15 (2022): 100144. <https://doi.org/10.1016/j.wroa.2022.100144>.

1117 Leonard, L. T., Vanzin, G. F., Garayburu-Caruso, V. A., Lau, S. S., Beutler, C. A., Newman, A. W.,
 1118 ... & Sharp, J. O. (2022). Disinfection byproducts formed during drinking water treatment reveal
 1119 an export control point for dissolved organic matter in a subalpine headwater stream. *Water
 1120 Research X*, 15, 100144. <https://doi.org/10.1016/j.wroa.2022.100144>

1121 Liang, C., Amelung, W., Lehmann, J. and Kästner, M., 2019. Quantitative assessment of
 1122 microbial necromass contribution to soil organic matter. *Global change biology*, 25(11),
 1123 pp.3578-3590. <https://doi.org/10.1111/gcb.14781>

1124 Liu, X. and Biondi, F., 2021. Inter-specific transpiration differences between aspen, spruce, and
 1125 pine in a sky-island ecosystem of the North American Great Basin. *Forest Ecology and
 1126 Management*, 491, p.119157. <https://doi.org/10.1016/j.foreco.2021.119157>.

1127 Lucas, M., Schlüter, S., Vogel, H.J. and Vetterlein, D., 2019. Roots compact the surrounding soil
 1128 depending on the structures they encounter. *Scientific reports*, 9(1), p.16236.
 1129 <https://doi.org/10.1038/s41598-019-52665-w>

1130 Luo, C., Xu, G., Wang, Y., Wang, S., Lin, X., Hu, Y., Zhang, Z., Chang, X., Duan, J., Su, A. and Zhao,
 1131 X., 2009. Effects of grazing and experimental warming on DOC concentrations in the soil
 1132 solution on the Qinghai-Tibet plateau. *Soil Biology and Biochemistry*, 41(12), pp.2493-2500.
 1133 <https://doi.org/10.1016/j.soilbio.2009.09.006>

1134 Mambelli, S., Bird, J.A., Gleixner, G., Dawson, T.E. and Torn, M.S., 2011. Relative contribution of
 1135 foliar and fine root pine litter to the molecular composition of soil organic matter after in situ
 1136 degradation. *Organic Geochemistry*, 42(9), pp.1099-1108.
 1137 <https://doi.org/10.1016/j.orggeochem.2011.06.008>

1138 Mainka, M., Summerauer, L., Wasner, D., Garland, G., Gripentrog, M., Berhe, A.A., Doetterl, S.
 1139 2022. Soil geochemistry as a driver of soil organic matter composition: insights from a soil
 1140 chronosequence. *Biogeosciences* 19:1675-1689. <https://doi.org/10.5194/bg-19-1675-2022>

1141 Makiel, M. *et al.* (2022) 'Formation of iron oxyhydroxides as a result of glauconite weathering in
 1142 soils of temperate climate', *Geoderma*, 416, p. 115780. Available at:
 1143 <https://doi.org/10.1016/j.geoderma.2022.115780>.

1144 Mataix-Solera, J., Cerdà, A., Arcenegui, V., Jordán, A. and Zavala, L.M., 2011. Fire effects on soil
 1145 aggregation: a review. *Earth-Science Reviews*, 109(1-2), pp.44-60.
 1146 <https://doi.org/10.1016/j.earscirev.2011.08.002>

1147 Mauer, O. and Palátová, E., 2012. Root system development in Douglas fir (*Pseudotsuga*
 1148 *menziesii* [Mirb.] Franco) on fertile sites. *Journal of Forest Science*, 58(9), pp.400-
 1149 409. <https://doi.org/10.17221/94/2011-JFS>.

1150 Mekontchou, C.G., Houle, D., Bergeron, Y., Drobyshev, I. 2020. Contrasting root system
 1151 structure and belowground interactions between black spruce (*Picea mariana* (Mill.) B.S.P) and
 1152 trembling aspen (*Populus tremuloides* Michx) in boreal mixed woods of eastern Canada.
 1153 *Forests*. 11:127. <https://doi.org/10.3390/f11020127>

1154 Menzel, A. and Fabian, P., 1999. Growing season extended in Europe. *Nature*, 397(6721),
 1155 pp.659-659. <https://doi.org/10.1038/17709>

1156 Mikutta, R., Turner, S., Schippers, A., Gentsch, N., Meyer-Stüve, S., Condrón, L.M., Peltzer, D.A.,
 1157 Richardson, S.J., Eger, A., Hempel, G. and Kaiser, K., 2019. Microbial and abiotic controls on
 1158 mineral-associated organic matter in soil profiles along an ecosystem gradient. *Scientific*
 1159 *reports*, 9(1), p.10294. <https://doi.org/10.1038/s41598-019-46501-4>.

