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Research Article

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Posted Date: August 7th, 2026

DOI: https://doi.org/10.21203/rs.3.rs-10094488/v1

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Abstract

Aims

Boreal forests store large amounts of soil organic carbon (SOC), to which fine roots contribute through belowground carbon inputs and stabilization mechanisms. However, the effects of partial cuts on fine root traits and their consequences for SOC dynamics remain poorly understood. We investigated long-term partial cut effects on fine root morphological, architectural and chemical traits and their link to SOC stocks and stability.

Methods

We studied twelve black spruce stands (Picea mariana [Mill.] B.S.P.) in two contrasting regions of Québec, Canada: Abitibi (warmer, Luvisols) and Côte-Nord (colder, Podzols) comparing control and thinned stands. SOC stability was assessed through incubation estimating bioreactive (C_{bioR}) and recalcitrant carbon (C_{recal}), and physical fractionation quantifying particulate organic (POC) and mineral-associated organic carbon (MAOC).

Results

Results showed depth-dependent thinning effects and trait–SOC relationships. In the forest floor, thinning decreased fine root cellulose and C/N, yet cellulose was positively related to C_{recal}, suggesting a decrease in C stability through root litter quality modification. In the 0-15 cm mineral layer, thinning reduced understory specific root length which was negatively correlated with SOC stocks. Lower C/N was associated with higher C_{recal} and MAOC, highlighting microbial-mediated stabilization. In the 15-30 cm mineral layer, fine root traits were unrelated to SOC stocks but predicted stability with root mass density,

tissue density and dead root dry mass content controlling fresh carbon inputs, selective preservation and microbial-mineral stabilization.

Conclusions

These findings show that partial cuts reshape belowground carbon dynamics through depth-specific changes in fine root traits, with implications for forest management.

Keywords: Fine root traits, Soil organic carbon, MAOC, Partial cut, Thinning, Boreal forest

Abbreviations

AIC: Akaike Information Criterion

ANOVA: Analysis of Variance

BD: Bulk Density

C: Carbon

C/N: Ratio Carbon/Nitrogen

C_{bioR}: Bioreactive Carbon

C_{recal}: Recalcitrant Carbon

DOC: Dissolved Organic Carbon

GLM: Generalized Linear Model

MAOC: Mineral Associated Organic Carbon

MEMS: Microbial Efficiency–Matrix Stabilization

N: Nitrogen

PCA: Principal Component Analysis

POC: Particulate Organic Carbon

RD: Root Diameter

RDMC: Root Dry Mass Content

RES: Root Economic Spectrum

RL: Root Length

RLD: Root Length Density

RMD: Root Mass Density

RTD: Root Tissue Density

SEM: Standard Error of Mean

SOC: Soil Organic Carbon

SRL: Specific Root Length

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Introduction

Boreal forests represent one of the largest terrestrial carbon (C) reservoirs, holding about 30% of global forest C, primarily sequestered belowground as soil organic carbon (SOC) (Pan et al., 2011). Fine roots (diameter ≤ 2 mm) are critical drivers of the C cycle in forest ecosystems (Matamala et al., 2003; Weemstra et al., 2016). For example, in black spruce (*Picea mariana* [Mill.] B.S.P.) forests, the dominant tree species of the Canadian boreal forest, fine roots can contribute up to 71% of annual net primary production (NPP) (Kalyn & Van Rees, 2006). Fine roots influence C cycling through a range of processes, including root turnover and litter input, root exudation and rhizosphere priming effects, root respiration, and symbiotic relationships with mycorrhizal fungi and bacteria (Chari & Taylor, 2022; Hopkins et al., 2013; Keiluweit et al., 2015; Kwatcho Kengdo et al., 2025; Pausch & Kuzyakov, 2018; Solly et al., 2018).

To better understand how fine roots influence SOC dynamics, trait-based approaches have become useful tools for characterizing plant belowground strategies in response to environmental change (McCormack et al., 2017). Fine root traits are commonly categorized into: (i) morphological traits (*e.g.* specific root length (SRL) and root tissue density (RTD)) which indicate resource acquisition efficiency (Freschet et al., 2021b; McCormack & Iversen, 2019); (ii) architectural traits (*e.g.* root length density (RLD) and root mass density (RMD)), which define the spatial exploration of the soil volume and the intensity of belowground foraging (Freschet et al., 2021a; Stokes et al., 2009); and (iii) chemical traits (*e.g.* soluble compounds and lignin), which govern tissue decomposability and the quality of organic matter inputs to the soil (Bardgett et al., 2014; Prieto et al., 2016; Saha et al., 2023). Despite the recognized importance of fine roots for SOC dynamics, it remains

poorly understood how forest management alters these different trait categories and whether such changes translate into shifts in soil C storage and stability.

Partial cuts such as commercial thinning are widely used to improve residual tree growth and wood quality (Drobyshev et al., 2019; Garcia-Gonzalo et al., 2007; Vincent et al., 2009) but they also modify the belowground environment by altering light penetration, soil temperature and moisture, nutrient availability, and understory vegetation development (Dang et al., 2018; Lull et al., 2020; Trentini et al., 2017; Wang et al., 2019) which in turn can indirectly influence fine root traits. The literature reports highly contrasting results depending on species, thinning intensity, and post-thinning recovery time. For example, RMD decreased by 14% in *Pinus massoniana* Lamb. plantations 2 years after 20% thinning (Tian DaLun et al., 2010) while it remained unchanged in *Pinus resinosa* Aiton plantations (Hwang et al., 2007). Wang et al. (2021b) found that RLD and RTD increased 4 years post-thinning but decreased SRL in a Chinese fir (*Cunninghamia lanceolata*) plantation. For chemical traits, thinning increased fine root carbon concentration (RCC) in *Pinus massoniana* Lamb. plantations after 14 years (Zhao et al., 2024b), while it decreased with increasing thinning intensity (Wang et al., 2021b). These divergences are best understood through the root economic spectrum (RES) framework, which reflects the strategy of plant root systems to balance nutrient acquisition and resource conservation (Reich, 2014). Acquisitive roots are typically thinner, with higher SRL and root nitrogen concentration (RNC), lower RTD and shorter lifespan, which allows rapid soil exploration and resource uptake. By contrast, conservative roots are thicker, more structurally reinforced, with lower SRL and longer lifespans, thereby favoring resource conservation (de la Riva et al., 2021; Freschet et al., 2021b; McCormack et al., 2012; Roumet et al., 2016; Weemstra et al., 2020).

Thinning may shift fine root traits along this acquisitive to conservative gradient depending on which resource becomes less limiting after canopy opening, such as light, soil nutrients or water availability. Additionally, thinning can stimulate understory vegetation, which may compete with trees for resources and potentially reshape belowground C inputs (Trentini et al., 2017; Wang et al., 2019). Moreover, long-term thinning effects, rarely studied beyond 10 years post-treatment in boreal forests, may diverge substantially from short-term responses as remaining trees reconstitute their root systems and understory communities reestablish (Qin et al., 2024), further underscoring the need for studies at this 20-year timescale.

Beyond silvicultural management, pedoclimatic conditions also dictate fine root traits. Generally, colder environments are often associated with slower fine root turnover (Solly et al., 2018) whereas in warmer environments higher fine root biomass has been observed (Wang et al., 2021a; Yuan & Chen, 2010). Moreover, reduced moisture availability tends to limit root diameter (RD) and accelerate turnover while increased precipitation stimulates fine root elongation (Sun et al., 2024; Wang et al., 2021a; Zhang et al., 2018). Soil type can further shape fine root traits by altering nutrient availability, water retention and mechanical resistance to root penetration (Neatrour et al., 2005; Schmid, 2002). These pedoclimatic contrasts may therefore modulate thinning effects on fine root traits, highlighting the need to assess thinning across contrasting soil and climate contexts.

Fine root traits are expected to influence both SOC storage and stability by regulating the amount and quality of root-derived C entering the soil. RMD has been shown to be positively correlated with SOC (Rabearison et al., 2025). High SRL has faster turn over and generates more frequent C input, while fine roots with high RTD decompose more

slowly and contribute to the gradual accumulation of persistent organic matter (Jimoh et al., 2024; McCormack et al., 2012; Saha et al., 2023). However, the relationship between fine root traits and SOC stocks is not straightforward. Fine roots with high SRL also release labile exudates that can stimulate rhizospheric priming, destabilizing old SOC and partially offsetting the positive effect of greater necromass inputs (Dijkstra et al., 2021; Malhotra et al., 2025).

SOC stability is regulated by multiple stabilization mechanisms including (i) intrinsic (or secondary) biochemical resistance, (ii) substrate accessibility to microbes and (iii) physicochemical protection through interaction with minerals (von Lützow et al., 2007). Two complementary approaches allow this stability to be partitioned empirically. Laboratory incubation quantifies bioreactive carbon (C_{bioR}), the readily mineralizable C, and recalcitrant carbon (C_{recal}), the fraction resistant to microbial degradation (Andrieux et al., 2020; Paré et al., 2022). Physical fractionation distinguishes particulate organic carbon (POC), mainly composed of partially decomposed plant fragments, from mineral-associated organic carbon (MAOC), derived primarily from microbial necromass and metabolites adsorbed onto mineral surfaces (Cotrufo et al., 2019; Lavallee et al., 2020). Labile C (C_{bioR} and POC) has a short residence time while stable C (C_{recal} and MAOC) can persist for centuries to millennia, thus exerting a more durable climate change mitigation (Lavallee et al., 2020; Lehmann & Kleber, 2015). Fine root traits can govern the pathway by which root-derived C enter these SOC stability fractions (Poirier et al., 2018; Rinehart et al., 2026; Sokol et al., 2022). The microbial efficiency matrix stabilization (MEMS) framework predicts that high quality, nitrogen-rich residues, maximize microbial carbon use efficiency (CUE) and generate microbial necromass that can be stabilized in the soil

by mineral interaction (Cotrufo et al., 2013; Poirier et al., 2018; Sokol et al., 2019). Despite this theoretical framework, studies that simultaneously link fine roots morphological, architectural, and chemical traits to both SOC storage and multiple indicators of SOC stability remain rare, particularly in boreal forests and across both forest floor and mineral layers.

This study aimed to evaluate long-term thinning effects on fine root traits in black spruce stands and to link these traits with SOC storage and stability across forest floor and mineral layers in two contrasting pedoclimatic regions. Specifically, our objectives were to: (1) assess the long-term effects of thinning on fine root morphological, architectural, and chemical traits; (2) determine how these traits are related to SOC stocks; (3) examine how they are associated with SOC stability using two complementary approaches, namely incubation-derived and fractionation-derived. We hypothesized that long-term thinning would shift fine root traits toward more acquisitive strategies (higher SRL, higher RNC) but that this response would vary with soil depth and pedoclimatic region. Furthermore, we expected that architectural traits (RMD and RLD) would be the strongest predictors of SOC stocks. Finally, we hypothesized that high quality fine roots (low C/N ratios and high RNC) would be positively associated with stable C, consistent with the MEMS framework.

Methodology

Regional context and site selection

The study was conducted across two contrasted bioclimatic regions of the black spruce-feathermoss domain in Québec, Canada: (i) The Abitibi region (Western Québec, 49.1567° N, 78.8648° W, Fig. 1), characterized by lacustrine clay deposits from the glacial Lake Barlow-Ojibway and soils generally classified as gray Luvisols (Soil Classification Working Group, 1998), and (ii) the Côte-Nord region (Eastern Québec, 49.7190° N, 69.9431° W, Fig. 1) characterized by glacial till deposits with a silty sand texture and humo-ferric Podzols as the most common soil type. The climate in Abitibi is relatively warmer (mean annual temperature, MAT: 0.8°C) and drier (904 mm) compared to the Côte-Nord site that has colder (MAT: -1°C) and wetter (1119 mm) summers conditions. The growing season typically spans 155 days with 1327-degree days per year in Abitibi and about 145 days and 1190-degree days per year in Côte-Nord (Environment Canada, 2020).

In each region, six black spruce stands were selected based on the provincial forest inventory, ensuring consistent topography and fire origin (1920 and 1919 respectively for Abitibi and Côte-Nord). Half of these stands underwent partial cuts, specifically, commercial thinning between 2002 and 2005, while the remaining three stands served as unmanaged controls. “Commercial thinning” is referred as “thinning” herein. More information about the site characteristics can be found in Ratsimandresiarivo et al. (2026).

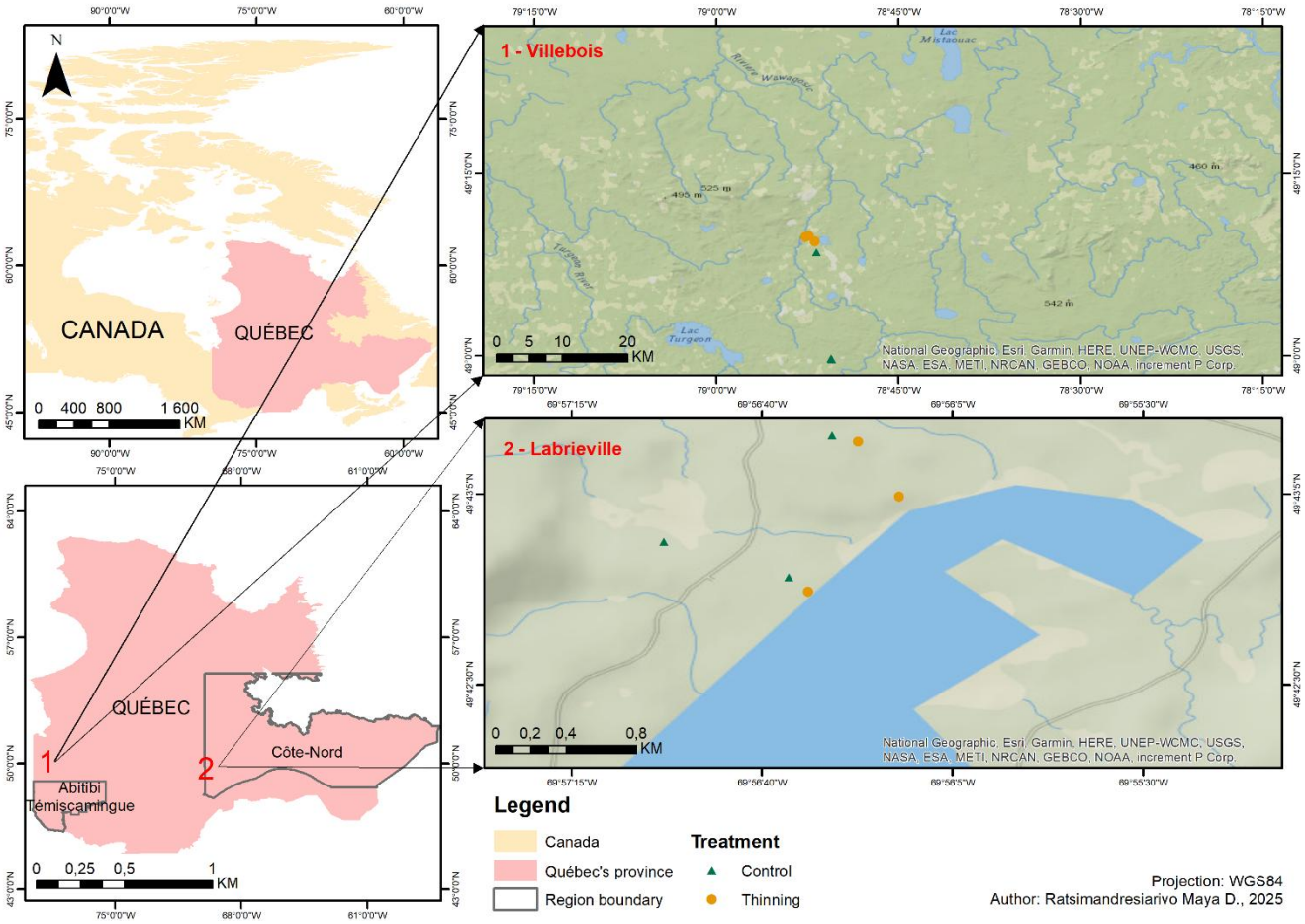

Fig. 1: Localization of study areas

Experimental design and fieldwork

In June 2023, approximately 20 years post-thinning, a 400 m² plot was installed in each of the 12 stands, where we established three pairs of adjacent quadrats (pseudo-replicates): one for soil collection and one for root extraction. This paired-quadrat approach was essential to preserve the integrity of the soil matrix required for C stability incubations and subsequent physico-chemical analyses, as the intensive washing and sieving process used to isolate fine roots results in the loss of the surrounding soil structure. These three pairs were distributed systematically in the control plots. We employed a stratified sampling

design for the thinned plot to capture the spatial heterogeneity introduced by mechanized harvesting: three pairs within the skidding strips (25% of the surface area) where all trees were removed and machinery passed and an additional three pairs within the residual strips (75% of the surface area) where only limited selective harvesting was conducted.

