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Key Points:

- Theoretical framework and hypothesis about the variation of C and N isotopic ratios of organic matter (OM) in permafrost cores are developed
- OM accumulated under C limitation, but contrasting accumulation pathways shaped mineral and organic soils
- Past conditions of OM accumulation may influence the decomposition of permafrost OM while permafrost thaws

Supporting Information:

Supporting Information may be found in the online version of this article.

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C and N Isotopic Fractionation Along Permafrost Profiles: A Theoretical Framework and Empirical Tests Across the Arctic

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Abstract Anticipating the decomposition of permafrost organic matter (OM) following thaw is critical for improving projections of climate-carbon feedbacks. Stable carbon (C) and nitrogen (N) isotope profiles provide integrated records of the environmental and biogeochemical processes that shaped OM during its accumulation and may therefore improve our understanding of the factors controlling its future vulnerability to decomposition. Here, we compiled isotope data from 122 soil units across 42 Arctic sites and used Bayesian hierarchical models to test whether relationships between stable isotope signatures and soil C/N ratios varied along a gradient of soil organic carbon (SOC) content. Nitrogen isotope fractionation remained consistent across the SOC gradient, with $\delta^{15}\text{N}$ increasing as C/N decreased. In contrast, carbon isotope fractionation differed markedly between mineral and organic soils. In mineral soils, $\delta^{13}\text{C}$ increased with decreasing C/N, indicating extensive microbial processing and recycling of OM during accumulation. In organic soils, $\delta^{13}\text{C}$ decreased with decomposition, consistent with the preferential preservation of relatively ^{13}C -depleted plant-derived compounds under waterlogged conditions. These contrasting isotope patterns reveal distinct OM accumulation pathways in mineral and organic permafrost soils. Our results provide a revised conceptual framework linking long-term OM accumulation pathways to the properties of permafrost OM exposed by thaw, improving the interpretation of Arctic soil isotope records and their implications for permafrost carbon vulnerability.

Plain Language Summary Arctic permafrost stores enormous amounts of organic matter (OM) that could be released as carbon dioxide and methane as the climate warms. However, not all permafrost OM is equally vulnerable to decomposition after thawing. To understand why, we examined natural variations in the stable isotope signatures of carbon and nitrogen, which preserve information about how OM accumulates over thousands of years. We compiled data from 122 soil units across 42 Arctic sites and analyzed how isotope signatures changed as OM decomposed. Nitrogen isotope patterns were remarkably consistent across Arctic soils, whereas carbon isotope patterns differed strongly between mineral and organic soils. These contrasting patterns indicate that OM followed different accumulation pathways before becoming frozen. Mineral soils show evidence of extensive microbial processing, whereas organic soils mainly preserve plant-derived material that accumulated under waterlogged conditions. Rather than directly predicting future decomposition, our study provides a new framework for interpreting Arctic soil isotope records. By revealing how past environmental conditions shaped the composition of permafrost OM, our results help improve predictions of how Arctic carbon stocks may respond to permafrost thaw and future climate change.

1. Introduction

1.1. Context

The oxidation of permafrost C will determine whether the Arctic will become a sink or a source of C as climate changes (Miner et al., 2022). Arctic soils contain up to 800 Pg of C in the first 3 m (Hugelius et al., 2014), a quantity comparable to the atmospheric pool (Canadell et al., 2021). Most of this Arctic C is durably stored in frozen soil horizons, but it may be respired if the active layer deepens (Koven et al., 2011) and permafrost thaws (Schneider Von Deimling et al., 2015; Schuur et al., 2009). Both decomposability and temperature sensitivity will influence the respiration of permafrost C (Davidson & Janssens, 2006; Koven et al., 2015). The decomposability of permafrost organic matter (OM) is thought to depend not only on current environmental conditions after thaw but also on the conditions under which it originally accumulated. Environmental factors such as climate, soil water saturation, and vegetation composition influence the chemical composition and preservation of OM during

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soil formation (e.g., Grosse et al., 2011; Sjögersten et al., 2016; Vaughn & Torn, 2019). Because these past conditions are partly recorded in soil properties, including stable isotope signatures, reconstructing OM accumulation histories may help explain why some permafrost carbon stocks are more vulnerable to decomposition than others following thaw.

The conditions under which permafrost OM accumulated can only be reconstructed through proxies preserved in soil profiles. Among these, stable carbon and nitrogen isotope profiles have been widely used to infer the history of OM accumulation and decomposition because isotopic fractionation integrates biogeochemical processes occurring over time (Baisden et al., 2002; Ehleringer et al., 2000). Their interpretation is well established in unfrozen soils, where depth generally reflects increasing OM age and decomposition (Trumbore, 2000). This relationship underpins the interpretation of depth profiles of stable C and N isotopes, which have been used to infer OM turnover (O'Brien & Stout, 1978), the stability of different OM pools (Acton et al., 2013), shifts in vegetation and N cycling during soil formation (Andersson et al., 2012; Tahmasebi et al., 2018), and to improve the calibration of land surface models (Camino-Serrano et al., 2019). Isotopic enrichment with depth is generally attributed to fractionation during decomposition together with lateral and vertical translocation of OM (Ehleringer et al., 2000).

In permafrost soils, depth does not necessarily reflect the decomposition stage. Because permafrost OM is preserved since its freezing, each layer captures the signal of the vegetation (Andersson et al., 2012; Pastukhov et al., 2018) and conditions prevailing during soil formation (Alewell et al., 2011; Hutchings et al., 2019; Strauss et al., 2015) rather than advanced decay (Schuur et al., 2009). Cryoturbation further disrupts the link between depth, age, and decomposition by redistributing OM both upward and downward in the profile (Gentsch, Mikutta, Alves, et al., 2015; Xu et al., 2009). In addition, slow microbial turnover and long-term retention of C and N in microbial biomass can alter isotope dynamics relative to unfrozen soils (Ravn et al., 2017; Sorensen et al., 2008a).

As a result, frameworks developed to interpret isotopic soil profiles in temperate systems cannot be applied directly to Arctic soils. A better understanding of how carbon and nitrogen isotopes record soil formation and OM processing under permafrost conditions is needed to assess the fate of frozen carbon. The goal of this study is to develop a framework for interpreting C and N stable isotope profiles in Arctic soils. We derive hypotheses from a modeling approach that incorporates current knowledge of fractionation processes and test them using a pan-Arctic data set of isotope profiles from active layers and permafrost cores.