1160 Mitchell, P.J., Lane, P.N. and Benyon, R.G., 2012. Capturing within catchment variation in
 1161 evapotranspiration from montane forests using LiDAR canopy profiles with measured and
 1162 modelled fluxes of water. *Ecohydrology*, 5(6), pp.708-720. <https://doi.org/10.1002/eco.255>

1163 Moldrup, P., Deepagoda, T.C., Hamamoto, S., Komatsu, T., Kawamoto, K., Rolston, D.E. and de
 1164 Jonge, L.W., 2013. Structure-dependent water-induced linear reduction model for predicting
 1165 gas diffusivity and tortuosity in repacked and intact soil. *Vadose Zone Journal*, 12(3).
 1166 <https://doi.org/10.2136/vzj2013.01.0026>

1167 Monteith, D.T., Stoddard, J.L., Evans, C.D., De Wit, H.A., Forsius, M., Høgåsen, T., Wilander, A.,
 1168 Skjelkvåle, B.L., Jeffries, D.S., Vuorenmaa, J. and Keller, B., 2007. Dissolved organic carbon
 1169 trends resulting from changes in atmospheric deposition chemistry. *Nature*, 450(7169), pp.537-
 1170 540. <https://doi.org/10.1038/nature06316>

1171 Moore, T.R., Trofymow, J.A., Prescott, C.E., Fyles, J. and Titus, B.D., 2006. Patterns of carbon,
 1172 nitrogen and phosphorus dynamics in decomposing foliar litter in Canadian forests. *Ecosystems*,
 1173 9, pp.46-62. <https://doi.org/10.1007/s10021-004-0026-x>.

1174 Morbidelli, R., Saltalippi, C., Flammini, A. and Govindaraju, R.S., 2018. Role of slope on
 1175 infiltration: A review. *Journal of hydrology*, 557, pp.878-886.
 1176 <https://doi.org/10.1016/j.jhydrol.2018.01.019>

1177 Morgan, M.D., 1969. Ecology of aspen in Gunnison County, Colorado. *American Midland*
 1178 *Naturalist*, pp.204-228. <https://doi.org/10.2307/2423831>

1179 Morris, D. P., Zagarese, H., Williamson, C. E., Balseiro, E. G., Hargreaves, B. R., Modenutti, B., ...
 1180 & Queimalinos, C. (1995). The attenuation of solar UV radiation in lakes and the role of
 1181 dissolved organic carbon. *Limnology and Oceanography*, 40(8), 1381-1391.
 1182 <https://doi.org/10.4319/lo.1995.40.8.1381>

1183 Nadelhoffer, K.J., Fry, B., 1988. Nitrogen-15 and carbon-13 abundances in forest soil organic
 1184 matter. *Soil Science Society of America Journal* 52:1633-1640.
 1185 <https://doi.org/10.2136/sssaj1988.03615995005200060024x>

1186 Nédeltcheva, T.H., Piedallu, C., Gégout, J.C., Stussi, J.M., Boudot, J.P., Angeli, N. and Dambrine,
 1187 E., 2006. Influence of granite mineralogy, rainfall, vegetation and relief on stream water
 1188 chemistry (Vosges Mountains, north-eastern France). *Chemical Geology*, 231(1-2), pp.1-15.
 1189 <https://doi.org/10.1016/j.chemgeo.2005.12.012>

1190 Neris, J., Jiménez, C., Fuentes, J., Morillas, G. and Tejedor, M., 2012. Vegetation and land-use
 1191 effects on soil properties and water infiltration of Andisols in Tenerife (Canary Islands, Spain).
 1192 *Catena*, 98, pp.55-62. <https://doi.org/10.1016/j.catena.2012.06.006>

1193 Neville, J., Tessier, J.L., Morrison, I., Scarratt, J., Canning, B. and Klironomos, J.N., 2002. Soil
 1194 depth distribution of ecto-and arbuscular mycorrhizal fungi associated with *Populus*
 1195 *tremuloides* within a 3-year-old boreal forest clear-cut. *Applied Soil Ecology*, 19(3), pp.209-216..
 1196 [https://doi.org/10.1016/S0929-1393\(01\)00193-7](https://doi.org/10.1016/S0929-1393(01)00193-7).