We sampled soil and roots across three depths in each quadrat: forest floor, 0-15 cm and 15-30 cm mineral layers. For soil sampling, the entire forest floor was collected within a 10 × 10 cm frame, and its total thickness was recorded. For the mineral layers, we extracted with an Eijkelkamp volumetric auger (8 cm diameter, 15 cm length). We used a metal corer with a 5 cm diameter for root sampling. The sampling length in the forest floor was adjusted to match its variable thickness, whereas the mineral layers were sampled at 15 cm intervals. Fewer samples were collected at 15–30 cm to balance the higher sampling effort required against the typically lower vertical variation in fine root and C distribution (Fig. 2). A total of 288 samples were collected [2 sample types × 2 regions × (3 quadrats × 3 controls × 2 soil depth + 2 quadrats × 3 controls × 1 soil depth) + (3 quadrats × 2 locations (residual and skidding) × 3 thinned × 2 soil depth + 2 quadrats × 2 locations × 3 thinned × 1 soil depth], sealed in plastic bags, and maintained at 4°C to minimize roots and microbial activity prior to analysis.

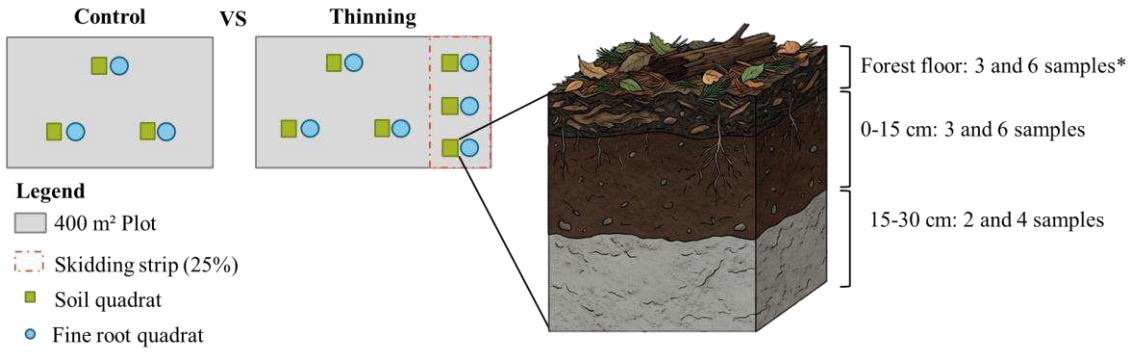

*Fig. 2: Experimental design and sampling for soil and fine roots. *3 and 6 samples for control and thinning respectively*

Root analysis

First, we washed the fine roots to remove all adhering soil particles and only roots with a diameter <2 mm were kept for analysis. We sorted fine roots of live (LBS) and dead (DBS) black spruce roots from understory vegetation (UV). The distinction between live and dead black spruce fine roots was based on visual and physical criteria: live roots were reddish-brown and flexible, while dead roots were black and brittle. We collected reference samples of the most common understory species at each site to develop morphological distinction criteria and ensure accurate identification.

Morphological Traits Analysis

Fine root morphological traits were analyzed following the methodology described by Roumet et al. (2016). We spread clean and live fine roots of black spruce and understory species into a transparent tray (30 × 43 cm) filled with distilled water to minimize root overlap. The roots were scanned at a resolution of 400 dpi using a scanner equipped with a transmitted light source to eliminate shadows (Epson Expression LA2400; Epson, Ontario, Canada). The resulting images were analyzed using WinRHIZO Pro software (v.2023c; Regent Instruments, Québec, Canada) to determine mean root diameter (RD, mm) and total root length (RL, cm). Then, all fine root samples were oven-dried at 60°C for 48 hours to determine root dry mass (RDM, g). Specific root length (SRL, $m.g^{-1}$) was calculated as the ratio of RL to RDM. Root dry matter content (RDMC, $mg.g^{-1}$) was calculated as the ratio of RDM to root fresh mass. Root tissue density (RTD, $g.cm^{-3}$) was calculated as RDM divided by root volume.

Architectural traits analysis

Root mass density (RMD, $g.cm^{-3}$) and root length density (RLD, $m.m^{-3}$) was calculated as the ratio of total RDM and total RL, respectively, by the volume of the soil core from which the roots were extracted.

Chemical traits analysis

Chemical traits were analyzed exclusively for the live black spruce fine root samples. First, dried root samples were pulverized at 2 mm sieve with a mixer mill (MM400, Retsch, Haan, Germany). Then, we quantified the concentrations of water-soluble compounds, hemicellulose, cellulose, and lignin using the Van Soest method (1991) with a fiber analyzer (Fibersac 24; Ankom, Macedon, NJ, USA). Additionally, fine root total C and N concentrations (RCC and RNC) were determined by dry combustion with a LECO CNS-928 analyzer (St. Joseph, MI, USA). Root material was insufficient in the 15–30 cm layer, therefore, C and N concentrations were not measured for this depth. Sample availability was prioritized for the analysis of soluble and structural compounds. Fine root C/N and lignin/N ratios were also calculated when data were available.

Soil analysis

We pooled all pseudo-replicate soil samples from the same depth within a plot to generate representative composite samples and to capture variability within each plot. We prepared composite samples separately for the skidding strip and residual strip of the thinned stands. Area-weighted averages were later applied for plot-level estimates.

Soil organic carbon storage

Soil samples were air-dried and sieved (6 mm for forest floor; 2 mm for mineral layers) and ground at 0.5 mm (Nelson et al., 2026) before determining total C and N concentrations by dry combustion (LECO CNS-928; St. Joseph, MI, USA). Bulk density (BD) was determined on an oven-dried basis (105°C) with correction for the presence of rock fragments in the mineral layers. SOC stock (Mg C ha^{-1}) at each depth was calculated using the Eq. 1 (Poeplau et al., 2017):

$$SOC_{stock} = SOC_{concentration} * BD * d * (1 - \delta) * 0.1 \quad (1)$$

Where $SOC_{concentration}$ is the soil organic carbon concentration ($g.kg^{-1}$), BD is the soil bulk density ($g.cm^{-3}$), d is the depth (cm) and δ is the rock fragment volume fraction (%/100).

Soil organic carbon stability

SOC stability was assessed using two complementary approaches: First, incubation-derived indicators were determined from long-term laboratory incubations under standard conditions and fitted with kinetic models to estimate: (i) the proportion of mineralizable C in each soil sample, defined as C_{bioR}, and (ii) the remaining C fraction, defined as C_{recal} (Andrieux et al., 2020; Laganière et al., 2013; Paré et al., 2006). Second, physical fractionation was used to separate POC from MAOC. This dual approach provides complementary insights into SOC vulnerability to mineralization and into stabilization pathways. Detailed descriptions of the incubation and fractionation settings can be found in Ratsimandresiarivo et al. (Submitted).

Laboratory incubation

We conducted a 355-day laboratory incubation at 26°C and 85% water-holding capacity to determine C_{bioR} and C_{recal}. We prepared 54 microcosms to represent the experimental design [3 controls + (3 thinned × 2 strips)) × 3 layers × 2 regions]. Periodic CO_2 efflux measurements were performed using a LI-6400 gas analyzer (LI-COR, Lincoln, NE, USA). To estimate the size of the C_{bioR} pool and its mineralization rate, we fitted a first-order kinetic model (Paré et al., 2006):

$$C(t) = C_0 * 1 - e^{-k_0 t} \quad (2)$$

where C(t) is the specific cumulative C mineralized at time t (mg $C.g^{-1}$ C_{tot}), C_0 represents the bioreactive C (mg $C.g^{-1}$ C_{tot}) and k_0 is the decomposition rate. C_{recal} (mg $C.g^{-1}$ C_{tot}) was defined as the difference between total organic C and C_{bioR}.

Bioreactive and recalcitrant C stocks (C_{bioR}, C_{recal}, Mg $C.ha^{-1}$), for each soil depth were computed using:

$$C_{bior\ stock} = C_{bior}\ concentration * BD * d * 0.1 \quad (3)$$

$$C_{recal\ stock} = C_{recal} concentration * BD * d * 0.1 \quad (4)$$

where C_{bioR} and C_{recal} concentration is the bioreactive and recalcitrant C concentration respectively, obtained from the model (g $C.kg^{-1}$ soil), BD is the bulk density ($g.cm^{-3}$) and d is soil depth (cm).

Physical fractionation

Soil physical fractionation was performed following the procedure of Carter & Gregorich (2007) and applied to the mineral layers (0–15 cm and 15–30 cm), as MAOC is considered negligible in the forest floor due to the absence of significant mineral particles (Lavallee et al., 2020). Dispersed 25 g of soil samples were passed through a 53 µm sieve

to separate the POC (>53 µm) from MAOC (<53 µm). Resulting fractions were oven-dried at 50°C, weighed and their C concentrations were determined by dry combustion using a LECO CNS-928 analyzer. POC and MAOC stocks (Mg C.ha^{-1}) were then calculated as:

$$POC_{stock} = POC_{conc} * BD * d * 0.1 \quad (5)$$

$$MAOC_{stock} = MAOC_{conc} * BD * d * 0.1 \quad (6)$$

where POC_{conc} and $MAOC_{conc}$ are POC and MAOC concentration in soil respectively (g. kg^{-1} soil), BD is the bulk density (g.cm^{-3}) and d is layer depth (cm).

Statistical analysis

All statistical analyses were performed in RStudio version 2026.01.1+403 (R Core Team, 2026). Fine root trait values and SOC variables were calculated at the plot level using area-weighted measurements obtained separately in the residual and skidding strips. We evaluated the effects of region, thinning treatment, and their interaction on fine root traits (morphological, architectural, and chemical) using ANOVA for each soil depth separately. As SOC storage and stability had previously shown clear depth dependent patterns (Ratsimandresiarivo et al., Submitted; Ratsimandresiarivo et al., 2026), all analyses were conducted separately for each soil depth. Linear models (*lm*) were used to quantify region and thinning effects, when the interaction was not significant, the model was simplified to retain only main effects. Model assumptions, including normality, homoscedasticity, and residual independence, were verified using diagnostic plots and Shapiro-Wilk tests. When necessary, response variables were log or square root transformed and if transformations failed to satisfy model assumptions, generalized linear models (*glm*, Gamma family) were used (Supplementary Table 1). Statistical significance

was assessed at $\alpha = 0.05$, and significant effects were followed by Tukey's post-hoc pairwise comparisons using the *emmeans* package. The fine root traits presented in the main text were selected based on (i) the significant effect of region and/or thinning effects, (ii) their functional relevance to fine root strategies and SOC dynamics, (iii) their non-redundancy with other correlated traits, and (iv) their relationships with SOC storage and stability indicators. Complete results for all traits tested are provided in Supplementary Table 1.

To examine the links between fine root traits and SOC dynamics, we analyzed the relationships between fine root traits (morphological, architectural and chemical) and: (i) SOC stocks; and (ii) SOC stability indicators (C_{BioR}, C_{recal}, POC, and MAOC). These relationships were done separately for each soil depth using linear regression models, with the same diagnostic procedures, transformations, and GLM alternatives as described above. For each SOC response variable, fine root traits were tested individually as predictors, and candidate models were compared using the p-values, the lowest Akaike Information Criterion (AIC) (and $\Delta AIC < 2$) and the highest R^2 (Supplementary Tables 2, 3, 4) to identify the fine root traits that best explained variation in SOC storage and stability.

Results

Effect of partial cut on fine root traits

Among the three fine root traits categories, only chemical traits responded consistently to thinning in the forest floor. Specifically, cellulose and C/N ratio both decreased in thinned stands across the two regions (Fig. 3). Fine roots from the warmer and drier region (Abitibi) had higher soluble compound concentrations than those from the colder and wetter region (Côte-Nord) in both the forest floor and the 0–15 cm mineral layer (Fig. 3). In contrast, cellulose concentration was higher in Côte-Nord than in Abitibi in the forest floor. However, neither region nor thinning changed fine root chemical traits in the 15-30 cm mineral layer (Fig 3).