1.2. Theoretical Framework

1.2.1. Decomposition

Let's consider a pool of OM entering the soil at time 0. During its presence in the soil, it will be submitted to decomposition. During decomposition, complex organic molecules are degraded, and the associated C and N are assimilated by microorganisms. A part of this plant derived C and N returns to the soil OM as microbial-derived products after mineralization (Parnas, 1975). A fraction of the assimilated C will be lost during cellular respiration, stored as dissolve organic carbon in water or lost through CO₂ released in the atmosphere (Moore et al., 2008), while a part of N will be excreted as mineral N, partly to maintain microbial stoichiometry (Dijkstra et al., 2008). During microbial activity and turnover, the exoenzymes and the necromass will rejoin the OM pool, transforming its composition from plant residuals to microbially originated OM through time (Paul, 2016). We can describe the dynamic of the C and N pools in time (*t*) in a simplistic way with the following ordinary differential equations:

$$\begin{aligned}\frac{\delta C}{\delta t} &= -p_C \cdot k \cdot C \\ \frac{\delta N}{\delta t} &= -p_N \cdot k \cdot N\end{aligned}\quad (1)$$

With C and N being respectively the size of the C and N pools (g·kg⁻¹), *k* (yr⁻¹) the decomposition rate, *p_C* and *p_N* (0–1) the proportion of decomposed C and N not returned to OM during decomposition, lost by respiration and mineralization, respectively. In other words, *p_C* and *p_N* are negatively related to C and N use efficiency (Mooshammer et al., 2014; Sinsabaugh et al., 2013). We assume that the proportion of C lost during microbial respiration is higher than the proportion of N mineralized and excreted (*p_C* > *p_N*). Therefore, the C/N ratio of OM

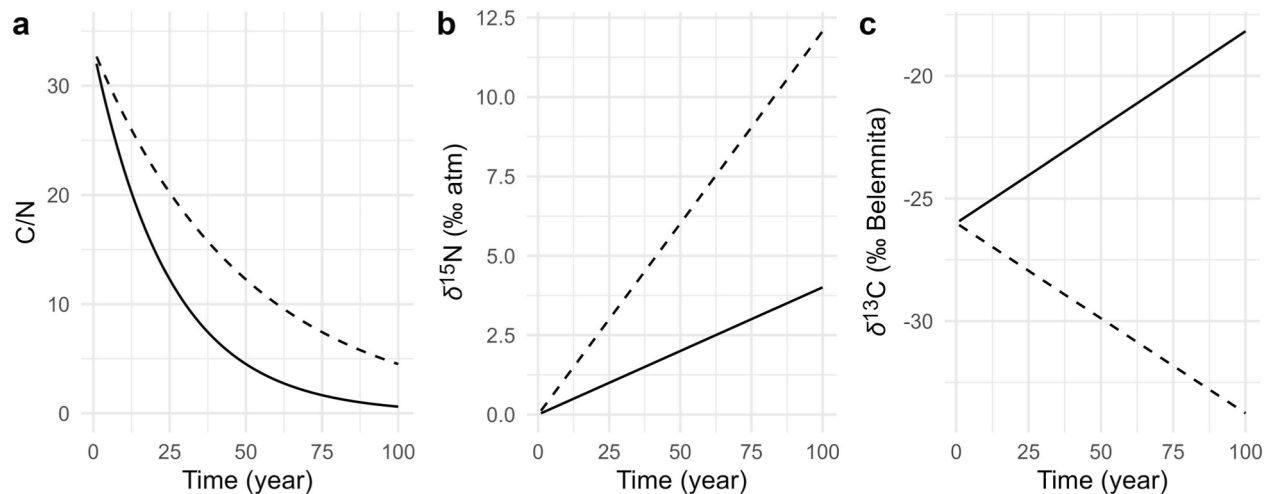


Figure 1. Evolution of organic matter (OM) (a) C/N, (b) $\delta^{15}\text{N}$ and (c) $\delta^{13}\text{C}$ with time in a simple exponential decay model under different fractionation scenarios. In panel (a) and (b), dashed lines and plain lines present the result of the model with $p_N = 0.3$ and $p_N = 0.2$, respectively. A lower value indicates a lower proportion of N excreted by microorganisms during decomposition, as explained in Section 1.2.2. In panel (b), dashed and plain lines present the result of the model with $\alpha_N = 0.998$ and $\alpha_N = 0.999$, respectively. A lower value indicates a stronger fractionation, micro-organisms retaining more ^{15}N and excreting more ^{14}N in proportion. In panel (c), the dashed and plain lines present the simulations with $\alpha_C = 0.1001$ and $\alpha_C = 0.999$, respectively. A value of $\alpha_C > 1$ indicates the preferential preservation of ^{13}C -depleted compounds during decomposition. A value of $\alpha_C < 1$ indicates progressive enrichment of soil OM in ^{13}C , which may arise from microbial reassimilation of ^{13}C -enriched soil CO_2 , fractionation during decomposition, or changes in plant $\delta^{13}\text{C}$ associated with the Suess effect.

decreases with time, as represented in Figure 1a (Parnas, 1975). During all the simulations, the value of p_C was fixed to 0.4, indicating a 40% loss of carbon during decomposition.

1.2.2. Nitrogen Stable Isotopes

The $^{15}\text{N}/^{14}\text{N}$ ratio of plant tissues entering the soil system is highly variable because of the various strategies plants have developed to grow in this N-limited environment (Hobbie et al., 2009; Nadelhoffer et al., 1996). Fixing the $^{15}\text{N}/^{14}\text{N}$ ratio of the atmosphere as a standard ($^{15}R_0$), isotopic ratios are generally computed as a more readable isotopic value ($\delta^{15}\text{N}$) using the isotopic ratio of the sample ($^{15}R_s$) and $^{15}R_0$:

$$\delta^{15}\text{N} = \frac{^{15}R_s}{^{15}R_0} - 1 \quad (2)$$

Because no fractionation occurs during atmospheric N fixation, plants relying on atmospheric fixation have the same isotopic ratio as the atmospheric N_2 ($\delta^{15}\text{N} \sim 0$, Craine et al., 2015), whereas mycorrhizal plants are highly ^{15}N depleted (highly negative $\delta^{15}\text{N}$, < -4) in ^{15}N relative to the atmosphere (Hobbie & Ouimet, 2009). Non-mycorrhizal plants may have a wide variety of isotopic signatures depending upon where they uptake N in the soil column and depending upon the molecules they uptake. Plants with shallower roots, mosses and lichens may profit from N contained in water runoff or N deposition (potentially slightly more depleted in ^{15}N than the atmosphere), whereas plants with deep roots may exploit more decomposed OM at depth (potentially more enriched in ^{15}N , Nadelhoffer et al., 1996).