1197 Nicoll, B.C., Berthier, S., Achim, A., Gouskou, K., Danjon, F. and Van Beek, L.P.H., 2006. The
 1198 architecture of *Picea sitchensis* structural root systems on horizontal and sloping terrain. *Trees*,
 1199 20, pp.701-712. <https://doi.org/10.1007/s00468-006-0085-z>.

1200 Nikolakopoulou, M., Argerich, A., Drummond, J.D., Gacia, E., Martí, E., Sorolla, A. and Sabater,
 1201 F., 2018. Emergent macrophyte root architecture controls subsurface solute transport. *Water*
 1202 *Resources Research*, 54(9), pp.5958-5972. <https://doi.org/10.1029/2017WR022381>

1203 Nimmo, J.R. and Perkins, K.S., 2002. 2.6 Aggregate stability and size distribution. *Methods of soil*
 1204 *analysis: part 4 physical methods*, 5, pp.317-328. <https://doi.org/10.2136/sssabookser5.4.c14>

1205 Nye, P.H., 1981. Changes of pH across the rhizosphere induced by roots. *Plant and soil*, 61,
 1206 pp.7-26. <https://doi.org/10.1007/BF02277359>

1207 Norris, C. E., Quideau, S. A., & Oh, S. W. (2016). Microbial utilization of double-labeled aspen
 1208 litter in boreal aspen and spruce soils. *Soil Biology and Biochemistry*, 100, 9-20.
 1209 <https://doi.org/10.1016/j.soilbio.2016.05.013>

1210 Oades, J.M., 1984. Soil organic matter and structural stability: mechanisms and implications for
 1211 management. *Plant and soil*, 76, pp.319-337. <https://doi.org/10.1007/BF02205590>

1212 Okada, H. (1971). Classification of sandstone: analysis and proposal. *The Journal of Geology*,
 1213 79(5), 509-525. <https://doi.org/10.1306/D42692BA-2B26-11D7-8648000102C1865D>

1214 Ouyang, N., Zhang, Y., Sheng, H., Zhou, Q., Huang, Y. and Yu, Z., 2021. Clay mineral composition
 1215 of upland soils and its implication for pedogenesis and soil taxonomy in subtropical China.
 1216 *Scientific Reports*, 11(1), p.9707. <https://doi.org/10.1038/s41598-021-89049-y>.

1217 Pagano, T., Bida, M., & Kenny, J. E. (2014). Trends in levels of allochthonous dissolved organic
 1218 carbon in natural water: a review of potential mechanisms under a changing
 1219 climate. *Water*, 6(10), 2862-2897. <https://doi.org/10.3390/w6102862>

1220 Panhwar, Q.A., Naher, U.A., Shamshuddin, J., Othman, R. and Ismail, M.R., 2016. Applying
 1221 limestone or basalt in combination with bio-fertilizer to sustain rice production on an acid
 1222 sulfate soil in Malaysia. *Sustainability*, 8(7), p.700. <https://doi.org/10.3390/su8070700>

1223 Paré, D. and Bergeron, Y., 1996. Effect of colonizing tree species on soil nutrient availability in a
 1224 clay soil of the boreal mixedwood. *Canadian Journal of Forest Research*, 26(6), pp.1022-1031.
 1225 <https://doi.org/10.1139/x26-113>

1226 Popenoe, J.H., Bevis, K.A., Gordon, B.R., Sturhan, N.K. and Hauxwell, D.L., 1992. Soil-vegetation
 1227 relationships in Franciscan terrain of northwestern California. *Soil Science Society of America*
 1228 *Journal*, 56(6), pp.1951-1959. <https://doi.org/10.2136/sssaj1992.03615995005600060050x>

1229 Ramesh, T., Bolan, N.S., Kirkham, M.B., Wijesekara, H., Kanchikerimath, M., Rao, C.S., Sandeep,
 1230 S., Rinklebe, J., Ok, Y.S., Choudhury, B.U. and Wang, H., 2019. Soil organic carbon dynamics:
 1231 Impact of land use changes and management practices: A review. *Advances in agronomy*, 156,
 1232 pp.1-107. <https://doi.org/10.1016/bs.agron.2019.02.001>.