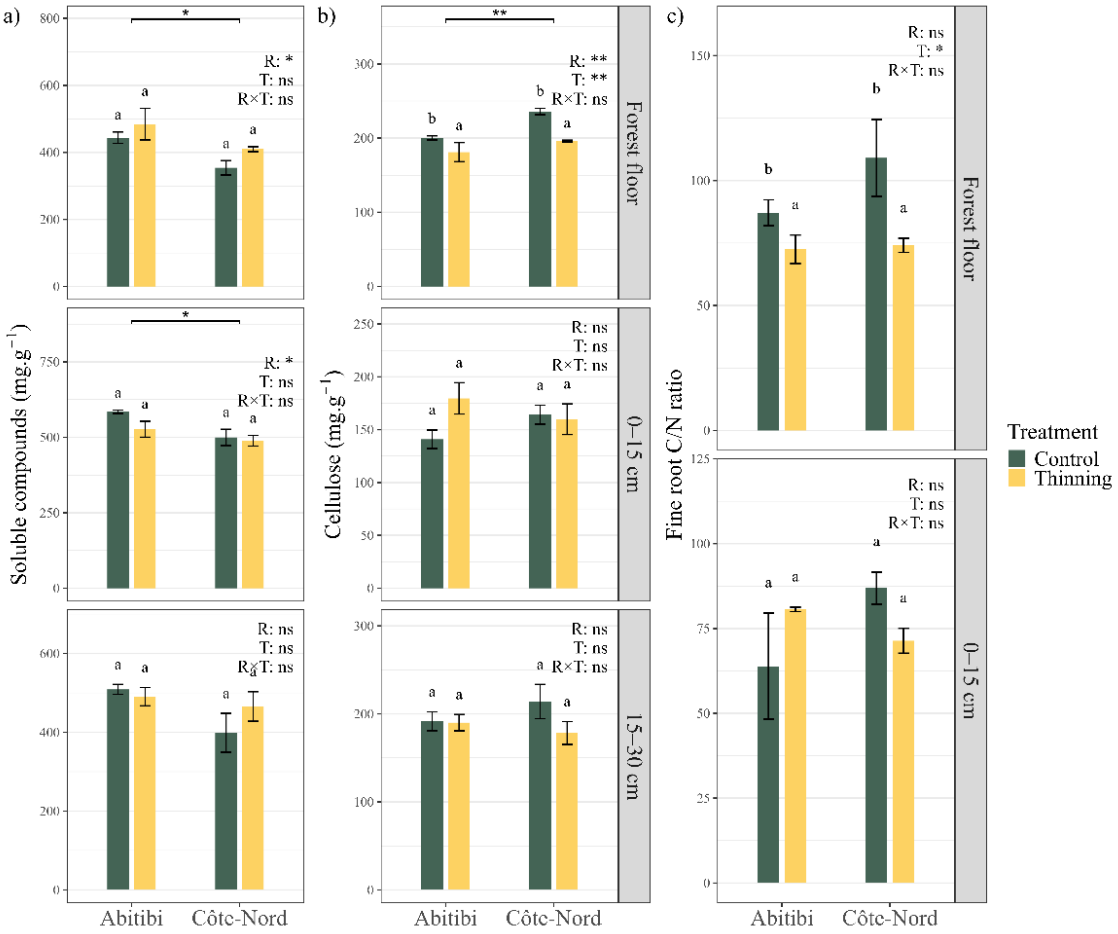

*Fig. 1: Mean chemical fine root traits between regions and treatments across soil depth. Within each soil depth, different letters indicate significant differences between region, treatment or their interaction, according to the significance of effects in the statistical models (R: region; T: Treatment; R x T: region x treatment interaction). Significant levels are indicated as follows: ns: not significant; ***: p <0.001; **: p <0.01; *: p <0.05.*

Most morphological and architectural fine root traits were unaffected by thinning across soil depths. The only exceptions involved understory vegetation fine roots: SRL_{UV} was lowered in thinned stands than in control stands only in Côte-Nord region, whereas $RDMC_{UV}$ was higher in thinned stands in Abitibi but remained unchanged in Côte-Nord (Fig 4). Regional effects were more pronounced than thinning effects for several morphological and architectural fine root traits of live and dead black spruce and understory vegetation. Live and dead fine roots of black spruce SRL and RLD (SRL_{LBS}, SRL_{DBS}, RLD_{LBS}, RLD_{DBS}, respectively) were similar across regions and at all depths (Fig.

4). In contrast, only SRL_{UV} and RLD_{UV} were lower in Abitibi compared to Côte-Nord in the 0-15 cm mineral layer and in the forest floor, respectively (Fig. 4). Additionally, $RDMC_{UV}$, $RDMC_{LBS}$ and $RDMC_{BDS}$ were consistently lower in Abitibi relative to Côte-Nord at the three depths. The same regional pattern was observed for the RMD_{UV} and RMD_{DBS} (Fig. 4).

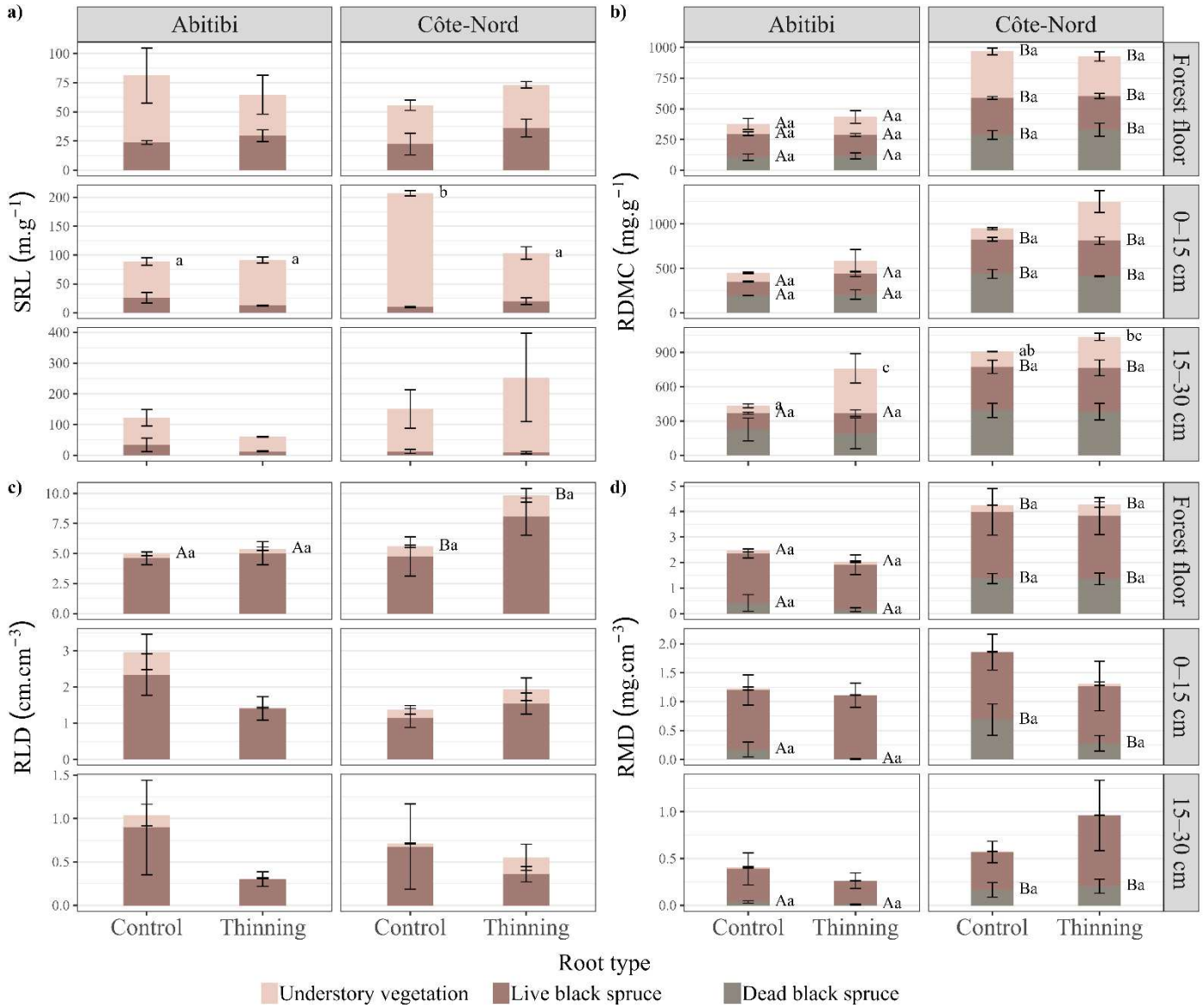

*Fig. 2: Mean SRL (a), RDMC (b), RLD (c) and RMD (d) for understory vegetation (UV), live and dead black spruce (LBS and DBS) between regions and treatments across soil depth. Within each soil depth, only significant differences were noted. Uppercase letters indicate significant differences between regions and lowercase letter indicate significant differences between thinning ($P<0.05$). $RDMC_{UV}$ in the 15-30 cm mineral layer was the only significant interaction (region*thinning). SRL: Specific root length, RDMC: Root dry mass content, RLD: Root length density, RMD: Root mass density.*

Relationships between SOC storage and fine root traits

Separate analyses by soil depth identified different categories of fine root predictors of SOC stocks across the soil profile (Table 1). Chemical and morphological traits were

strongly associated with SOC stocks in the forest floor, which increased with both fine root cellulose content ($R^2 = 0.70$, $p < 0.001$; Fig. 5a) and RTD_{LBS} ($R^2 = 0.56$, $p < 0.01$; Fig. 5b). In contrast, the strongest predictor of SOC stocks in the 0-15 cm mineral layer was the morphological trait SRL_{UV}, with SOC stocks declining as SRL_{UV} increased ($R^2 = 0.46$, $p < 0.05$; Fig. 5c). The lignin/N ratio ratios was also one of the best predictors at this depth, as its model had a $\Delta AIC \leq 2$ compared with the best-supported model (Table 1). None of our fine root traits was significantly related to SOC stocks in the deeper mineral layer (15–30 cm) (Table 1).

Table 1: Model selection between soil organic carbon (SOC) stocks and fine root traits ranged by AIC values with p value (Pr>F) at each depth.

Soil depth	Predictor	AIC	ΔAIC	Estimate	R^2	p-value
Forest floor	Cellulose	97.67	0.00	0.75	0.70	**<0.001**
	Lignin/N ratio	101.70	4.03	1.16	0.58	**0.004**
	RTD LBS	102.28	4.61	125.78	0.56	**0.005**
	Compound soluble	105.54	7.87	-0.21	0.42	**0.023**
	RNC	106.10	8.43	-108.59	0.39	**0.030**
	Fine root C/N ratio	106.11	8.43	0.65	0.39	**0.030**
	RDMC LBS	106.80	9.13	0.20	0.35	**0.042**
	RDMC UV	106.91	9.23	0.09	0.35	**0.044**
	RMD DBS	107.67	10.00	6.14	0.30	0.063
0–15 cm	SRL UV	77.54	0.00	-0.22	0.45	**0.049**
	Lignin/N ratio	78.53	0.99	-1.12	0.68	**0.003**
	Fine root C/N ratio	80.34	2.81	-0.81	0.62	**0.007**
	RNC	81.40	3.86	153.26	0.58	**0.011**
	RDMC DBS	82.32	4.78	-0.11	0.59	**0.009**
	Lignin	94.80	17.26	-0.24	0.66	**0.001**
	Compound soluble	97.59	20.05	0.27	0.57	**0.004**
	Hemicellulose	98.61	21.08	0.62	0.53	**0.007**
	RTD LBS	102.29	24.75	-84.77	0.37	**0.037**
	RDMC LBS	102.38	24.85	-0.09	0.36	**0.039**
	RL LBS	102.39	24.86	0.05	0.36	**0.039**
	RLD LBS	102.39	24.86	14.32	0.36	**0.039**
	RMD DBS	105.63	28.09	-19695.88	0.16	0.195
15–30 cm	RMD UV	78.89	0.00	527521.45	0.29	0.086

RDMC DBS	81.46	2.57	-0.03	0.28	0.095

Fine root traits presented here include those with significant *P* values, the best non-significant from each fine root trait category or those explicitly related to the study hypotheses. Complete model selection results for all fine root traits are provided in Supplementary Table 2. Values in bold are significant at $P < 0.05$. RTD: Root tissue density, RDMC: Root dry mass content, RL: Root length, RMD: Root mass density, RLD: Root length density, RNC: Root nitrogen concentration, LBS: Live black spruce, DBS: Dead black spruce, UV: Understory vegetation.

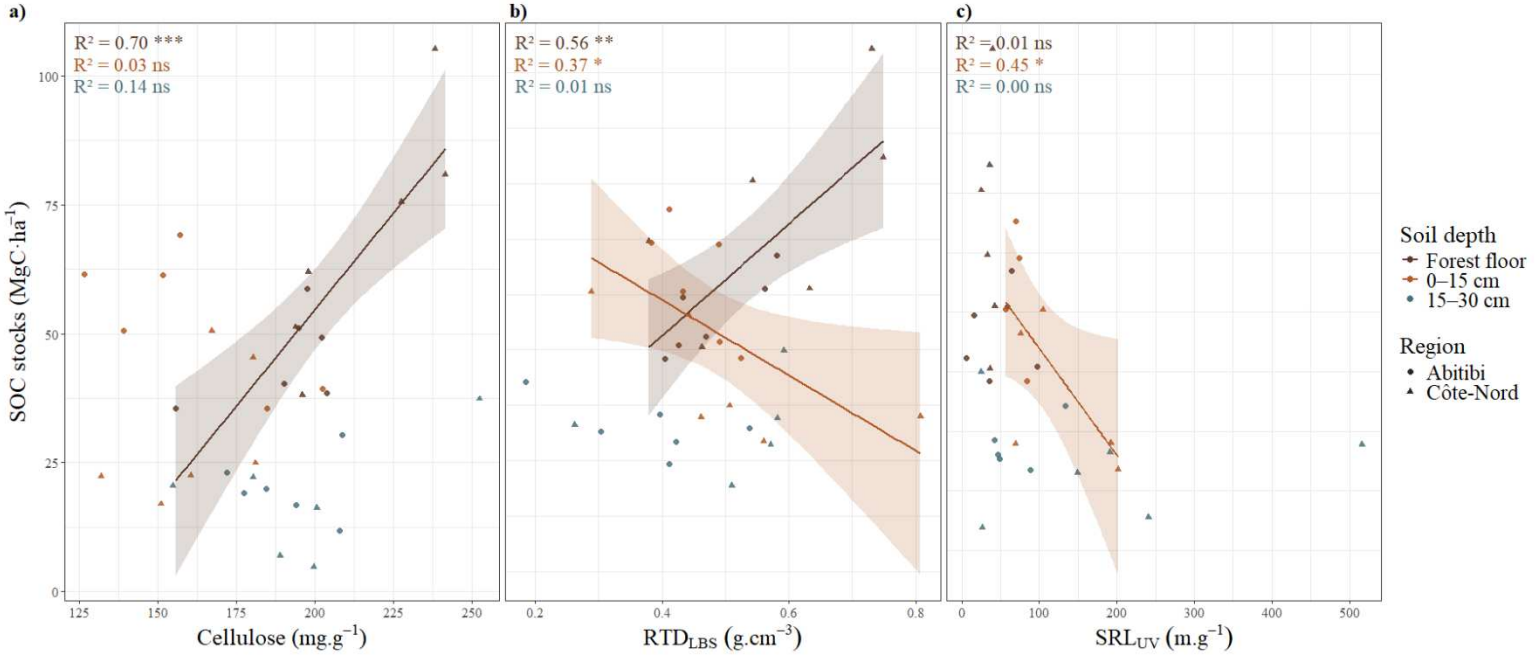

*Fig. 3: Relationship between soil organic carbon (SOC) stocks with significant and best model of fine root traits at each soil depth. Significant levels are indicated as follows: ns: not significant; ***: p <0.001; **: p <0.01; *: p <0.05. RTD_{LBS}: Root tissue density of live black spruce, SRL_{UV}: Specific root length of understory vegetation.*

Relationships between SOC stability and fine root traits

The category of fine root traits associated with labile C differed among soil depths when each layer was considered separately (Table 2). Relationships between measured fine root traits and incubation-derived C_{bioR} were absent in the forest floor. Higher morphological trait $RDMC_{DBS}$ was associated with lower C_{bioR} ($R^2 = 0.52$, $p<0.05$, Fig. 6a) whereas higher architectural trait RMD_{UV} was related with the lower POC ($R^2 = 0.87$, $p<0.001$, Fig. 6c) in the 0-15cm mineral layer. In contrast, higher architectural trait

374 RMD_{LBS} was related with higher C_{bioR} (R^2 = 0.71, p <0.001; Fig. 6b) whereas higher
375 chemical trait compound soluble was associated with lower POC (R^2 = 0.45, p <0.05; Fig.
376 6d) in the 15-30 cm mineral layer.