Once the OM enters the soil columns, N-containing molecules may be subjected to fractionation following OM mineralization and lixiviation (Baisden et al., 2002; Craine et al., 2015). Fractionation occurs in living systems mostly because of the kinetic effects slowing the displacement, excretion and transformation of molecules containing a higher proportion of the heavier isotopes (Sulzman, 2008). Following Amundson and Baisden (2000), we can express the variation in ^{15}N with time by adding an apparent fractionation factor α_N to Equation 2:

$$\frac{\delta^{15}\text{N}}{\delta t} = -\alpha_N \cdot p_N \cdot k \cdot ^{15}\text{N} \quad (3)$$

$\alpha_N < 1$ implies an enrichment in the heavier isotope with time and decomposition, while $\alpha_N > 1$ implies a loss of ^{15}N . The results of the N and ^{15}N mass balance equations were then divided to obtain the $^{15}\text{N}/^{14}\text{N}$ ratio and converted into $\delta^{15}\text{N}$ to ease the interpretation.

Dijkstra et al. (2008) proposed that in a highly C limiting environment, microbial biomass will face an excessive assimilation of N while degrading OM to obtain energy from C bounds. To maintain their stoichiometric ratio and avoid damages caused by N-rich molecules such as ammonium (NH_4^+), they will excrete excess N. Because of preferential mineralization and excretion of ^{14}N , microbial biomass becomes enriched in ^{15}N in C limited environments, as will the OM ultimately derived from it ($\alpha_N < 1$). In N-limited environments, this enrichment will be slower, where N excretion is not favorable and NH_4^+ is maintained in microbial cells ($\alpha_N = 1$). Following such a framework, OM should become more enriched in ^{15}N while decomposition advances in C-limited environments, whereas no or weaker fractionation should occur in N-limited environments. This would lead the relationships between $\delta^{15}\text{N}$ and depth and C/N to be steeper in a C-limited environment (Figure 1b, $\alpha_N = 0.998$, $p_N = 0.3$) than in the N-limited environment (Figure 1b, $\alpha_N = 0.999$, $p_N = 0.2$).

Strong fractionation also occurs during NH_3 volatilization, nitrification, and denitrification, but these processes are not explicitly included in the present conceptual framework. They generally produce ^{15}N -depleted inorganic products, potentially enriching microbial biomass and derived OM in ^{15}N (Craine et al., 2015). Dijkstra et al. (2008) suggested that, in many soils, their overall contribution to soil OM $\delta^{15}\text{N}$ is smaller than that associated with microbial NH_4^+ excretion. The intensity of these processes varies with environmental conditions such as soil moisture, nitrate availability, and permafrost disturbance (Abbott & Jones, 2015; Chapin, 1996; Repo et al., 2009). Because these controls cannot be quantified consistently from the compiled literature data, they were not explicitly incorporated into our theoretical framework and are considered as potential sources of variability around the expected isotopic patterns.

1.2.3. Carbon Stable Isotopes

Variation of ^{13}C with decomposition can also be modeled with an exponential decay formula:

$$\frac{\delta^{13}\text{C}}{\delta t} = -\alpha_C \cdot p_C \cdot k \cdot ^{13}\text{C} \quad (4)$$

Where α_C is the apparent fractionation factor potentially changing the isotopic ratio during decomposition. The results of the C and ^{13}C mass balance equations were then divided to obtain the $^{12}\text{C}/^{13}\text{C}$ ratio and converted into $\delta^{13}\text{C}$ to ease the interpretation.

The $\delta^{13}\text{C}$ value of different plant tissues and compounds are partly correlated with their lability (Nadelhoffer & Fry, 1998). More recalcitrant compounds such as lignin or lipids are generally depleted in ^{13}C relative to bulk plant tissues (by $\sim -3\text{‰}$ and $\sim -4\text{‰}$, on average), while more labile compounds such as sugars, starch, or cellulose are generally enriched in ^{13}C (by ~ 1 , 2 and 2‰ , respectively) (Bowling et al., 2008).

In anoxic environments, compound-specific variability in plant $\delta^{13}\text{C}$ plays a major role in the isotopic evolution of soil OM during decomposition. Recalcitrant ^{13}C enriched plant compounds are degraded slowly and incorporated in soil OM pools (Moore & Basiliko, 2006). Soil OM $\delta^{13}\text{C}$ becomes close to the signature of recalcitrant ^{13}C depleted plant compounds when decomposition occurs, causing a depletion in ^{13}C with time (Benner et al., 1987). This leads to an apparent fractionation factor $\alpha_C > 1$ (Figure 1, dashed line).

Compound-specific variability in plant $\delta^{13}\text{C}$ play a weaker role in oxic environments than in anoxic ones. At the first stage of decomposition, ^{13}C enriched labile molecules are preferentially respired, leading to a decrease of the $\delta^{13}\text{C}$ of OM (Melillo et al., 1989). At later stages, recalcitrant compounds are consumed as microbial community changes, reestablishing original OM $\delta^{13}\text{C}$ (Lerch et al., 2011) or increasing it, as discussed in the next paragraphs.

No kinetic fractionation effect seems to occur during the aerobic respiration of soil OM. While mitochondrial respiration was hypothesized to favor the emission of $^{12}\text{C}\text{-CO}_2$, direct tests and review studies report a wide and unconvulsive range of fractionation (Ehleringer et al., 2000; Werth & Kuzyakov, 2010). Breecker et al. (2015) concluded that there was no fractionation during aerobic respiration of well-preserved soil samples, while disturbances during manipulations may cause misleading results.

Limited microbial reassimilation of soil CO₂ may also contribute to ¹³C enrichment during OM decomposition (Ehleringer et al., 2000). This process refers to the incorporation of a small fraction of interstitial soil CO₂ into microbial biomass during heterotrophic metabolism rather than photosynthetic C fixation. In Arctic soils, Šantrůčková et al. (2018) showed that this process represents a small but measurable fraction of respired CO₂, representing approximately 1.0% of the CO₂ respired in mineral and cryoturbated horizons, and up to 16.1% in mineral permafrost horizons, while remaining negligible in organic layers. Because diffusion through soil pores generally enriches interstitial CO₂ in ¹³C relative to soil OM (Amundson et al., 1998), microbial reassimilation may gradually introduce ¹³C-enriched carbon into microbial biomass and, ultimately, into microbial necromass accumulating in the finest soil OM pools. Over centuries of decomposition, this process could therefore contribute to a progressive enrichment of OM in ¹³C (Šantrůčková et al., 2018). Within our theoretical framework, this mechanism is represented by an apparent fractionation factor $\alpha_C < 1$ (Figure 1c, solid line).