1233 Reisman, D., Rutkowski, T., Smart, P., Gusek, J. and Sieczkowski, M., 2009. Passive treatment
 1234 and monitoring at the standard mine superfund site Crested Butte, CO. *Proceedings America*
 1235 *Society of Mining and Reclamation*, pp.1107-1128.

1236 Rhoades, A.M., Ullrich, P.A. and Zarzycki, C.M., 2018. Projecting 21st century snowpack trends
 1237 in western USA mountains using variable-resolution CESM. *Climate Dynamics*, 50(1-2), pp.261-
 1238 288. <https://doi.org/10.1007/s00382-017-3606-0>.

1239 Riveros-Iregui, D.A., McGlynn, B.L., Marshall, L.A., Welsch, D.L., Emanuel, R.E. and Epstein, H.E.,
 1240 2011. A watershed-scale assessment of a process soil CO₂ production and efflux model. *Water*
 1241 *Resources Research*, 47(10). <https://doi.org/10.1029/2010WR009941>

1242 Roulet, N. and Moore, T.R., 2006. Browning the waters. *Nature*, 444(7117), pp.283-284.
 1243 <https://doi.org/10.1038/444283a>

1244 Burnett, B. N., Meyer, G. A., & McFadden, L. D. (2008). Aspect-related microclimatic influences
 1245 on slope forms and processes, northeastern Arizona. *Journal of Geophysical Research: Earth*
 1246 *Surface*, 113(F3). <https://doi.org/10.1029/2010WR009941>

1247 Dobarco, M. R., & Van Miegroet, H. (2014). Soil Organic Carbon Storage and Stability in the
 1248 Aspen-Conifer Ecotone in Montane Forests in Utah, USA. *Forests*, 5(4), 666-688.
 1249 <https://doi.org/10.3390/f5040666>

1250 Román Dobarco, M., Jacobson, A.R. and Van Miegroet, H., 2021. Chemical composition of soil
 1251 organic carbon from mixed aspen-conifer forests characterized with Fourier transform infrared
 1252 spectroscopy. *European Journal of Soil Science*, 72(3), pp.1410-1430.
 1253 <https://doi.org/10.1111/ejss.13065>.

1254 Rossi, A.M., Hirmas, D.R., Graham, R.C. and Sternberg, P.D., 2008. Bulk density determination
 1255 by automated three-dimensional laser scanning. *Soil Science Society of America Journal*, 72(6),
 1256 pp.1591-1593. <https://doi.org/10.2136/sssaj2008.0072N>

1257 Rutter, E.B., Ruiz Diaz, D. and Hargrave, L.M., 2022. Evaluation of Mehlich-3 for determination
 1258 of cation exchange capacity in Kansas soils. *Soil Science Society of America Journal*, 86(1),
 1259 pp.146-156. <https://doi.org/10.1002/saj2.20354>

1260 Sadnes, A., Eldhuset, T.D., Wollebaek, G. 2005. Organic acids in root exudates and soil solution
 1261 of Norway spruce and silver birch. *Soil Biology and Biochemistry* 37:259-k269.
 1262 <https://doi.org/10.1016/j.soilbio.2004.07.036>

1263 Sae-Tun, O., Bodner, G., Rosinger, C., Zechmeister-Boltenstern, S., Mentler, A. and Keiblinger,
 1264 K., 2022. Fungal biomass and microbial necromass facilitate soil carbon sequestration and
 1265 aggregate stability under different soil tillage intensities. *Applied Soil Ecology*, 179, p.104599.
 1266 <https://doi.org/10.1016/j.apsoil.2022.104599>