377 *Table 2: Model selection between labile C: (i) bioreactive C; (ii) particulate organic C*
378 *(POC) and fine root traits ranged by AIC values with p value (Pr>F) at each depth.*

Response	Soil depth	Predictor	AIC	ΔAIC	Estimate	R^2	p-value
Bioreactive C	Forest floor	RTD LBS	77.64	2.27	1.89	0.27	0.111
		Lignin	80.23	4.85	0.00	0.10	0.332
	0–15 cm	RDMC DBS	40.60	0.00	0.00	0.52	**0.016**
		RD UV	57.76	17.16	-19.94	0.55	**0.006**
		RDMC LBS	58.73	18.13	0.00	0.31	**0.041**
		Lignin	59.51	18.91	-0.01	0.27	**0.032**
		RMD UV	60.75	20.15	-44237.49	0.16	0.219
	15–30 cm	RMD LBS	22.59	0.00	2066.91	0.71	**<0.001**
		RLD UV	23.25	0.66	2.36	0.40	**0.030**
		RL UV	23.76	1.18	0.01	0.38	**0.041**
		RMD DBS	25.48	2.89	3139.99	0.29	**0.025**
		Compound soluble	27.28	4.70	0.00	0.18	0.147
POC	0–15 cm	RMD UV	44.90	0.00	-16900.09	0.87	**<0.001**
		RDMC UV	54.68	9.78	0.01	0.15	0.306
		RCC	59.60	14.70	-0.24	0.15	0.270
	15–30 cm	Compound soluble	74.81	0.00	-0.06	0.45	**0.017**
		Lignin	76.70	1.60	0.06	0.35	**0.042**
		RLD UV	77.12	2.15	20.78	0.33	0.051
		RMD LBS	77.67	2.56	8624.49	0.30	0.066
		SRL LBS	81.78	-75.52	-0.03	0.01	0.734

379 Fine root traits presented here include those with significant *P* value, the best nonsignificant
380 from each fine root trait category or those explicitly related to the study hypotheses.
381 Complete model selection results for all fine root traits are provided in Supplementary
382 Table 3. Values in bold are significant at *P* <0.05. RTD: Root tissue density, RDMC: Root
383 dry mass content, RL: Root length, RD: Root diameter, RMD: Root mass density, RLD:
384 Root length density, LBS: Live black spruce, DBS: Dead black spruce, UV: Understory
385 vegetation.

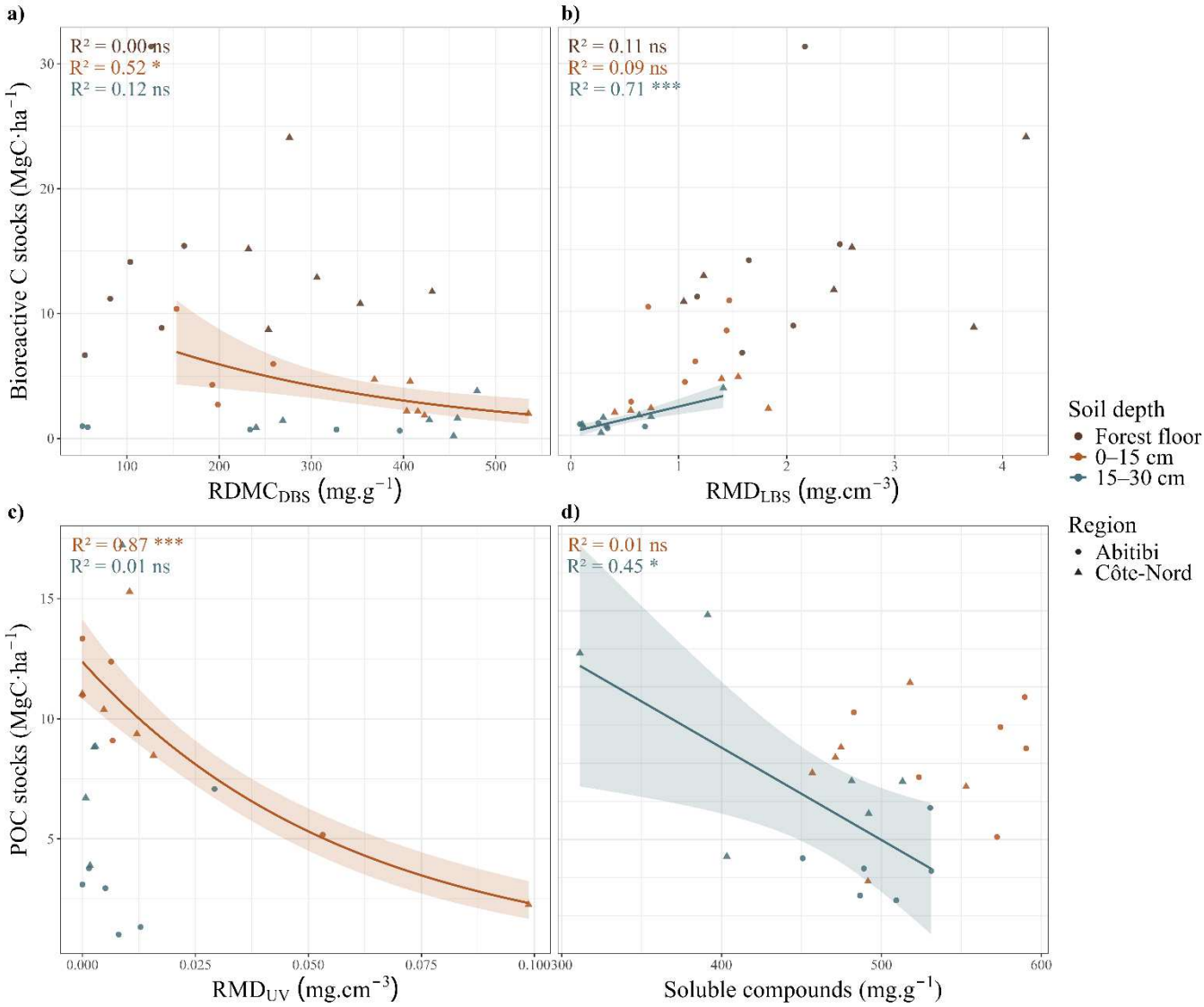

*Fig. 4: Relationship between labile C: (i) bioreactive C (a, b); (ii) particulate organic C (POC) (c, d) with significant and best model of fine root traits at each soil depth. Significant levels are indicated as follows: ns: not significant; ***: p <0.001; **: p <0.01; *: p <0.05. RDMC: Root dry mass content, RMD: Root mass density, RTD: Root tissue density, LBS: Live black spruce, DBS: Dead black spruce, UV: Understory vegetation.*

386

387 Depth-specific analyses revealed distinct fine root predictors of stable C in the
388 forest floor and mineral layers (Table 3). The chemical trait cellulose was the strongest
389 predictor of C_{recal} in the forest floor with higher cellulose content associated with higher
390 C_{recal} (R^2 = 0.75, p <0.001; Fig. 7a). Relationships with chemical traits were again more

significant in the 0-15 cm mineral layer, as the C/N ratio was the best predictor of both C_{recal} and MAOC. At this depth, increasing C/N was associated with lower C_{recal} ($R^2 = 0.63$, $p < 0.01$; Fig. 7b) and lower MAOC ($R^2 = 0.88$, $p < 0.001$; Fig. 7d). In contrast, morphological traits were most closely related to stable C in the 15-30 cm mineral layer: higher RTD_{UV} was associated with higher C_{recal} ($R^2 = 0.46$, $p < 0.05$; Fig. 7c), whereas higher $RDMC_{DBS}$ was related with lower MAOC ($R^2 = 0.36$, $p < 0.05$; Fig. 7e).

Table 3: Model selection between stable C: (i) recalcitrant C; (ii) mineral associated organic C (MAOC) and fine root traits ranged by AIC values with p value (Pr>F) at each depth.

Response	Soil layer	Predictor	AIC	ΔAIC	Estimate	R^2	p-value
Recalcitrant C	Forest floor	Cellulose	93.46	0.00	0.72	0.75	**<0.001**
		Lignin/N ratio	96.41	2.95	1.17	0.68	**<0.001**
		Compound soluble	99.53	6.06	-0.23	0.58	**0.004**
		RCC	101.75	8.29	35.60	0.50	**0.010**
		RDMC UV	102.89	9.43	0.09	0.45	**0.017**
		RTD LBS	103.63	10.17	100.33	0.42	**0.024**
		Fine root C/N ratio	104.39	10.93	0.59	0.38	**0.033**
		Lignin	104.50	11.03	77.16	0.37	**0.035**
		RNC	104.68	11.22	-96.57	0.36	**0.038**
		RDMC LBS	104.70	11.23	0.19	0.36	**0.039**
		RMD DBS	107.21	13.75	4.73	0.21	0.131
	0–15 cm	Fine root C/N ratio	79.65	0.00	-0.79	0.63	**0.006**
		Lignin/N ratio	79.96	0.31	-1.04	0.62	**0.007**
		RNC	82.28	2.63	141.95	0.52	**0.019**
		RCC	83.97	4.32	-1.65	0.43	**0.039**
		RDMC DBS	84.01	4.36	-0.10	0.49	**0.023**
		Lignin	95.18	15.53	-0.22	0.61	**0.003**
		Hemicellulose	96.46	16.81	0.60	0.57	**0.005**
		Compound soluble	98.12	18.47	0.24	0.50	**0.010**
		RTD LBS	100.13	20.48	-85.07	0.41	**0.025**
		RL UV	101.55	21.90	0.07	0.34	**0.049**
		RMD DBS	104.82	25.17	-16576.08	0.13	0.255
	15–30 cm	RTD UV	75.33	0.00	24.21	0.40	**0.035**
		RMD UV	78.24	2.92	516037.93	0.29	0.084
		Cellulose	85.13	9.81	0.15	0.22	0.121
MAOC	0–15 cm	Fine root C/N ratio	62.37	0.00	-0.70	0.88	**<0.001**

		RNC	64.27	1.90	5.60	0.81	**<0.001**
		Lignin/N ratio	69.97	7.61	-0.85	0.75	**0.001**
		RCC	74.63	12.26	-1.45	0.60	**0.009**
		RDMC DBS	81.72	19.36	-23.06	0.43	**0.040**
		Hemicellulose	89.39	27.02	0.52	0.64	**0.002**
		Lignin	89.57	27.20	-0.18	0.63	**0.002**
		Compound soluble	92.73	30.37	0.01	0.37	**0.024**
		RMD LBS	98.06	35.70	-189.91	0.03	0.600
	15–30 cm	RDMC DBS	77.92	4.15	0.00	0.36	**0.030**
		RMD UV	79.98	6.21	895464.80	0.52	**0.013**
		SRL LBS	81.96	8.20	0.43	0.67	**0.001**
		RD LBS	83.70	9.94	-3.81	0.34	**0.046**
		Cellulose	88.22	14.46	0.01	0.05	0.518

Fine root traits presented here include those with significant *P* values, the best non significant from each fine root trait category or those explicitly related to the study hypotheses. Complete model selection results for all fine root traits are provided in Supplementary Table 4. Values in bold are significant at $P < 0.05$. RTD: Root tissue density, RDMC: Root dry mass content, RMD: Root mass density, RCC: Root carbon concentration, RNC: Root nitrogen concentration, LBS: Live black spruce, DBS: Dead black spruce, UV: Understory vegetation.

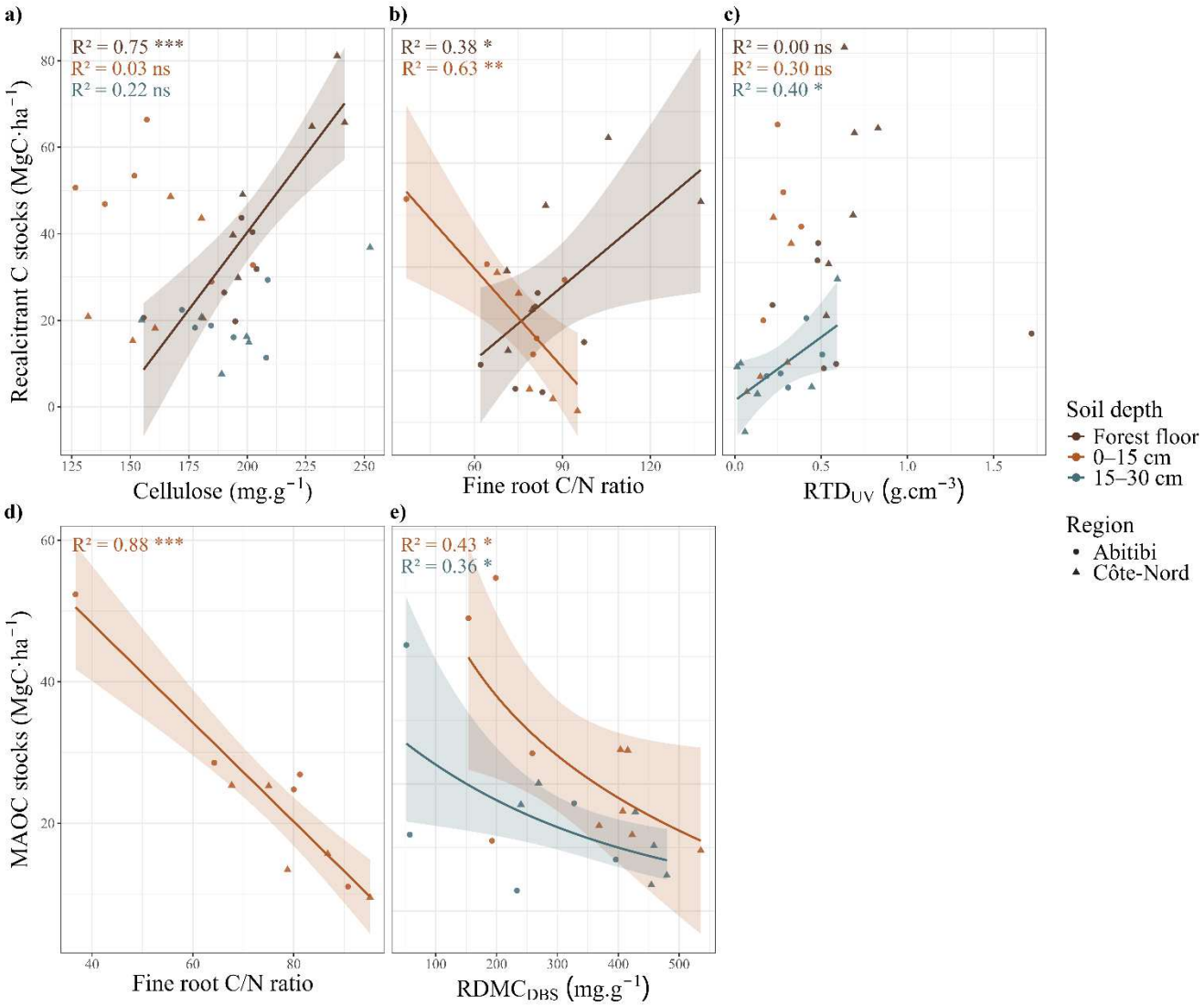

*Fig. 5: Relationship between stable C: (i) recalcitrant C (a, b, c); (ii) mineral associated organic C (MAOC) (c, e) with significant and best model of fine root traits at each soil depth. Significant levels are indicated as follows: ns: not significant; ***: p <0.001; **: p <0.01; *: p <0.05. RDMC: Root dry mass content, RTD: Root tissue density, DBS: Dead black spruce.*

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Discussion

Structurally reinforced fine roots linked with SOC accumulation and recalcitrant C in the forest floor

Our results indicate that the fine root traits most strongly linked to both SOC storage and stability were soil depth-dependent, with chemical traits as the main predictors in the forest floor and upper mineral layer, whereas morphological and architectural traits were more important in the deeper mineral layer.