Special care should be taken when studying the recent time OM accumulation. Fossil combustible burning since the industrial era has increasingly depleted the atmospheric CO₂ in ¹³C relative to the international standard (Figure S1a in Supporting Information S1; Rubino et al., 2013; Graven et al., 2017). Older OM is thus enriched in ¹³C relative to the recent OM (e.g., Lamarque et al., 2023). This difference in ¹³C concentration leads to an apparent fractionation factor $\alpha_C < 1$, $\delta^{13}\text{C}$ values being higher in older OM, even if no fractionation occurs during decomposition (Ehleringer et al., 2000, Figures S1b and S1c in Supporting Information S1). Atmospheric ¹³C composition is far less certain in the pre-industrial era, but no tendency of such magnitude has been discovered during the last millennium (Rubino et al., 2013).

1.2.4. Consideration of Arctic Conditions

Syngenetic permafrost contains most of Arctic permafrost OM (Hugelius et al., 2014). In these soils, accumulation of peat and deposition and stabilization of sediments capture soil OM rapidly after its formation. Freezing at the bottom of the active layer following such surface aggradation allows SOM to be durably preserved at temperatures below the freezing point. This must be contrasted with epigenetic permafrost formation in which case permafrost forms after sedimentary deposition or OM formation, with limited freezing and protection of newly produced OM (Ping et al., 2015). This study will focus on the case of syngenetic permafrost, which represents most of the soil profiles currently described in the literature. We will contrast syngenetic permafrost processes occurring in high OM soils from peat accumulation, to processes occurring in mineral soils, more plausibly aggraded because of sediment deposition.

To produce theoretically grounded hypotheses, it is necessary to add a movement process to the system of differential equation above (Equation 1) to account for OM movement with depth. An advective term should represent a respectable approximation of syngenetic permafrost aggradation, the depth of a given OM pool increasing as it is covered by new sediments or organic layers (like what is used to represent OM accumulation at the bottom of lakes or ocean, Soetaert & Herman, 2009). We will thus add advective terms ($\delta C/\delta z$, $\delta N/\delta z$, $\delta^{15}\text{N}/\delta z$ and $\delta^{13}\text{C}/\delta z$) to Equation 1, representing the variation of C, N, ¹⁵N and ¹³C along depth:

$$\begin{aligned}\frac{\delta C}{\delta t} &= -v \cdot \frac{\delta C}{\delta z} - p_C \cdot k \cdot C \\ \frac{\delta N}{\delta t} &= -v \cdot \frac{\delta N}{\delta z} - p_N \cdot k \cdot N \\ \frac{\delta^{15}\text{N}}{\delta t} &= -v \cdot \frac{\delta^{15}\text{N}}{\delta z} - \alpha_C \cdot p_C \cdot k \cdot ^{15}\text{N} \\ \frac{\delta^{13}\text{C}}{\delta t} &= -v \cdot \frac{\delta^{13}\text{C}}{\delta z} - \alpha_C \cdot p_C \cdot k \cdot ^{13}\text{C}\end{aligned}\tag{5}$$

With v being the advection rates (0.03 cm·yr⁻¹, Table S1 in Supporting Information S1, Fortier et al., 2006; Wetterich et al., 2020; Zhu et al., 2016). Considering the variation of temperature, soil moisture, oxygen, and other unresolved processes with depth, we considered an exponentially decreasing decomposition rate with depth, defined as:

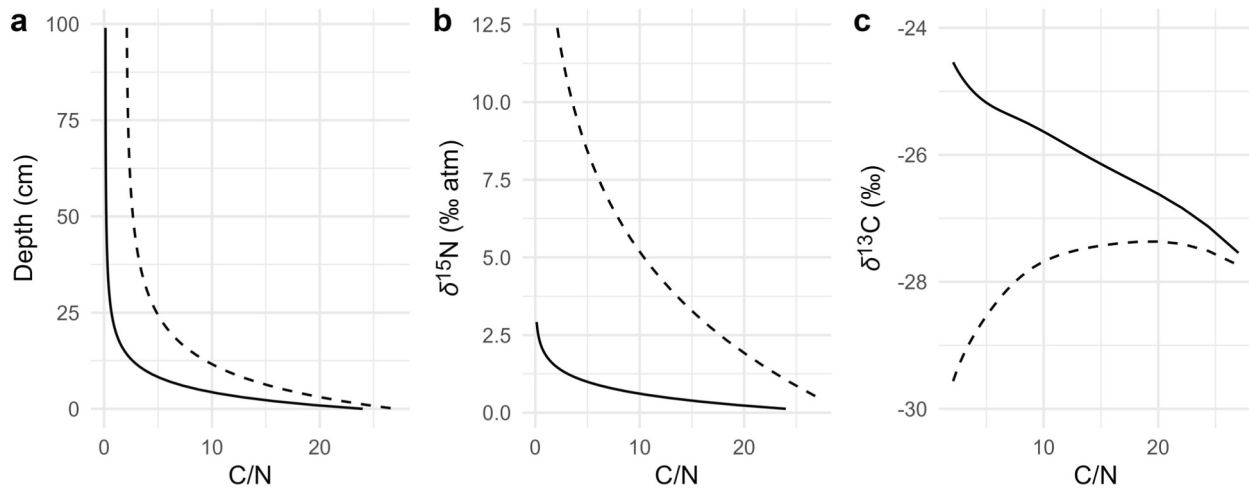


Figure 2. Evolution of (a) organic matter (OM) C/N with depth, and relationships OM C/N and (b) $\delta^{15}\text{N}$ and (c) $\delta^{13}\text{C}$ with time in a simple exponential decay model under different fractionation scenarios. In panel (a) and (b), dashed lines and plain lines present the result of the model with $p_N = 0.3$ and $p_N = 0.2$, respectively. A lower value indicates a lower proportion of N excreted by microorganisms during decomposition, as explained in Section 1.2.2. In panel (b), dashed and plain lines present the result of the model with $\alpha_N = 0.9995$ and $\alpha_N = 0.9985$, respectively. A lower value indicates a stronger fractionation, micro-organisms retaining more ^{15}N and excreting more ^{14}N in proportion. In panel (c), the dashed and plain lines present the results of the model with $\alpha_C = 0.1.0003$ and $\alpha_C = 0.9998$, respectively. The negative value indicates that micro-organisms conserve ^{13}C depleted compounds during decomposition. A positive value indicates micro-organisms become enriched in ^{13}C , either because of limited microbial reassimilation of CO_2 , fractionation during decomposition, or trends in plant material due to depletion of atmospheric CO_2 after fossil fuel consumption. The variable ^{13}C concentration due to fossil fuel burning is included in the model under a dynamic boundary condition, leading to irregular lines. For all the simulations, the basal decomposition parameter, k_0 , was set to 0.05 years^{-1} , and the advection rate, v , to 0.03 mm.yr^{-1} .

$$k = k_0 \cdot \exp\left(-\frac{z}{z_h}\right) \quad (6)$$

Where k_0 (year^{-1}) is the base decomposition rate at the surface and z_h (cm) is the depth control parameter representing the depth at which k_0 is halved. In all the simulations, z_h (20 cm) was chosen to ensure almost null decomposition below an active layer of approximately 50 cm (Table S1 in Supporting Information S1).