1267 Scharlemann, J.P., Tanner, E.V., Hiederer, R. and Kapos, V., 2014. Global soil carbon:
 1268 understanding and managing the largest terrestrial carbon pool. *Carbon management*, 5(1),
 1269 pp.81-91. <https://doi.org/10.4155/cmt.13.77>

1270 Schjønning, P., Thomsen, I.K., Møberg, J.P., de Jonge, H., Kristensen, K. and Christensen, B.T.,
 1271 1999. Turnover of organic matter in differently textured soils: I. Physical characteristics of
 1272 structurally disturbed and intact soils. *Geoderma*, 89(3-4), pp.177-198.
 1273 [https://doi.org/10.1016/S0016-7061\(98\)00083-4](https://doi.org/10.1016/S0016-7061(98)00083-4)

1274 Schneider, C.A., Rasband, W.S. and Eliceiri, K.W., 2012. NIH Image to ImageJ: 25 years of image
 1275 analysis. *Nature methods*, 9(7), pp.671-675. <https://doi.org/10.1038/nmeth.2089>

1276 Schoeneberger, P.J., D.A. Wysocki, E.C. Benham, and Soil Survey Staff. 2012. Field book for
 1277 describing and sampling soils, Version 3.0. Natural Resources Conservation Service, National
 1278 Soil Survey Center, Lincoln, NE.

1279 Seyfried, G.S., Canham, C.D., Dalling, J.W. and Yang, W.H., 2021. The effects of tree-mycorrhizal
 1280 type on soil organic matter properties from neighborhood to watershed scales. *Soil Biology and*
 1281 *Biochemistry*, 161, p.108385. <https://doi.org/10.1016/j.soilbio.2021.108385>.

1282 Shand, C.A., Williams, B.L., Coutts, G., 2008. Determination of N-species in soil extracts using
1283 microplate techniques. *Talanta* 74 ,648-654; [10.1016/j.talanta.2007.06.039](https://doi.org/10.1016/j.talanta.2007.06.039)

1284 Shen, R., Pennell, K.G. and Suuberg, E.M., 2013. Influence of soil moisture on soil gas vapor
1285 concentration for vapor intrusion. *Environmental Engineering Science*, 30(10), pp.628-637.
1286 <https://doi.org/10.1089/ees.2013.0133>

1287 Shepperd, W., Rogers, P.C. and Bartos, D., 2006. Ecology, management, and restoration of
1288 aspen in the Sierra Nevada. <https://doi.org/10.2737/RMRS-GTR-178>.

1289 Silver, W.L., Lugo, A.E. and Keller, M., 1999. Soil oxygen availability and biogeochemistry along
1290 rainfall and topographic gradients in upland wet tropical forest soils. *Biogeochemistry*, 44,
1291 pp.301-328. <https://doi.org/10.1007/BF00996995>.

1292 Singer, M.J., Southard, R.J., Warrington, D.N. and Janitzky, P., 1992. Stability of synthetic sand-
1293 clay aggregates after wetting and drying cycles. *Soil Science Society of America Journal*, 56(6),
1294 pp.1843-1848. Le Bissonnais, Y., 1996. Aggregate stability and assessment of soil crustability and
1295 erodibility: I. Theory and methodology. *Eur. J. Soil Sci.* 47 (4), 425–437.
1296 <https://doi.org/10.2136/sssaj1992.03615995005600060032x>

1297 Singh, S.H.I.P.R.A., 2018. Understanding the role of slope aspect in shaping the
1298 vegetation attributes and soil properties in Montane ecosystems. *Tropical Ecology*, 59(3),
1299 pp.417-430.

1300 Sinsabaugh, R.L. and Moorhead, D.L., 1994. Resource allocation to extracellular enzyme
1301 production: a model for nitrogen and phosphorus control of litter decomposition. *Soil biology
1302 and biochemistry*, 26(10), pp.1305-1311. [https://doi.org/10.1016/0038-0717\(94\)90211-9](https://doi.org/10.1016/0038-0717(94)90211-9).