We had predicted that architectural traits would best predict SOC stocks, however we found that SOC stocks were positively correlated with fine root cellulose content and RTD_{LBS} in the forest floor. This result contrasts with patterns commonly reported for mineral layers and emphasizes that trait–SOC relationships are strongly depth dependent. For example, negative correlations were found between RTD and SOC stocks in the top mineral layer of hybrid poplar plantations (Rabearison et al., 2025). High RTD is often associated with longer fine root lifespan and slower fine root turnover, therefore less organic C release into the soil (Eissenstat & Yanai, 1997; Roumet et al., 2016). However, it appears that this mechanism differs for the forest floor of black spruce stands: higher RTD at this depth may primarily reflect denser and more persistent tissues with slower decomposition, favoring the accumulation of plant-derived organic matter (Prescott & Vesterdal, 2021; Yin et al., 2025). Indeed, C_{bioR} stocks were higher in the forest floor compared to the upper mineral layer (Supplementary Figure 1). Additionally, cellulose content was positively correlated with incubation-derived C_{recal}, suggesting that sites retaining more cellulose-rich fine roots also have more recalcitrant C. This pattern supports a litter-centered hypothesis of SOC

stabilization, which posits that recalcitrant litter (high cellulose and lignin) contributes to more SOC stabilization than high quality litter, since it resists enzymatic attack and has lower mineralization (Parton et al., 1987; Poirier et al., 2018; Wardle et al., 2004).

Understory vegetation fine root exploration is linked to SOC loss, whereas fine root quality favors stable C formation in the upper mineral layer

In the 0-15 cm mineral layer, the relationships between fine root traits and SOC dynamics suggest that SOC storage and stability are governed by a balance between rhizosphere-driven C losses and the quality of fine root inputs contributing to MAOC stabilization. The negative relationship between SRL of understory vegetation (*i.e.* SRL_{UV}) and SOC stocks in the 0–15 cm mineral layer is, at first glance, counter-intuitive: higher SRL implies more root length per unit biomass, more rhizodeposition, and generally more C inputs (Pausch & Kuzyakov, 2018; Weemstra et al., 2020; Zhao et al., 2024a). However, fine root effects on SOC can be a double-edged sword as new C input in soil can also promote SOC decomposition by rhizosphere positive priming effect (Dijkstra et al., 2021). Higher SRL can intensify rhizosphere activity and might stimulate decomposition of older SOC (Bernard et al., 2022; Li et al., 2020; Perveen et al., 2019) leading to a net SOC loss even when belowground C inputs increase. Interestingly, SOC stocks were specifically correlated with SRL_{UV} rather than other black spruce fine root traits, suggesting that understory vegetation exploration strategies were the primary biotic drivers of SOC in the upper mineral layer. Understory vegetation fine root systems may be more plastic than tree fine roots and more tightly coupled to canopy-opening-induced variation in near-surface

453 microsites (Jiang et al., 2018; Noguchi et al., 2021; Zheng et al., 2024). They strongly
454 respond to local changes in light, moisture and substrate conditions (Koelemeijer et al.,
455 2024; Majasalmi & Rautiainen, 2020; Su et al., 2019).

456 In agreement with our third hypothesis, the negative relationships between fine root
457 C/N ratio and stable C, MAOC and C_{recal}, further highlight the dominance of the microbial-
458 mediated stabilization pathway. Our results follows the MEMS hypothesis predicting that
459 fine roots with lower C/N ratios (higher N content) are generally decomposed more
460 efficiently by microbes (higher carbon use efficiency), allowing a greater proportion of fine
461 root-derived C to be associated with minerals and promote MAOC (Cotrufo et al., 2013;
462 Sokol & Bradford, 2019). Together, these findings suggest that SRL_{UV} regulates C losses
463 via priming while root chemical quality (C/N) is the primary driver determining the C
464 stabilization in the upper mineral layer.

465 Different fine root traits categories regulate SOC stability in the
466 deeper mineral layer

467 There was a lack of significant correlation between any fine root traits and SOC stocks
468 in the deeper mineral layer (15-30 cm), suggesting a functional dissociation between
469 current organic matter inputs and long-term C storage in deeper soil layers. In boreal forest
470 soils, SOC in deeper layers often represents a legacy of long-term pedogenic processes (eg.
471 iron and aluminium oxides or clay content) or vertical leaching of dissolved organic carbon
472 (DOC) rather than shorter-term fine root inputs (Kalbitz & Kaiser, 2008; Rumpel & Kögel-
473 Knabner, 2011). Moreover, RMD_{LBS} at this depth was lower than in forest floor
474 (Supplementary Figure 2). However, fine root traits emerged as significant predictors for

475 SOC stability indicators, revealing that they influence soil C fractions more than SOC
476 storage in deeper mineral layer.

477 The positive correlation between RTD_{UV} and C_{recal} in the 15-30 cm mineral layer
478 suggests that denser understory vegetation fine roots were associated with greater
479 recalcitrant C. This pattern aligns with the "litter-centered" hypothesis, where the structural
480 robustness of fine root tissues dictates their persistence (Poirier et al., 2018). High RTD
481 can reflect an investment in thicker cell walls that resist enzymatic decomposition (Roumet
482 et al., 2016), thereby increasing recalcitrant C. In contrast, the negative relationship
483 between $RDMC_{DBS}$ and MAOC, consistent with the MEMS hypothesis, suggests that dead
484 fine root tissues with higher dry matter content were less favorable to microbial conversion
485 into MAOC. Rather than depending on fine root chemistry alone, MAOC formation can
486 also be constrained by morphological traits such as RDMC when these may be associated
487 with slower decomposition (Jimoh et al., 2024) which in turn might produce fewer
488 microbial substrates processed into MAOC. Rather than a contradiction, these results
489 suggest that SOC stability in deeper soil may be influenced through two pathways:
490 selective preservation of dense understory vegetation fine roots contributing into C_{recal} and
491 reduced microbial transformation of conservative dead black spruce fine roots into MAOC.

492 The positive relationships of RMD_{LBS} with C_{bioR} suggest that denser black spruce fine
493 root mass increased fresh fine root-derived C in the deeper mineral layer. Because of the
494 reduced influence of aboveground litter at this depth, greater RMD_{UV} was likely an
495 important factor in enhancing C supply (Clemmensen et al., 2013; Ding et al., 2021;
496 Noguchi et al., 2021) through higher fine root biomass and turnover (Garrett et al., 2024)
497 and rhizodeposition (Pausch & Kuzyakov, 2018), thereby increasing the bioreactive C. The

negative relationship between fine root soluble compounds content and POC also reinforces this interpretation by suggesting that chemically labile fine roots were less likely to remain as particulate residues.

Together, these results suggest that SOC stability in the 15–30 cm mineral layer was jointly regulated by multiple fine root categories. Architectural traits (RMD) mainly regulated fresh C inputs, morphological traits (RTD and RDMC) influenced whether this C was preserved in C_{recal} or contributed less into MAOC formation, and chemical traits (soluble compounds) affected the persistence of particulate residues.

Partial cuts alter fine root traits and their relationships with SOC dynamics across soil layers

Our results indicate that the long-term impact of thinning on fine root traits is depth dependent, shifting from a chemical response in the forest floor to a morphological response in the mineral layer. Specifically, the finding that thinning only reduced the fine root chemical traits cellulose and C/N of the forest floor across both regions suggests a shift toward reduced cell wall thickness and more N-enriched tissues (Freschet et al., 2021b; McCormack et al., 2015), supporting our first hypothesis. Although the thinning effect was consistent across regions, the decrease appeared more pronounced in Côte-Nord than in Abitibi, indicating a potentially stronger shift in fine root chemistry in the colder and wetter region. A driver of the lower C/N in fine roots could be linked to an increase in post-thinning soil N availability through thinning residue decomposition and reduced competition between residual trees (Zhou et al., 2021). Higher soil N availability may have increased N absorption in fine roots, lowering fine root C/N, as soil N and RNC tended to

520 be correlated within region and treatment combined ($R^2 = 0.38$, $p = 0.057$, Supplementary
521 Table 5). In parallel, plants may reduce cell walls thickness (cellulose and lignin rich tissue)
522 with greater nutrient availability and increase metabolic compounds (Hendricks et al.,
523 2000; Prieto et al., 2016), which is coherent with a decline in cellulose content.
524 From a "litter-centered" hypothesis, lower cellulose and C/N ratios means that the fine root
525 litter is more easily transformed by decomposers and therefore contributes to lower SOC
526 stability (Poirier et al., 2018). In a previous study conducted at the same sites, we found
527 that thinning also reduced forest floor C_{recal} in Côte-Nord (Ratsimandresiarivo et al.,
528 Submitted), suggesting that this shift in more decomposable fine root litter may have
529 contributed to this loss of recalcitrant C.
530 These thinning-induced shifts in fine root chemistry carry direct implications for the SOC
531 dynamics described in the previous section. As established above, cellulose-rich fine roots
532 were associated with higher C_{recal} in the forest floor, suggesting that the reduction in
533 cellulose after thinning may therefore reduce recalcitrant C. Consistently, in a previous
534 study conducted at the same sites, we found that thinning also reduced forest floor C_{recal} in
535 Côte-Nord (Ratsimandresiarivo et al., Submitted), supporting the interpretation that the
536 shift toward more decomposable fine root litter contributed to this loss of recalcitrant C.
537 In the 0-15 cm mineral layer, thinning only decreased morphological trait SRL_{UV} at
538 Côte-Nord sites which can be interpreted as a reduced need for soil exploration by
539 understory vegetation after thinning increased local resource availability following canopy
540 opening (Wang et al., 2026; Zhou et al., 2021). SRL is highly plastic to environmental
541 change and can decrease under fertilization, supporting the idea that producing long and
542 thin roots become less profitable when nutrients are more accessible (McCormack et al.,

543 2012; Ostonen et al., 2007). As discussed in Sec. 4.2, higher SRL_{UV} was associated with
544 lower SOC stocks in this layer, the thinning-induced decline in SRL_{UV} is therefore
545 consistent with the tendency of greater SOC retention in the upper mineral soil.
546 Higher SRL is typically associated with finer, more acquisitive root which increases the
547 root surface area per unit biomass (McCormack et al., 2015) and expands root-soil contact,
548 rhizodeposition volume, and therefore root-derived C input to the mineral layer (Pausch &
549 Kuzyakov, 2018; Weemstra et al., 2020; Zhao et al., 2024a). In the 0-15 cm mineral layer,
550 SRL_{LBS} showed contrasting responses to thinning between regions, tending to decrease in
551 Abitibi but to increase in Côte-Nord ($p = 0.06$, Supplementary Table 1; Fig. 4a).
552 Interestingly, this regional divergence followed the same direction of SOC stock responses
553 in a previous study observed within the same sites, where thinning tended to reduce SOC
554 stocks of the upper mineral soil in Abitibi but increase them in Côte-Nord
555 (Ratsimandresiarivo et al., 2026), suggesting that thinning may have promoted different
556 belowground foraging strategies between regions. In the warmer and more fertile region
557 (Abitibi), nutrient release through residue decomposition and reduced inter-trees
558 competition after thinning may have shifted residual trees to invest more in conservative
559 fine root traits (McCormack et al., 2012; Ostonen et al., 2007), reducing SRL_{LBS} and SOC
560 stocks in the 0-15 cm mineral layer. Conversely, in the cooler, more humid and less fertile
561 region (Côte-Nord), where nutrient limitation dominates (Ratsimandresiarivo et al., 2026),
562 residual trees might maximize exploratory absorptive roots, potentially supporting the post-
563 thinning increase in tree growth reported by Andrianirinarimanana et al.
564 (Andrianirinarimanana et al., 2026) within the same study sites. This increase in SRL_{LBS}
565 may also have enhanced rhizodeposition and necromass inputs in the upper mineral layer

(Lugli et al., 2020; Wu et al., 2025; Zhao et al., 2024a) which could contribute to increase SOC stocks. Indeed, higher SRL_{LBS} tended to be associated with higher SOC stocks (R^2 = 0.26, p = 0.08, Supplementary Table 2).

Taken together, in the forest floor, fine roots with lower cellulose and C/N ratios, reflecting more acquisitive traits, were associated with lower SOC storage. In contrast, in the 0-15 cm mineral layer, higher SRL_{LBS} tended to be associated with higher SOC stocks. This divergence suggests that the dominant mechanisms of SOC storage differ between organic and mineral layers, with an important role of litter quality in the forest floor and root-derived C fluxes in the mineral layer.

In the 15-30 cm mineral layer, thinning only increased the morphological root trait $RDMC_{UV}$ in Abitibi. It was previously shown that RDMC increased in water limited contexts to enhance resistance to desiccation and maintain function (de Vries et al., 2016; Lozano et al., 2020; Reinelt et al., 2023). Clay-rich Luvisol in Abitibi are denser soils than those in Côte-Nord and more difficult for roots to penetrate (Bengough et al., 2011; Lardy et al., 2022; Lavkulich & Arocena, 2011), requiring greater mechanical penetration strength to explore this deep soil layer (Clark et al., 2003; Tomobe et al., 2023). Taken together with the lower SRL_{UV} observed in the 0-15 cm mineral layer, these results suggest that thinning in Abitibi promoted a more conservative root strategy in understory vegetation fine roots across the mineral soil profile.

Conclusion

This study provided a comprehensive evaluation of how forest thinning interacts with different pedoclimatic conditions to shape fine root traits and, consequently, SOC dynamics in black spruce forests. Our findings revealed depth specific C stabilization mechanisms and showed that thinning altered fine root traits involved in them. In the forest floor, higher structural quality of fine root inputs (cellulose and RTD) was associated with higher SOC storage, consistent with a "litter-centered" preservation pathway. Thinning shifted this pathway by reducing fine root cellulose and C/N, thereby promoting more decomposable litter and reduced recalcitrant C at this depth. In the upper mineral layer, higher understory vegetation SRL was associated with lower SOC stocks, whereas lower fine root C/N were associated with greater MAOC formation. Black spruce SRL also tended to be positively associated with SOC stocks. Thinning modified this balance by reducing understory SRL in Côte-Nord, consistent with greater SOC retention, while region-specific changes in black spruce SRL paralleled regional SOC stock patterns. In the deeper mineral layer, fine root traits were no longer related to SOC storage, but remained linked to SOC stability, with higher understory vegetation RTD associated with greater C_{recal}, lower black spruce fine root RDMC associated with greater MAOC, and higher black spruce RMD associated with greater C_{bioR}. Together, these results show that fine root traits regulate distinct SOC pathways across soil depths, and that thinning can redirect these pathways over the long term.