To simulate from this model, we consider constant input flux I_C and I_N as boundary conditions at the soil surface. To keep our model simple, we deliberately chose to ignore root input, assuming it would not qualitatively change the hypothesis we could derive from our framework:

$$\begin{aligned} -v \frac{\delta C}{\delta z} \Big|_{z=0} &= I_C \\ -v \frac{\delta N}{\delta z} \Big|_{z=0} &= I_N \\ -v \frac{\delta^{15}\text{N}}{\delta z} \Big|_{z=0} &= R_N \cdot I_N \\ -v \frac{\delta^{13}\text{C}}{\delta z} \Big|_{z=0} &= R_C \cdot I_C \end{aligned} \quad (7)$$

With R_N and R_C being the $^{14}\text{N}/^{15}\text{N}$ and $^{12}\text{C}/^{13}\text{C}$ ratio of OM at the surface.

Cryoturbation does not allow to substitute depth for time, as it can be done in southern soils (see e.g., O'Brien & Stout, 1978). Frequent freezing-thawing events may cause surficial, young and slightly degraded OM to be buried at depth, where it may become protected in permafrost (Bockheim, 2007; Gentsch, Mikutta, Alves, et al., 2015; Xu et al., 2009). To solve this difficulty, we will use C/N as a proxy of decomposition rather than depth. We postulate that C/N captures the decomposition stage of an OM pool even if it has been displaced in the soil column. The relationship between OM C/N and $\delta^{15}\text{N}$ (Figure 2b) and between C/N and $\delta^{13}\text{C}$ (Figure 2c) are

represented for a hypothetical Arctic soil column, following the fractionation scenarios described in Sections 1.2.2 *Nitrogen stable isotopes* and 1.2.3 *Carbon stable isotopes*.

Figure 2a presents the evolution of C/N as a function of depth for different values of parameters at equilibrium. We numerically solved the models containing advective terms using the *ode.ID* function in the *deSolve R* package (Soetaert et al., 2010). The complete model is illustrated in Figure S2 in Supporting Information S1.

Spatial and temporal variation of plant input signature may alter isotopic values in Arctic soil profiles. All Arctic plants perform C3 photosynthesis (Billings, 1987). The intensity of fractionation during C3 photosynthesis is controlled by the ratio between intra-cellular and ambient CO₂ pressure related to stomatal closure in vascular plants (Farquhar et al., 1989). This causes tissues of water stressed vascular plant to be more enriched in ¹³C (higher $\delta^{13}\text{C}$) than non-water-stressed vascular plants on average, because they should fractionate less during photosynthesis. Even if bryophytes also perform C3 photosynthesis, the diffusive process behind CO₂ acquisition makes their signature less intuitive. It has been shown $\delta^{13}\text{C}$ of mosses increases with wetness because of slower diffusion of ¹³C in water (the opposite relationship than vascular plants, Loisel et al., 2009; Price et al., 1997), while it decreases with air temperature (Skrzypek et al., 2007). Change in surface condition, for example, if the surface dries after soil uplifting, may thus change the signature of plant inputs, with or without change in fractionation during decomposition. Concretely, this could lead to noisy relationships between C/N and isotopic values.

Carbon isotope fractionation during methanogenesis is unlikely to substantially modify the $\delta^{13}\text{C}$ signature of bulk OM preserved in permafrost soils. Methane emissions are generally low in well-drained tundra but may still occur during shoulder seasons or within wetter microsites, whereas they can represent up to 6.3% of ecosystem respiration in saturated Arctic soils (Olefeldt et al., 2013). Strong isotope fractionation occurs during the final steps of methanogenesis, producing CH₄ that is highly depleted in ¹³C while leaving methanogenic biomass relatively enriched (Conrad, 2005). However, fractionation during the earlier conversion of OM into acetate and CO₂ is comparatively small (Blaser & Conrad, 2016). Consequently, the $\delta^{13}\text{C}$ signature of residual bulk OM is expected to be only weakly affected by methanogenesis itself. Although ¹³C-enriched methanogenic necromass could contribute to soil OM, microbial-derived compounds represent only a small fraction of the organic carbon pool in Arctic organic soils (Hutchings et al., 2019; Pastukhov et al., 2018; Prater et al., 2020). We therefore consider methanogenesis as a secondary process that may contribute to variability in $\delta^{13}\text{C}$, but whose influence is likely smaller than the preferential preservation of ¹³C-depleted compounds under anoxic conditions.

1.3. Hypotheses

Our objective is not to use stable isotopes as direct indicators of OM decomposability. Instead, we propose that isotope signatures preserve the integrated imprint of the environmental and biogeochemical processes that shape OM during its accumulation. Because these processes determine the composition and degree of transformation of OM, they are also expected to influence its vulnerability to decomposition following permafrost thaw. Therefore, we derive the following hypotheses regarding isotope fractionation during OM accumulation.

We expect a negative relationship between $\delta^{15}\text{N}$ and C/N ratio of OM in soils with low mean C/N (Figure 2b, dashed line), where C should have been limiting for microbial biomass during decomposition (Table 1). We expect the slope of the $\delta^{15}\text{N}$ -C/N relationship to approach zero as mean soil C/N increases (Figure 2b, plain line). We thus derive:

H_N: a positive relationship between the $\delta^{15}\text{N}$ -C/N slope and the mean C/N of soil.

Because high soil organic carbon (SOC) soils generally appear in low-redox conditions, when decomposition is slowed down, we expect a positive $\delta^{13}\text{C}$ -C/N relationship in high SOC soils (Figure 2c, dashed line). In low SOC soils, we expect young horizons to have a negative $\delta^{13}\text{C}$ -C/N relationship because of recent depletion of atmospheric CO₂, and older horizons to have the same relationship because of long-term limited microbial re-assimilation of ¹³C-enriched interstitial soil CO₂ (Table 1, Figure 3c, plain line). We thus derive:

H_C: a positive relationship between the $\delta^{13}\text{C}$ -C/N slope and the C content of the soil.