1303 Six, J., Bossuyt, H., Degryze, S. and Denef, K., 2004. A history of research on the link between
1304 (micro) aggregates, soil biota, and soil organic matter dynamics. *Soil and tillage research*, 79(1),
1305 pp.7-31. <https://doi.org/10.1016/j.still.2004.03.008>

1306 Six, J., Conant, R.T., Paul, E.A. and Paustian, K., 2002. Stabilization mechanisms of soil organic
1307 matter: implications for C-saturation of soils. *Plant and soil*, 241, pp.155
1308 176. <https://doi.org/10.1023/A:1016125726789>

1309 Six, J. and Jastrow, J.D., 2002. Organic matter turnover. *Encyclopedia of soil science*, 10.

1310 Soil Survey Staff, Natural Resources Conservation Service, United States Department of
1311 Agriculture. Web Soil Survey. Available online at the following link:
1312 <http://websoilsurvey.sc.egov.usda.gov/>. Accessed [5/21/2023].

1313 Soil Survey, S., 2014,. Keys to soil taxonomy.

1314 Sokol, N.W., Whalen, E.D., Jilling, A., Kallenbach, C., Pett-Ridge, J. and Georgiou, K., 2022. Global
1315 distribution, formation and fate of mineral-associated soil organic matter under a changing
1316 climate: A trait-based perspective. *Functional Ecology*, 36(6), pp.1411-
1317 1429. <https://doi.org/10.1111/1365-2435.14040>

- 1318 Solly, E.F., Weber, V., Zimmermann, S., Walthert, L., Hagedorn, F. and Schmidt, M.W., 2020. A
1319 critical evaluation of the relationship between the effective cation exchange capacity and soil
1320 organic carbon content in Swiss forest soils. *Frontiers in Forests and Global Change*, 3,
1321 p.98.<https://doi.org/10.3389/ffgc.2020.00098>.
- 1322 Souza, L.F., Hirmas, D.R., Sullivan, P.L., Reuman, D.C., Kirk, M.F., Li, L., Ajami, H., Wen, H., Sarto,
1323 M.V., Loecke, T.D. and Rudick, A.K., 2023. Root distributions, precipitation, and soil structure
1324 converge to govern soil organic carbon depth distributions. *Geoderma*, 437, p.116569.
1325 <https://doi.org/10.1016/j.geoderma.2023.116569>
- 1326 Staff, S. S., 1999,. Soil taxonomy: a basic system of soil classification for making and interpreting
1327 soil surveys. *Agriculture handbook*, 436.
- 1328 Stanley, E. H., Powers, S. M., Lottig, N. R., Buffam, I., & Crawford, J. T. (2012). Contemporary
1329 changes in dissolved organic carbon (DOC) in human-dominated rivers: is there a role for DOC
1330 management?. *Freshwater Biology*, 57, 26-42.
- 1331 <https://doi.org/10.1111/j.1365-2427.2011.02613.x>
- 1332
- 1333 Stătescu, F., Zaucă, D.C. and Pavel, L.V., 2013. Soil structure and water-stable aggregates.
1334 *Environmental Engineering & Management Journal (EEMJ)*,
1335 12(4).<https://doi.org/10.30638/eemj.2013.091>.
- 1336 Sternberg, P.D., Anderson, M.A., Graham, R.C., Beyers, J.L. and Tice, K.R., 1996. Root
1337 distribution and seasonal water status in weathered granitic bedrock under chaparral.
1338 *Geoderma*, 72(1-2), pp.89-98.[https://doi.org/10.1016/0016-7061\(96\)00019-5](https://doi.org/10.1016/0016-7061(96)00019-5).
- 1339 Stone, E.L. and Kalisz, P.J., 1991. On the maximum extent of tree roots. *Forest ecology and*
1340 *management*, 46(1-2), pp.59-102. [https://doi.org/10.1016/0378-1127\(91\)90245-Q](https://doi.org/10.1016/0378-1127(91)90245-Q)
- 1341 Stone, M.M., DeForest, J.L. and Plante, A.F., 2014. Changes in extracellular enzyme activity and
1342 microbial community structure with soil depth at the Luquillo Critical Zone Observatory. *Soil*
1343 *Biology and Biochemistry*, 75, pp.237-247.<https://doi.org/10.1016/j.soilbio.2014.04.017>.
- 1344 Stump, L.M. and Binkley, D., 1993. Relationships between litter quality and nitrogen availability
1345 in Rocky Mountain forests. *Canadian Journal of Forest Research*, 23(3), pp.492-
1346 502. <https://doi.org/10.1139/x93-067>
- 1347 Sullivan, P. L., Godd  ris, Y., Shi, Y., Gu, X., Schott, J., Hasenmueller, E. A., ... & Brantley, S. L.
1348 (2019). Exploring the effect of aspect to inform future earthcasts of climate-driven changes in
1349 weathering of shale. *Journal of Geophysical Research: Earth Surface*, 124(4), 974-993.
1350 <https://doi.org/10.1029/2017JF004556>
- 1351 Sullivan, P.L., Billings, S.A., Hirmas, D., Li, L., Zhang, X., Ziegler, S., Murenbeeld, K., Ajami, H.,
1352 Guthrie, A., Singha, K. and Gim  nez, D., 2022. Embracing the dynamic nature of soil structure: A