An important finding of this research was the major role of understory vegetation in shaping mineral SOC dynamics. Its fine root traits were linked to SOC storage and

608 stability, highlighting understory vegetation as a functional component of belowground C
609 cycling in black spruce forests.

610 Finally, this work demonstrates that partial cuts like thinning have long-lasting
611 belowground effects. By altering the fine root functional traits of both trees and understory
612 vegetation, management practices redirect the pathways of SOC storage and stabilization.
613 For forest managers and earth system modelers, integrating these depth-dependent fine root
614 strategies is essential for predicting the future of the boreal C sink under changing
615 management and climate regimes.

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Acknowledgements

We are grateful to our funding partners for their collaboration throughout this project: Ministry of Natural Resources and Forestry (MRNF), Sept-Iles's Economic Development, Boisaco, Chantiers Chibougamau Ltd. and Natural Sciences and Engineering Research Council of Canada (NSERC). We would like to thank our field assistants Zoé Rhéaume, Nicolas Cito, Marion Noualhaguet and Fatou Diabi for their invaluable help during data collection. We also acknowledge Benjamin Andrieux for his help with the soil incubation experiment and Sébastien Dagnault, Fanny Michaud, Olivier Jeffrey, Mathieu Létourneau and Esther Pouliot of the Forest Soil Lab at the Laurentian Forestry Centre (LFC) for their support with sample processing and analysis.

Supplementary materials

Fine root traits mediate the effects of long-term partial cuts on soil organic carbon storage and stability in boreal black spruce forests

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Supplementary Table 1: Analysis of variance (p-values; Pr> F) of fine root traits (morphological, architectural and chemical) between region and treatment and their interaction in each depth

Fine root categories	Soil depth	Variables	Model type	Transformation	Region	Treatment	Region*Treatment
Morphological	Forest floor	RD LBS	lm	none	0.494	0.160	0.867
		RD UV	lm	none	0.441	0.775	0.498
		RL LBS	lm	none	0.103	0.914	0.886
		RL UV	lm	none	<0.001	0.544	0.475
		RDMC DBS	lm	none	<0.001	0.487	0.658
		RDMC LBS	lm	none	<0.001	0.156	0.848
		RDMC UV	lm	none	<0.001	0.923	0.161
		RTD LBS	lm	none	0.125	0.195	0.146
		RTD UV	lm	log	0.516	0.316	0.094
		SRL LBS	lm	none	0.704	0.172	0.556
		SRL UV	lm	none	0.476	0.549	0.405
	0-15 cm	RD LBS	lm	none	0.689	0.495	0.416
		RD UV	lm	none	0.575	0.741	0.238
		RL LBS	lm	none	0.203	0.506	0.122
		RL UV	lm	none	0.827	0.591	0.181
		RDMC DBS	lm	none	**0.001**	0.875	0.673
		RDMC LBS	lm	none	<0.001	0.170	0.252
		RDMC UV	lm	none	0.194	0.145	0.259
		RTD LBS	lm	none	0.335	0.251	**0.019**
		RTD UV	lm	none	0.189	0.428	**0.037**
		SRL LBS	lm	none	0.471	0.748	0.063
		SRL UV	lm	none	<0.001	**0.003**	<0.001

	15-30 cm	RD LBS	lm	none	0.668	0.566	0.950
		RD UV	lm	none	**0.022**	0.807	0.101
		RL LBS	lm	none	0.831	0.253	0.720
		RL UV	lm	log (y+1)	0.366	0.259	**0.021**
		RDMC DBS	lm	none	0.087	0.805	0.901
		RDMC LBS	lm	none	**0.002**	0.704	0.740
		RDMC UV	lm	log	0.263	<0.001	**0.022**
		RTD LBS	lm	none	0.192	0.748	0.208
		RTD UV	lm	none	0.443	0.310	0.744
		SRL LBS	lm	none	0.300	0.303	0.485
		SRL UV	lm	none	0.213	0.725	0.442
Architectural	Forest floor	RLD LBS	lm	none	0.240	0.175	0.277
		RLD UV	lm	none	**0.016**	0.173	0.185
		RMD DBS	lm	none	**0.001**	0.548	0.585
		RMD LBS	lm	none	0.299	0.801	0.992
		RMD UV	lm	none	**0.005**	0.153	0.161
	0-15 cm	RLD LBS	lm	none	0.203	0.506	0.122
		RLD UV	lm	none	0.966	0.483	0.223
		RMD DBS	lm	none	**0.045**	0.119	0.481
		RMD LBS	lm	none	0.965	0.880	0.700
	15-30 cm	RLD LBS	lm	none	0.831	0.253	0.720
		RLD UV	lm	sqrt	0.432	0.992	0.174
		RMD DBS	lm	none	**0.018**	0.903	0.565
		RMD LBS	lm	none	0.241	0.587	0.334
Chemical	Forest floor	Cellulose	lm	none	**0.007**	**0.003**	0.176
		RCC	lm	none	**0.027**	0.402	0.550
		Fine root C/N ratio	lm	none	0.214	**0.022**	0.275

	RNC	lm	none	0.278	**0.010**	0.404
	Hemicellulose	lm	none	0.500	0.644	0.233
	Lignin	lm	none	**0.042**	0.483	0.706
	Lignin/N	lm	none	**0.011**	**0.004**	0.262
	Compound soluble	lm	none	**0.017**	0.117	0.790
0-15 cm	Cellulose	lm	none	0.887	0.194	0.113
	RCC	glm	none (GLM Gamma)	0.653	0.393	0.265
	Fine root C/N ratio	lm	none	0.542	0.957	0.180
	RNC	lm	none	0.529	0.606	0.218
	Hemicellulose	lm	none	0.086	0.508	0.382
	Lignin	lm	none	**0.020**	0.746	0.684
	Lignin/N	lm	none	0.135	0.472	0.179
	Compound soluble	lm	none	**0.019**	0.143	0.302
15-30 cm	Cellulose	lm	none	0.707	0.209	0.247
	Hemicellulose	lm	none	0.178	0.226	0.611
	Lignin	lm	none	**0.034**	0.793	0.528
	Compound soluble	lm	none	0.080	0.493	0.240

LBS: Live Black Spruce; DBS: Dead Black Spruce; UV: Understory vegetation; RD: Root Diameter; RL: Root Length; RDMC: Root Dry Mass Content; RTD: Root Tissue Density; SRL: Specific Root Length; RLD: Root Length Density; RMD: Root Mass Density; RCC: Root Carbon Concentration; RNC: Root Nitrogen Concentration

Supplementary Table 2: Relationship between SOC stock and fine root traits (morphological, architectural and chemical) ranged by AIC values with p value (Pr>F)

Soil depth	Predictor	AIC	ΔAIC	Estimate	R^2	p-value
Forest floor	Cellulose	97.67	0.00	0.75	0.70	**<0.001**
	Lignin/N ratio	101.70	4.03	1.16	0.58	**0.004**
	RTD LBS	102.28	4.61	125.78	0.56	**0.005**
	Compound soluble	105.54	7.87	-0.21	0.42	**0.023**
	RNC	106.10	8.43	-108.59	0.39	**0.030**
	Fine root C/N ratio	106.11	8.43	0.65	0.39	**0.030**
	RDMC LBS	106.80	9.13	0.20	0.35	**0.042**
	RDMC UV	106.91	9.23	0.09	0.35	**0.044**
	RCC	107.62	9.94	30.25	0.31	0.061
	RMD DBS	107.67	10.00	6.14	0.30	0.063
	RL UV	107.71	10.03	11.09	0.30	0.064
	RL LBS	108.55	10.88	0.01	0.25	0.097
	RDMC DBS	108.87	11.20	0.09	0.23	0.114
	Lignin	109.11	11.43	0.22	0.22	0.128
	RMD LBS	109.88	12.20	8581.76	0.16	0.192
	SRL LBS	111.04	13.37	-0.53	0.08	0.377
	RD UV	111.13	13.45	-93.19	0.07	0.399
	Hemicellulose	111.61	13.94	0.50	0.03	0.569
	SRL UV	111.85	14.18	-0.10	0.01	0.711
	RMD UV	111.88	14.20	13276.68	0.01	0.734
	RLD UV	111.92	14.25	2.56	0.01	0.775
	RLD LBS	111.95	14.28	-0.68	0.01	0.811
	D LBS	111.96	14.28	32.40	0.01	0.818
	RTD UV	112.02	14.35	0.51	0.00	0.978
0–15 cm	SRL UV	77.54	0.00	-0.22	0.45	**0.049**
	Lignin/N ratio	78.53	0.99	-1.12	0.68	**0.003**
	RTD UV	79.90	2.37	98.77	0.28	0.142
	Fine root C/N ratio	80.34	2.81	-0.81	0.62	**0.007**
	RNC	81.40	3.86	153.26	0.58	**0.011**
	RDMC DBS	82.32	4.78	-0.11	0.59	**0.009**
	RDMC UV	82.83	5.29	-0.01	0.00	0.869
	RCC	85.71	8.17	-1.53	0.35	0.070
	Lignin	94.80	17.26	-0.24	0.66	**0.001**
	RMD UV	96.30	18.76	144990.14	0.08	0.412
	Compound soluble	97.59	20.05	0.27	0.57	**0.004**
	Hemicellulose	98.61	21.08	0.62	0.53	**0.007**
	RTD LBS	102.29	24.75	-84.77	0.37	**0.037**

	RDMC LBS	102.38	24.85	-0.09	0.36	**0.039**
	RL LBS	102.39	24.86	0.05	0.36	**0.039**
	RLD LBS	102.39	24.86	14.32	0.36	**0.039**
	SRL LBS	104.06	26.53	0.87	0.26	0.087
	RL UV	104.54	27.00	0.06	0.23	0.111
	RLD UV	105.52	27.99	14.47	0.17	0.185
	RMD DBS	105.63	28.09	-19695.88	0.16	0.195
	Cellulose	107.34	29.80	-0.14	0.03	0.571
	RD LBS	107.44	29.91	-36.36	0.02	0.627
	RD UV	107.66	30.13	-11.47	0.01	0.806
	RMD LBS	107.72	30.19	-1385.28	0.00	0.909
15–30 cm	RMD UV	78.89	0.00	527521.45	0.29	0.086
	RDMC DBS	81.46	2.57	-0.03	0.28	0.095
	RTD LBS	82.62	3.73	-4.61	0.01	0.821
	RTD UV	82.96	4.07	19.04	0.17	0.202
	RDMC UV	84.78	5.89	-0.01	0.02	0.643
	SRL UV	85.00	6.11	0.00	0.00	0.843
	RMD LBS	88.96	10.07	-11338.43	0.22	0.121
	RMD DBS	89.23	10.34	-34953.78	0.21	0.138
	SRL LBS	89.99	11.10	0.18	0.15	0.208
	Cellulose	90.25	11.36	0.14	0.14	0.239
	RD LBS	90.91	12.02	-24.80	0.09	0.352
	Lignin	91.54	12.65	-7.00	0.04	0.547
	RDMC LBS	91.56	12.67	0.01	0.04	0.555
	RL UV	91.63	12.74	-0.03	0.03	0.588
	RL LBS	91.64	12.75	0.01	0.03	0.594
	RLD LBS	91.64	12.75	2.58	0.03	0.594
	RLD UV	91.70	12.81	-8.58	0.02	0.629
	Hemicellulose	91.98	13.09	0.02	0.00	0.910
	RD UV	91.99	13.10	1.58	0.00	0.927
	Compound soluble	92.21	13.32	0.00	0.00	0.961

LBS: Live Black Spruce; DBS: Dead Black Spruce; UV: Understory vegetation; RD: Root Diameter; RL: Root Length; RDMC: Root Dry Mass Content; RTD: Root Tissue Density; SRL: Specific Root Length; RLD: Root Length Density; RMD: Root Mass Density; RCC: Root Carbon Concentration; RNC: Root Nitrogen Concentration

Supplementary Table 3: Relationship between labile C indicators (bioreactive C and POC) and fine root traits (morphological, architectural and chemical) ranged by AIC values with p value (Pr>F)

Response	Soil depth	Predictor	AIC	ΔAIC	Estimate	R^2	p-value
Bioreactive C	Forest floor	RTD LBS	77.64	2.27	1.89	0.27	0.111
		Lignin	80.23	4.85	0.00	0.10	0.332
		RCC	80.79	5.42	-0.28	0.06	0.485
		Fine root C/N ratio	80.88	5.51	0.01	0.06	0.485
		RL LBS	81.01	5.63	0.00	0.05	0.574
		RL UV	81.14	5.76	0.00	0.04	0.577
		RDMC LBS	81.14	5.77	0.00	0.04	0.585
		Compound soluble	81.29	5.91	0.00	0.02	0.659
		Cellulose	81.31	5.93	0.00	0.02	0.688
		RDMC UV	81.48	6.11	0.00	0.01	0.789
		RD LBS	81.51	6.13	0.81	0.01	0.804
		Hemicellulose	81.55	6.17	0.00	0.00	0.847
		Lignin/N ratio	81.56	6.19	0.00	0.00	0.896
		RTD UV	81.58	6.20	-0.05	0.00	0.909
		RDMC DBS	81.58	6.20	0.00	0.00	0.917
		RLD LBS	81.58	6.21	-0.01	0.00	0.923
		RLD UV	81.59	6.22	-0.01	0.00	0.973
		RD UV	82.52	7.15	-56.01	0.23	0.112
		RMD DBS	84.16	8.78	3670.84	0.12	0.267
		RMD LBS	84.36	8.98	2314.20	0.11	0.300
		SRL LBS	84.47	9.09	-0.20	0.10	0.321
		RNC	84.83	9.45	-15.50	0.07	0.402
		RMD UV	85.35	9.98	-6949.22	0.03	0.593
		SRL UV	85.54	10.17	0.03	0.01	0.716
	0–15 cm	RDMC DBS	40.60	0.00	0.00	0.52	**0.016**
		RDMC UV	43.36	2.76	0.00	0.10	0.434
		RTD UV	44.27	3.67	0.64	0.01	0.814
		SRL UV	48.58	7.98	-0.01	0.03	0.640
		RNC	50.62	10.02	2.35	0.09	0.323
		RCC	53.81	13.21	0.14	0.11	0.358
		Lignin/N ratio	54.01	13.41	-0.07	0.09	0.405
		Fine root C/N ratio	54.93	14.33	0.00	0.00	0.974
		RD UV	57.76	17.16	-19.94	0.55	**0.006**
		RDMC LBS	58.73	18.13	0.00	0.31	**0.041**
		Lignin	59.51	18.91	-0.01	0.27	**0.032**
		RMD UV	60.75	20.15	-44237.49	0.16	0.219