Table 1
Summary of the Processes Influencing C and N Isotopic Ratios During Organic Matter Accumulation, and Its Impact on the Relationship Between C/N and Delta Values in Arctic Soils

Element	Mechanism	Isotopic ratio	α	Slope with C/N	Implications for OM accumulation
N	Mineralization of NH_4^+	Enriched in ^{15}N with decomposition	<1	Negative	Carbon-limited decomposition. Indicates extensive microbial processing of OM, generally associated with greater decomposition prior to burial and potentially lower availability of labile substrates after thaw.
	Conservation of NH_4^+	Stable ^{15}N with decomposition	~1	Null	Nitrogen-limited decomposition. Indicates limited microbial processing of OM, favoring the preservation of less transformed OM that may retain a larger proportion of labile compounds.
C	Fractionation during respiration	Enriched in ^{13}C with decomposition	=1	Null	Oxic mineral soils where decomposition proceeds with little net isotopic fractionation. Does not substantially modify the chemical quality of preserved OM.
	Microbial reassimilation of soil CO_2	Enriched in ^{13}C with C accumulation	<1	Negative	Predominantly oxic mineral soils. Reflects repeated microbial recycling of carbon and increasing microbial contribution to OM, indicative of more processed OM.
	Input of recent plant material (Suess effect)	Enriched in ^{13}C with C accumulation	<1	Negative	Active layer and recent plant inputs. Reflects changes in atmospheric $\delta^{13}\text{C}_{\text{CO}_2}$ rather than decomposition processes and should not be interpreted as a direct indicator of OM quality.
	Fractionation during methanogenesis	Enriched in ^{13}C with C accumulation	<1	Negative	Waterlogged, anoxic soils. Represents a potential secondary source of variability in $\delta^{13}\text{C}$ but is expected to contribute less to bulk OM composition than selective preservation of plant compounds.
	Preservation of ^{13}C depleted compounds	Depleted in ^{13}C with decomposition	>1	Positive	Anoxic organic soils. Indicates preferential preservation of chemically recalcitrant plant compounds and limited microbial transformation, potentially leading to OM with distinct decomposition trajectories after thaw.

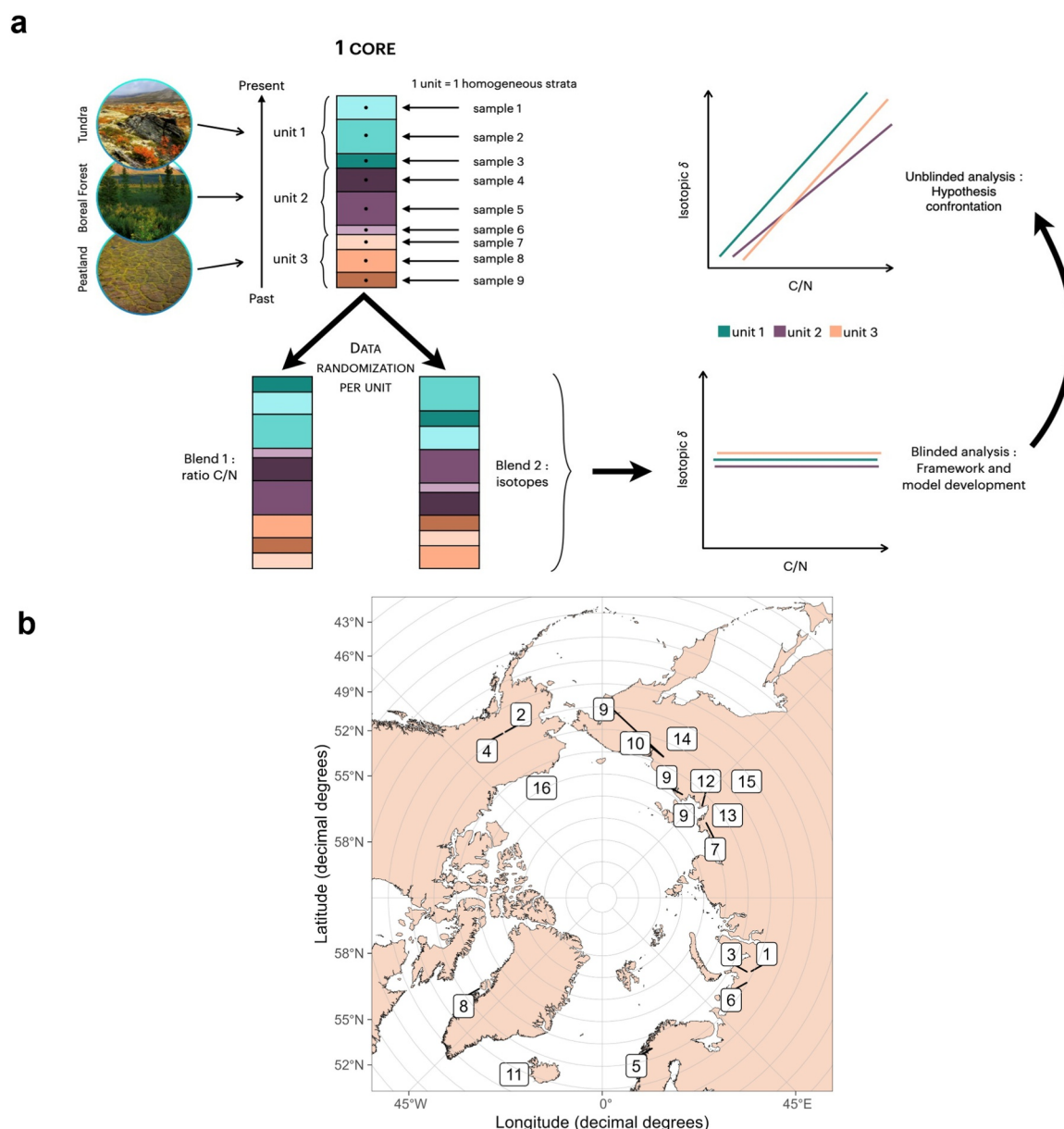


Figure 3. Schematic representation of the analysis framework (a) and map presenting the distribution of the analyzed studies (b). 1: Andersson et al. (2012); 2: Hicks Pries et al. (2012); 3: Hugelius et al. (2012); 4: Hutchings et al. (2019); 5: Krüger et al. (2014); 6: Pastukhov et al. (2018); 7: Prater et al. (2020); 8: Ravn et al. (2020); 9: Schirrmeister et al. (2011); 10: Schirrmeister et al. (2018a, 2018b); 11: Skrzypek et al. (2008); 12: Stapel et al. (2016b, 2016a); 13: Strauss et al. (2015); 14: Wetterich and Schirrmeister (2017a, 2017b, 2017c), Wetterich et al. (2018); 15: Windirsch et al. (2019, 2020); 16: Xu et al. (2009).