1353 paradigm illuminating the role of life in critical zones of the Anthropocene. *Earth-Science*
 1354 *Reviews*, 225, p.103873. <https://doi.org/10.1016/j.earscirev.2021.103873>.

1355 Tew, R.K., 1968. *Properties of soil under aspen and herb-shrub cover* (Vol. 78). US Department
 1356 of Agriculture, Forest Service, Intermountain Forest & Range Experiment Station.

1357 Tisdall, J.M. and OADES, J.M., 1982. Organic matter and water-stable aggregates in soils. *Journal*
 1358 *of soil science*, 33(2), pp.141-163. <https://doi.org/10.1111/j.1365-2389.1982.tb01755.x>
 1359

1360 von Lützow, M., Kögel-Knabner, I., Ludwig, B., Matzner, E., Flessa, H., Ekschmitt, K.,
 1361 Guggenberger, G., Marschner, B. and Kalbitz, K., 2008. Stabilization mechanisms of organic
 1362 matter in four temperate soils: Development and application of a conceptual model. *Journal of*
 1363 *Plant Nutrition and Soil Science*, 171(1), pp.111-124. <https://doi.org/10.1002/jpln.200700047>

1364

1365 Wadgyamar, S.M., Ogilvie, J.E., Inouye, D.W., Weis, A.E. and Anderson, J.T., 2018. Phenological
 1366 responses to multiple environmental drivers under climate change: insights from a long-term
 1367 observational study and a manipulative field experiment. *New Phytologist*, 218(2), pp.517-
 1368 529. <https://doi.org/10.1111/nph.15029>.

1369 Wainwright, Haruko M., Sebastian Uhlemann, Maya Franklin, Nicola Falco, Nicholas J. Bouskill,
 1370 Michelle E. Newcomer, Baptiste Dafflon et al. Watershed zonation through hillslope clustering
 1371 for tractably quantifying above-and below-ground watershed heterogeneity and functions.
 1372 *Hydrology and Earth System Sciences* 26, no. 2 (2022): 429-444. [https://doi.org/10.5194/hess-](https://doi.org/10.5194/hess-26-429-2022)
 1373 [26-429-2022](https://doi.org/10.5194/hess-26-429-2022), 2022

1374 Wang, Y., Gao, S., Li, C., Zhang, J. and Wang, L., 2016. Effects of temperature on soil organic
 1375 carbon fractions contents, aggregate stability and structural characteristics of humic substances
 1376 in a Mollisol. *Journal of Soils and Sediments*, 16, pp.1849-1857. [https://doi.org/10.1007/s11368-](https://doi.org/10.1007/s11368-016-1379-4)
 1377 [016-1379-4](https://doi.org/10.1007/s11368-016-1379-4)

1378 Wang, Q., Xiao, J., Ding, J., Zou, T. 2021. Differences in root exudate inputs and rhizosphere
 1379 effects on soil N transformation between deciduous and evergreen trees. *Plant and Soil* 458
 1380 <https://doi.org/10.1007/s11104-019-04156-0>

1381 Wasner, D., Abramoff, R., Griepentrog, M., Venegas, E.Z., Boeckx, P., & Doetterl, S. (2024) The role
 1382 of climate, mineralogy and stable aggregates for soil organic carbon dynamics along a
 1383 geoclimatic gradient. *Global Biogeochemical Cycles*, 38, e2023GB007934.
 1384 <https://doi.org/10.1029/2023GB007934>