		RTD LBS	63.46	22.86	0.08	0.00	0.964
		RLD UV	64.58	23.98	-3.01	0.21	0.133
		Compound soluble	64.59	23.99	0.03	0.21	0.134
		RL UV	65.16	24.56	-0.01	0.17	0.181
		RMD DBS	65.27	24.66	-3698.33	0.16	0.192
		RLD LBS	65.99	25.39	1.49	0.11	0.288
		RL LBS	65.99	25.39	0.01	0.11	0.288
		RMD LBS	66.25	25.65	2119.44	0.09	0.336
		SRL LBS	66.84	26.24	-0.07	0.05	0.502
		Hemicellulose	67.08	26.48	2.15	0.03	0.606
		RD LBS	67.16	26.56	6.28	0.02	0.653
		Cellulose	67.38	26.78	-1.29	0.00	0.862
	15–30 cm	RTD LBS	16.66	0.00	1.03	0.11	0.322
		RMD UV	17.91	1.25	1795.62	0.00	0.919
		RMD LBS	22.59	5.93	2066.91	0.71	**<0.001**
		RLD UV	23.25	6.59	2.36	0.40	**0.030**
		RL UV	23.76	7.11	0.01	0.38	**0.041**
		RMD DBS	25.48	8.82	3139.99	0.29	**0.025**
		Compound soluble	27.28	10.62	0.00	0.18	0.147
		RTD UV	27.67	11.01	1.08	0.09	0.372
		Lignin	28.06	11.40	0.00	0.13	0.262
		RDMC UV	28.34	11.68	0.00	0.04	0.518
		RD UV	28.40	11.74	1.58	0.10	0.239
		SRL UV	28.65	12.00	0.00	0.01	0.768
		RDMC LBS	28.79	12.13	0.00	0.07	0.450
		Cellulose	28.91	12.25	0.01	0.07	0.451
		RL LBS	29.51	12.85	0.00	0.02	0.686
		RLD LBS	29.51	12.85	0.18	0.02	0.686
		RD LBS	29.75	13.09	0.29	0.00	0.903
		Hemicellulose	29.78	13.12	0.00	0.00	0.997
		RDMC DBS	33.75	17.09	0.00	0.12	0.288
		SRL LBS	35.05	18.39	-0.46	0.17	0.180
POC	0–15 cm	RMD UV	44.90	0.00	-16900.09	0.87	**<0.001**
		RDMC UV	54.68	9.78	0.01	0.15	0.306
		SRL UV	56.01	11.11	-0.01	0.01	0.773
		RTD UV	56.11	11.21	1.47	0.00	0.929
		RCC	59.60	14.70	-0.24	0.15	0.270
		Fine root C/N ratio	60.23	15.32	-0.07	0.09	0.387
		RDMC DBS	60.68	15.77	0.00	0.01	0.795
		Lignin/N ratio	60.88	15.98	-0.06	0.03	0.611
		RNC	61.04	16.14	6.44	0.02	0.710

	RDMC LBS	68.65	23.75	-0.01	0.15	0.221
	RD UV	68.98	24.08	-10.64	0.12	0.267
	RMD LBS	69.57	24.67	2203.80	0.08	0.382
	Lignin	69.70	24.80	-0.02	0.07	0.415
	Cellulose	69.73	24.83	0.04	0.07	0.423
	RMD DBS	69.74	24.84	2634.71	0.06	0.427
	Hemicellulose	70.16	25.25	0.03	0.03	0.583
	RTD LBS	70.31	25.41	4.03	0.02	0.675
	RL LBS	70.36	25.46	0.00	0.01	0.708
	RLD LBS	70.36	25.46	0.61	0.01	0.708
	Compound soluble	70.36	25.46	0.01	0.01	0.711
	RD LBS	70.49	25.58	3.18	0.00	0.842
	SRL LBS	70.54	25.63	0.00	0.00	0.998
	RLD UV	73.94	29.03	-0.10	0.02	0.673
	RL UV	73.96	29.06	0.00	0.01	0.695
15–30 cm	RTD LBS	69.31	0.00	8.50	0.06	0.452
	RMD UV	69.96	0.66	45212.59	0.01	0.810
	RDMC LBS	71.49	2.19	0.00	0.27	0.113
	RMD DBS	72.20	2.89	3700.95	0.22	0.083
	RD UV	72.35	3.05	2.90	0.22	0.076
	Compound soluble	74.81	5.50	-0.06	0.45	**0.017**
	RL LBS	75.52	6.21	0.00	0.00	0.868
	RLD LBS	75.52	6.21	0.08	0.00	0.868
	RDMC DBS	75.54	6.23	0.01	0.05	0.519
	RD LBS	75.55	6.25	0.18	0.00	0.944
	RTD UV	75.81	6.50	0.76	0.02	0.650
	SRL UV	75.81	6.50	-0.01	0.02	0.650
	RDMC UV	76.07	6.76	0.00	0.00	0.943
	Lignin	76.70	7.40	0.06	0.35	**0.042**
	RLD UV	77.12	7.81	20.78	0.33	0.051
	RMD LBS	77.67	8.36	8624.49	0.30	0.066
	RL UV	78.08	8.78	0.07	0.27	0.081
	Cellulose	78.47	9.17	0.12	0.25	0.098
	Hemicellulose	81.24	11.94	-0.07	0.06	0.462
	SRL LBS	81.78	12.48	-0.03	0.01	0.734

LBS: Live Black Spruce; DBS: Dead Black Spruce; UV: Understory vegetation; RD: Root Diameter; RL: Root Length; RDMC: Root Dry Mass Content; RTD: Root Tissue Density; SRL: Specific Root Length; RLD: Root Length Density; RMD: Root Mass Density; RCC: Root Carbon Concentration; RNC: Root Nitrogen Concentration

Supplementary Table 4: Relationship between stable C indicators (recalcitrant C and MAOC) and fine root traits (morphological, architectural and chemical) ranged by AIC values with p value (Pr>F)

Response	Soil layer	Predictor	AIC	ΔAIC	Estimate	R^2	p-value
Recalcitrant C	Forest floor	Cellulose	93.46	0.00	0.72	0.75	**<0.001**
		Lignin/N ratio	96.41	2.95	1.17	0.68	**<0.001**
		Compound soluble	99.53	6.06	-0.23	0.58	**0.004**
		RCC	101.75	8.29	35.60	0.50	**0.010**
		RDMC UV	102.89	9.43	0.09	0.45	**0.017**
		RTD LBS	103.63	10.17	100.33	0.42	**0.024**
		Fine root C/N ratio	104.39	10.93	0.59	0.38	**0.033**
		Lignin	104.50	11.03	77.16	0.37	**0.035**
		RNC	104.68	11.22	-96.57	0.36	**0.038**
		RDMC LBS	104.70	11.23	0.19	0.36	**0.039**
		RDMC DBS	105.75	12.28	0.09	0.30	0.064
		RL UV	106.28	12.82	9.69	0.27	0.083
		RL LBS	106.87	13.41	0.01	0.23	0.110
		RMD DBS	107.21	13.75	4.73	0.21	0.131
		RMD LBS	108.60	15.14	6658.48	0.12	0.279
		SRL LBS	109.61	16.15	-0.34	0.04	0.542
		RMD UV	109.62	16.16	21560.27	0.04	0.547
		Hemicellulose	109.68	16.22	0.45	0.03	0.574
		SRL UV	109.80	16.34	-0.12	0.02	0.640
		RD UV	109.87	16.41	-42.11	0.02	0.684
		RLD UV	109.91	16.45	3.05	0.01	0.712
		RD LBS	110.04	16.58	23.49	0.00	0.857
		RLD LBS	110.04	16.58	-0.46	0.00	0.860
		RTD UV	110.08	16.61	-0.99	0.00	0.954
	0–15 cm	SRL UV	77.06	0.00	-0.22	0.45	0.060
		RTD UV	79.14	2.07	99.46	0.30	0.126
		Fine root C/N ratio	79.65	2.59	-0.79	0.63	**0.006**
		Lignin/N ratio	79.96	2.90	-1.04	0.62	**0.007**
		RNC	82.28	5.22	141.95	0.52	**0.019**
		RDMC UV	82.36	5.30	0.00	0.00	0.966
		RCC	83.97	6.90	-1.65	0.43	**0.039**
		RDMC DBS	84.01	6.95	-0.10	0.49	**0.023**
		RMD UV	93.22	16.16	185145.01	0.15	0.238
		Lignin	95.18	18.12	-0.22	0.61	**0.003**

		Hemicellulose	96.46	19.40	0.60	0.57	**0.005**
		Compound soluble	98.12	21.06	0.24	0.50	**0.010**
		RTD LBS	100.13	23.07	-85.07	0.41	**0.025**
		RL UV	101.55	24.49	0.07	0.34	**0.049**
		SRL LBS	101.71	24.65	0.91	0.33	0.052
		RL LBS	102.08	25.02	0.04	0.31	0.062
		RLD LBS	102.08	25.02	12.51	0.31	0.062
		RDMC LBS	102.28	25.22	-0.08	0.29	0.069
		RLD UV	102.86	25.80	16.98	0.26	0.091
		RMD DBS	104.82	27.76	-16576.08	0.13	0.255
		RMD LBS	105.74	28.68	-99.73	0.01	0.742
		Cellulose	106.05	28.99	-0.13	0.03	0.574
		RD LBS	106.06	29.00	-39.44	0.03	0.577
		RD UV	106.44	29.38	4.03	0.00	0.927
	15–30 cm	RTD UV	75.33	0.00	24.21	0.40	**0.035**
		RMD UV	78.24	2.92	516037.93	0.29	0.084
		RDMC DBS	78.56	3.24	-0.02	0.20	0.167
		SRL UV	80.53	5.20	-0.01	0.04	0.532
		RDMC UV	80.77	5.44	-0.01	0.02	0.653
		RTD LBS	82.00	6.68	-4.94	0.01	0.803
		Cellulose	85.13	9.81	0.15	0.22	0.121
		Compound soluble	87.15	11.83	-13.92	0.08	0.373
		RMD DBS	87.42	12.10	-15953.44	0.06	0.446
		RD LBS	87.48	12.16	-16.72	0.05	0.465
		RMD LBS	87.63	12.31	-4217.61	0.04	0.520
		SRL LBS	87.70	12.38	1.76	0.04	0.550
		RDMC LBS	87.73	12.41	0.01	0.03	0.562
		RLD UV	87.86	12.53	7.35	0.02	0.627
		RL LBS	87.91	12.58	0.01	0.02	0.659
		RLD LBS	87.91	12.58	1.82	0.02	0.659
		RL UV	87.94	12.62	0.02	0.02	0.682
		RD UV	87.96	12.63	5.77	0.02	0.692
		Lignin	88.13	12.80	0.01	0.00	0.886
		Hemicellulose	88.16	12.83	0.00	0.00	0.992
MAOC	0–15 cm	Fine root C/N ratio	62.37	0.00	-0.70	0.88	**<0.001**
		RNC	64.27	1.90	5.60	0.81	**<0.001**
		Lignin/N ratio	69.97	7.61	-0.85	0.75	**0.001**
		RCC	74.63	12.26	-1.45	0.60	**0.009**

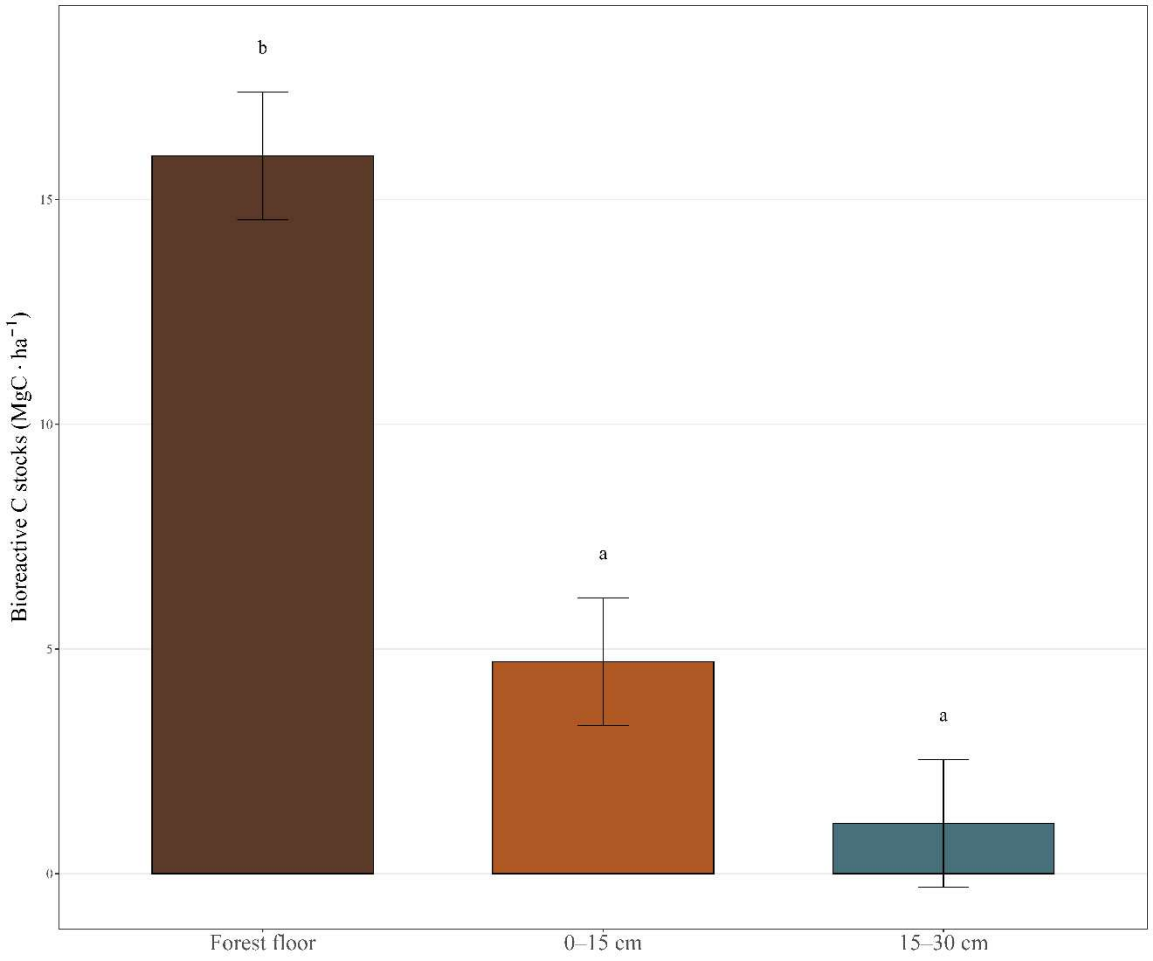
	SRL UV	77.88	15.51	-0.12	0.17	0.263
	RTD UV	79.42	17.05	22.31	0.02	0.713
	RDMC UV	79.58	17.22	0.00	0.00	0.898
	RDMC DBS	81.72	19.36	-23.06	0.43	**0.040**
	RMD UV	88.40	26.03	-28015.04	0.01	0.817
	Hemicellulose	89.39	27.02	0.52	0.64	**0.002**
	Lignin	89.57	27.20	-0.18	0.63	**0.002**
	Compound soluble	92.73	30.37	0.01	0.37	**0.024**
	RL LBS	96.34	33.97	0.00	0.15	0.270
	RLD LBS	96.34	33.97	0.29	0.15	0.270
	SRL LBS	97.55	35.18	0.70	0.29	0.074
	RL UV	97.95	35.58	0.05	0.26	0.090
	RMD LBS	98.06	35.70	-189.91	0.03	0.600
	RDMC LBS	98.73	36.36	-0.05	0.21	0.133
	RLD UV	98.83	36.46	12.33	0.20	0.140
	RTD LBS	100.37	38.00	-33.63	0.10	0.327
	RD LBS	100.45	38.09	-53.77	0.09	0.345
	RMD DBS	100.71	38.34	-10029.16	0.07	0.406
	RD UV	101.42	39.06	-12.61	0.01	0.726
	Cellulose	101.51	39.14	0.05	0.01	0.810
15–30 cm	RDMC DBS	77.92	4.15	0.00	0.36	**0.030**
	RMD UV	79.98	6.21	895464.80	0.52	**0.013**
	SRL LBS	81.96	8.20	0.43	0.67	**0.001**
	RTD UV	82.55	8.78	0.73	0.04	0.545
	SRL UV	83.02	9.26	0.00	0.00	0.874
	RD LBS	83.70	9.94	-3.81	0.34	**0.046**
	RL LBS	85.49	11.73	0.00	0.24	0.124
	RLD LBS	85.49	11.73	0.49	0.24	0.124
	RTD LBS	85.64	11.88	-33.34	0.19	0.176
	RMD LBS	86.68	12.92	-836.17	0.16	0.165
	RMD DBS	86.95	13.19	-2681.27	0.14	0.168
	RLD UV	87.09	13.33	1.60	0.13	0.170
	RL UV	87.72	13.96	0.00	0.09	0.290
	RD UV	88.13	14.37	1.11	0.06	0.422
	Cellulose	88.22	14.46	0.01	0.05	0.518
	Compound soluble	88.27	14.51	0.00	0.05	0.572
	RDMC UV	88.31	14.55	-0.01	0.02	0.701
	Hemicellulose	88.80	15.04	0.00	0.01	0.779
	RDMC LBS	88.94	15.18	0.00	0.00	0.961