2. Materials and Methods

2.1. Literature Search and Exclusion Criteria

We searched the Scopus database for any article reporting isotopic values, C/N and massic C content in Arctic soil cores or profiles. The query was performed on 20 October 2020, with the keywords (soil OR permafrost) AND (arctic) AND (13C OR 15N), leading to a total of 897 articles (Table 2). We excluded articles which (a) did not take place in terrestrial ecosystems; (b) did not measure massic C content, C/N and $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ at more than three depths in soil cores or profiles; (c) made inferences without reporting raw data or summary statistics at multiple depths. When necessary, data were digitized from plots using the WebPlotDigitizer software (Rohatgi, 2021).

Table 2

Summary of the Extracted Data From the 15 Publications Reporting Organic Matter C and N Isotopic Values, C/N and Soil Organic Carbon in Permafrost Cores or Profiles

Study	Number of sites	Number of cores	Number of units	SOC Mean (range)	Element	Data form	Active layer sampled
Andersson et al. (2012)	1	1	3	46.6 (45.2–48.1)	C, N	Statistics, Plots	No
Hicks Pries et al. (2012)	1	3	3	39.4 (38.4–39.9)	C, N	Statistics, Plots	Yes
Hugelius et al. (2012)	7	7	7	33.1 (6.9–46.8)	C, N	Raw data, Plots	No
Hutchings et al. (2019)	1	1	5	13.6 (0.56–34.4)	C	Raw data, Tables	No
Krüger et al. (2014)	12	36	36	45.2 (30.1–49.1)	C	Raw data, Plots	Yes
Pastukhov et al. (2018)	3	4	4	46.6 (44.0–48.4)	C, N	Raw data, Tables	Yes
Prater et al. (2020)	1	4	4	24.7 (23.7–27.0)	C, N	Raw data, Tables	No
Ravn et al. (2020)	1	1	1	9.28 (9.28–9.28)	C	Summaries, Tables	No
Schirrmeister et al. (2011)	5	15	26	3.16 (0–10.5)	C	Raw data, Plots	No
Schirrmeister et al. (2018a, 2018b)	1	8	8	9.96 (3.45–19.5)	C	Raw data, PANGAEA	No
Skrzypek et al. (2008)	1	1	1	16.3 (16.3–16.3)	C, N	Raw data, Plots	Yes
Stapel et al. (2016b, 2016a)	1	1	2	2.95 (2.42–3.94)	C	Raw data, PANGAEA	No
Strauss et al. (2015)	1	4	9	3.33 (0.68–10.0)	C	Raw data, Plots	No
Wetterich and Schirrmeister (2017a, 2017b, 2017c), Wetterich et al. (2018)	1	2	2	8.41 (6.18–12.0)	C	Raw data, PANGAEA	No
Windirsch et al. (2019, 2020)	1	2	6	0.52 (0.1–1.15)	C	Raw data, PANGAEA	No
Xu et al. (2009)	1	1	1	9.55 (9.55–9.55)	C, N	Raw data, Tables	No
17 studies	42	95	122	24.47 (0.1–49.1)	17C, 8N	–	–

Note. SOC represents the mean soil organic carbon of a unit.

Analysis was based on “units”, defined as sections of cores or profiles constituted during homogeneous vegetation and condition of decomposition (Figure 4). Units were delimited using stratigraphic information recovered in the text and figures of the paper. For example, the Late Glacial/Early Holocene thermokarst lake deposits of the Dmitry Laptev Strait (Figure 5 in Schirrmeister et al., 2011) is considered as a unit in this study, whereas the Holocene polygonal cover above it in the profile constitutes another unit. We considered units to combine into a “core”, and cores (or profiles) into “sites.” No selected article reported soil $\delta^{15}\text{N}$ only. Prater et al. (2020) reported C/N and isotopic values for soil fractions at different depths. Bulk soil values were calculated as the weighted average of each variable, with weights corresponding to the relative mass of each soil fraction.

2.2. Data Blinding Approach

To avoid the impact of confirmation bias during data preparation and model development (Nuzzo, 2015), we used a data blinding approach (Figure 4, MacCoun & Perlmutter, 2015). Values of each variable were randomized within units, breaking depth ordering and relationships among variables. Introduction, theoretical framework, hypothesis, model, and figures were then developed blind, the measured data set being used only once model formulation, model convergence and clarity of text and figure were recognized by all authors. Every change in analysis made after the discovery of real data is labeled as post-blinding.

2.3. Statistical Analysis

Both hypothesis (H_N and H_C) implies quantifying the relationship between OM C/N and isotopic values. We used a Bayesian hierarchical model to estimate this relationship for each soil unit (part of the profile accumulated during homogeneous conditions and vegetation). The i th isotopic value y_i in the unit u was modeled as