1385 Weil, R.R. and Brady, N.C., 2017. *The nature and properties of soils* (Fifteen Ed).

1386 White, T., Brantley, S., Banwart, S., Chorover, J., Dietrich, W., Derry, L., et al., 2015. The role of
 1387 critical zone observatories in critical zone science. In: *Developments in Earth Surface Processes*,
 1388 vol. 19. Elsevier, pp. 15–78. <https://doi.org/10.1016/B978-0-444-63369-9.00002-1>

1389 Witty, J.H., Graham, R.C., Hubbert, K.R., Doolittle, J.A. and Wald, J.A., 2003. Contributions of
1390 water supply from the weathered bedrock zone to forest soil quality. *Geoderma*, 114(3-4),
1391 pp.389-400.[https://doi.org/10.1016/S0016-7061\(03\)00051-X](https://doi.org/10.1016/S0016-7061(03)00051-X).

1392 Woldelessassie, M., Van Miegroet, H., Gruselle, M.C. and Hambly, N., 2012. Storage and stability
1393 of soil organic carbon in aspen and conifer forest soils of northern Utah. *Soil Science Society of*
1394 *America Journal*, 76(6), pp.2230-2240..<https://doi.org/10.2136/sssaj2011.0364>.

1395 Woolf, D., and Lehmann, J. 2019. Microbial models with minimal mineral protection can explain
1396 long-term soil organic carbon persistence. *Sci Rep* 9, 6522. [https://doi.org/10.1038/s41598-](https://doi.org/10.1038/s41598-019-43026-8)
1397 [019-43026-8](https://doi.org/10.1038/s41598-019-43026-8)

1398 Yang, J. Q., Zhang, X., Bourg, I. C., and Stone, H. A., 2021. 4D imaging reveals mechanisms of
1399 clay-carbon protection and release. *Nature communications*, 12(1), 622.

1400 Ye, C., Chen, D., Hall, S.J., Pan, S., Yan, X., Bai, T., Guo, H., Zhang, Y., Bai, Y. and Hu, S., 2018.
1401 Reconciling multiple impacts of nitrogen enrichment on soil carbon: plant, microbial and
1402 geochemical controls. *Ecology Letters*, 21(8), pp.1162-1173.<https://doi.org/10.1111/ele.13083>.

1403 Zhai, J., Liu, R., Liu, J., Zhao, G. and Huang, L., 2014. Radiative forcing over China due to albedo
1404 change caused by land cover change during 1990–2010. *Journal of Geographical Sciences*, 24,
1405 pp.789-801. <https://doi.org/10.1007/s11442-014-1120-4>

1406 Zhang, Y., Niu, J., Yu, X., Zhu, W. and Du, X., 2015. Effects of fine root length density and root
1407 biomass on soil preferential flow in forest ecosystems. *Forest Systems*, 24(1),
1408 p.12.<https://doi.org/10.5424/fs/2015241-06048>.

1409 Zhao, D., Xu, M., Liu, G., Ma, L., Zhang, S., Xiao, T. and Peng, G., 2017. Effect of vegetation type
1410 on microstructure of soil aggregates on the Loess Plateau, China. *Agriculture, ecosystems &*
1411 *environment*, 242, pp.1-8. <https://doi.org/10.1016/j.agee.2017.03.014>

1412 Zhi, W., Williams, K.H., Carroll, R.W., Brown, W., Dong, W., Kerins, D. and Li, L., 2020. Significant
1413 stream chemistry response to temperature variations in a high-elevation mountain watershed.
1414 *Communications Earth & Environment*, 1(1), p.43.[https://doi.org/10.1038/s43247-020-00039-](https://doi.org/10.1038/s43247-020-00039-w)
1415 [w](https://doi.org/10.1038/s43247-020-00039-w).

1416 Ziegler, S.E., Benner, R., Billings, S.A., Edwards, K.A., Philben, M., Zhu, X., Laganière, J. 2017.
1417 [Climate warming can accelerate carbon fluxes without changing soil carbon stocks](https://doi.org/10.1038/s41598-017-00002-0). *Frontiers in*
1418 *Earth Science* 5:2 doi: 10.3389/feart.2017.00002.