	Lignin	93.12	19.36	-0.07	0.16	0.204

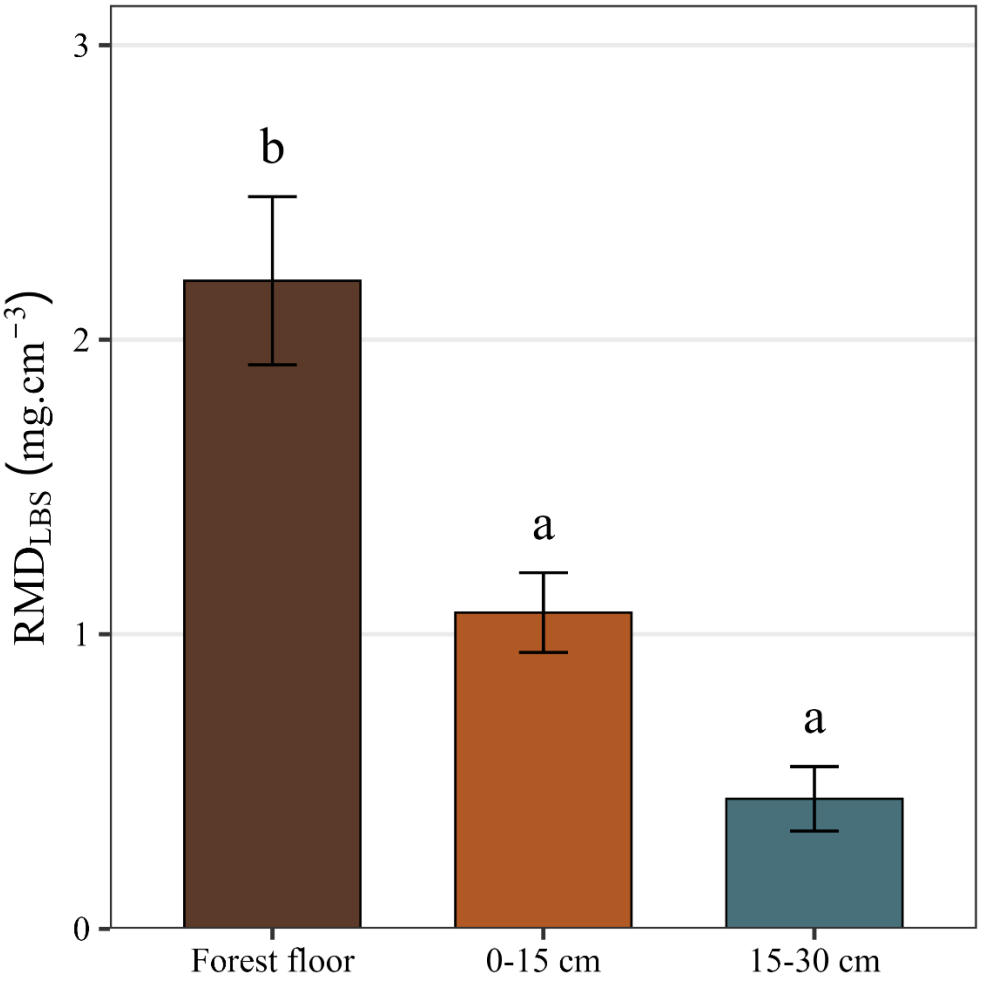
LBS: Live Black Spruce; DBS: Dead Black Spruce; UV: Understory vegetation; RD: Root Diameter; RL: Root Length; RDMC: Root Dry Mass Content; RTD: Root Tissue Density; SRL: Specific Root Length; RLD: Root Length Density; RMD: Root Mass Density; RCC: Root Carbon Concentration; RNC: Root Nitrogen Concentration

Supplementary Table 5: Relationship between soil N and fine root N concentration (RNC) with P value

Soil depth	Response	Predictor	R^2	p-value
Forest floor	N	RNC	0.08	0.374
0–15 cm	N	RNC	0.38	0.057



Supplementary Figure 1: Mean bioreactive C stocks between soil layers. Different letters indicate significant differences (P<0.05).



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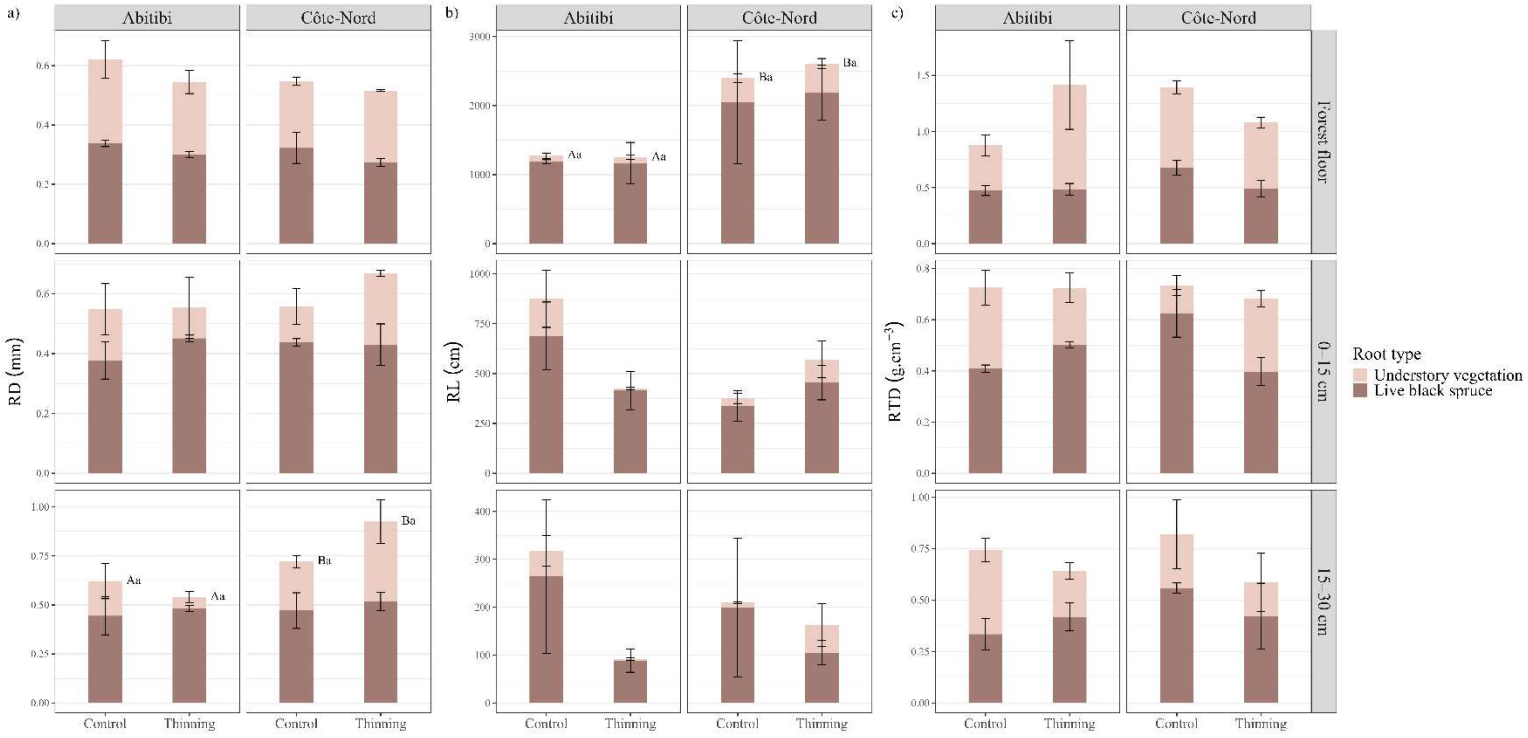
676 *Supplementary Figure 2: Mean root mass density (RMD) of black spruce between soil*
677 *layers. Different letters indicate significant differences (P<0.05).*

678 *Supplementary Table 6: Pairwise comparison of* $RDMC_{UV}$ *in 15-30 cm mineral layer.*
679 *Abbreviations: AT: Abitibi; CN: Côte-Nord*

Soil depth	Region	Treatment	emmean	.group
15-30 cm	AT	Control	4.11	a
	CN	Control	4.88	ab
	CN	Thinning	5.58	bc
	AT	Thinning	5.90	c



Supplementary Figure 3: Mean RD (a), RL (b) and RTD (c) for understory vegetation (UV) and live black spruce (LBS) between regions and treatments across soil depth. Within each soil depth, only significant differences were noted. Uppercase letters indicate significant differences between regions and lowercase letter indicate significant differences between thinning ($P<0.05$).

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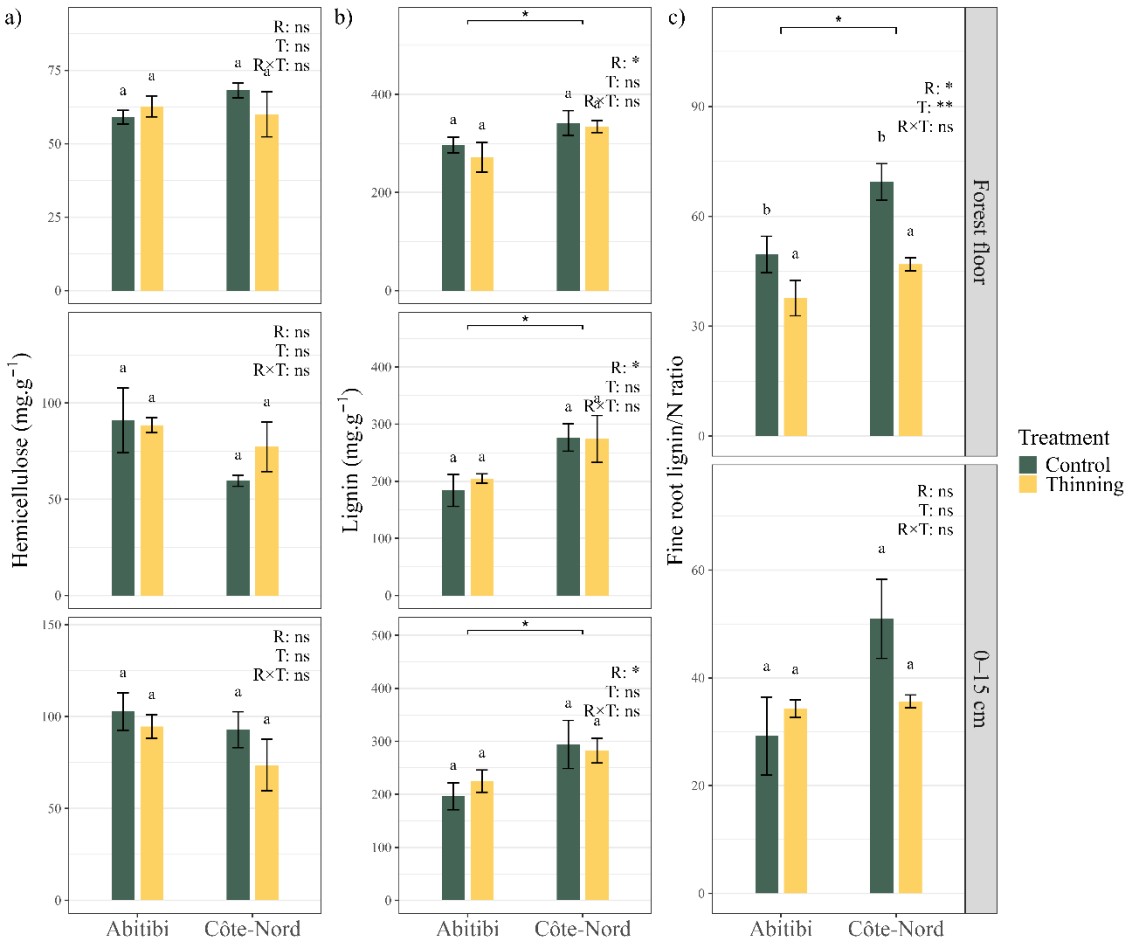

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682 *Supplementary Figure 4: Mean hemicellulose (a), lignin (b) and lignin/N ratio between*
683 *regions and treatments across soil depth. Within each soil depth, different letters indicate*
684 *significant differences between region, treatment or their interaction, according to the*
685 *significance of effects in the statistical models (R: region; T: Treatment; R x T: region x*
686 *treatment interaction). Significant levels are indicated as follows: ns: not significant; ***:*
687 *p <0.001; **: p <0.01; *: p <0.05.*

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Statements & Declarations

Funding

This work was supported by Natural Sciences and Engineering Research Council of Canada (NSERC) (Grant number: Alliance ALLRP 549166-19), Ministry of Natural Resources and Forestry (MRNF), Sept-Iles's Economic Development, Boisaco, Chantiers Chibougamau Ltd.

Competing interests

We declare that we have no knowledge of competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Author Contributions

Maya Disraëli Ratsimandresiarivo: Conceptualization, Data Curation, Formal analysis, Investigation, Methodology, Software, Visualization, Writing—original draft, Writing—review & editing. **Annie DesRochers**: Conceptualization, Methodology, Resources, Writing— review & editing, Supervision, Visualization. **Jérôme Laganière**: Methodology, Resources, Writing— review & editing. **Xavier Cavard**: Conceptualization, Methodology, Resources, Writing— review & editing, Supervision, Visualization, Project administration, Funding acquisition.

Data availability

The datasets are available from the corresponding author on reasonable request.