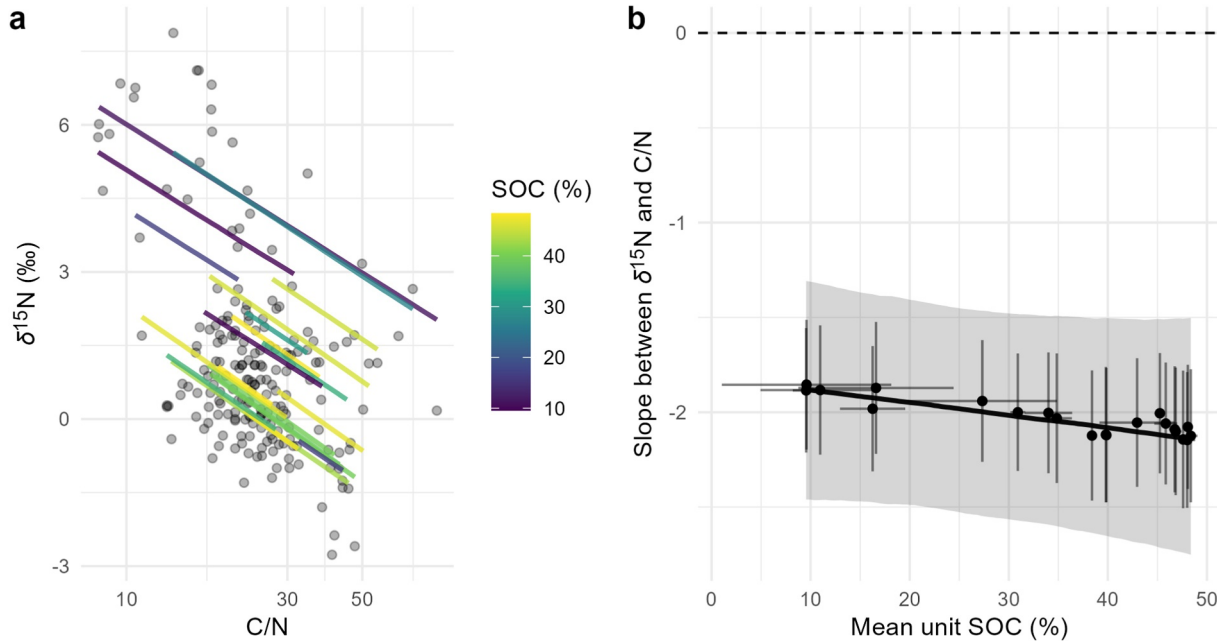


Figure 4. Relationships between (a) $\delta^{15}\text{N}$ and C/N for each soil unit and (b) $\delta^{15}\text{N}$ -C/N slopes and mean unit soil organic carbon (SOC). Colored lines represent the posterior median relationship estimated independently for each soil unit, illustrating the among-profile variability subsequently analyzed in panel (b). Points of panel (b) represent median estimated slopes and mean SOC of soil units, and the associated vertical and horizontal lines represent the mean absolute deviations around the median. Notice the logged x-axis in panel (a).

$$y_i \sim \text{Normal}(\mu_i, \sigma)$$

$$\mu_i = \alpha + \beta_{u(i)} + x_i \cdot \beta'_{u(i)}$$

$$\{\beta_{u(i)}, \beta'_{u(i)}\} \sim \text{MultiNormal}(\{0, \epsilon_{u(i)}\}, \Sigma) \quad (8)$$

Where x_i is the log of the C/N ratio of the i th observation, α the global intercept, $\beta_{u(i)}$ the hierarchical intercept of the unit of the observation i , and $\beta'_{u(i)}$ the hierarchical slope between C/N and the isotopic value in the unit of the observation i . μ_i and σ are the mean and the residual standard-deviation of the normal distribution, respectively. $\epsilon_{u(i)}$ is the linear predictor of the hierarchical slope of unit u , and Σ a 2×2 covariance matrix.

H_N expected a positive relationship between the $\delta^{15}\text{N}$ -C/N slope and the C content of the soil unit (SOC), the relationship between C/N and $\delta^{15}\text{N}$ being closer to zero in soil units with high mean SOC. We thus modeled the relationship between the slope of the C/N- $\delta^{15}\text{N}$ isotopic values relationship and C_u , the unit mean SOC, with γ and γ' being the intercept and slope of this hierarchical relationship, respectively.

$$\epsilon_u = \gamma + \gamma' \cdot C_u \quad (9)$$

H_C expected a positive relationship between the $\delta^{13}\text{C}$ -C/N slope and the C content of the soil unit, the relationship between C/N and $\delta^{13}\text{C}$ being negative in soil units with low mean C content, and positive in soil units with high mean C content. The hierarchical relationship presented in Equation 9 was first used to confront H_C . Potential issues related to the fundamental differences between mineral and organic soils were pointed out during the reviews. We thus fitted a second hierarchical model with different intercepts and slopes for mineral (mean unit C content $<30\%$) and organic soils (mean unit C content $\geq 30\%$).

We accounted for the uncertainty around the mean unit C content, estimating C_u as

$$C_i \sim \text{logNormal}(\log(C_{u(i)}), \sigma_C) \log(C_{u(i)}) \sim \text{Normal}(\lambda, \phi) \quad (10)$$

Where C_i is the C content of the i th observation, σ_C is the residual standard deviation around the log of C content of the units, and λ and φ the estimated mean and standard deviations of the population of estimated mean units C content.

We estimated parameters using the NUTS algorithm in *stan* (Stan Development Team, 2022) through the *cmdstanR* interface (Gabry & Češnovar, 2022) in the R 4.2.0 software (R Core Team, 2022). We sampled posterior parameter distribution with three chains of 2,000 warm-up and 2,000 sampling iterations. We realized careful prior predictive checks to ensure that priors avoided the prediction of impossible isotopic values while being not informative about the direction of the slopes. We ensured posterior distribution samplings to be unbiased (no divergent transition when setting the adapt delta argument to 0.9) and efficient (no warning about tree depth when setting the max tree depth argument to 12).

The ChatGPT 4-o model (OpenAI, 2024) was used in its free version to make suggestions to synthesize paragraphs of Section 1.1. Context section, and to spot issues with the structure and of some paragraphs of Section 1.2. Theoretical framework.

3. Results

The compiled data set captured an important variability of soil isotopic values. $\delta^{15}\text{N}$ varied between -2.77 and 7.87‰ , with a median at 0.9‰ , whereas $\delta^{13}\text{C}$ varied between -31.8 and -22.5‰ , with a median at -27.1‰ . In the data set used for ^{15}N analysis, C/N varied from 8.20 to 113, with a median at 22.7, whereas mean unit SOC varied between 9.55% and 48.4%, with a median at 39.8. In the data set used for ^{13}C analysis, C/N varied from 1.05 to 162 with a median at 21.0, whereas unit SOC varied between 0.12% and 49.1% with a median at 30.1%.

We detected a constant fractionation of N isotopes during past Arctic decomposition (Figures 4a and 4b), OM becoming more ^{15}N enriched when C/N decreased in all units (Figure 4a). The intercept and slope of the relationship between mean unit SOC and the $\delta^{15}\text{N}$ -C/N slopes were -1.82 (ci: -2.35 ; -1.28) and -0.007 (ci: -0.018 ; 0.005 , Figure 4). An outlier soil profile was removed, characterized by a positive tendency between CN and $\delta^{15}\text{N}$ (Figure S3 in Supporting Information S1). This trend was due to two points with very high $\delta^{15}\text{N}$ values (around 8) at high C/N, probably caused by the burying by cryoturbation of surface OM under particular vegetation, rather than by decomposition processes. Including this profile, the intercept of the relationship between mean unit SOC and $\delta^{15}\text{N}$ -C/N slopes was on average -1.33 (95% credible interval, ci: -1.93 ; -0.73), while the slope was slightly negative with high uncertainty (median: -0.007 , ci: -0.019 ; 0.008) (Figure S4b in Supporting Information S1).

On the other hand, C fractionation varied during past Arctic decomposition (Figure 5a) depending upon unit SOC (Figure 5b), corroborating H_C , with negative $\delta^{13}\text{C}$ -C/N slopes at low SOC and null or positive slopes at high SOC. The intercept of the relationship between mean unit SOC and the $\delta^{13}\text{C}$ -C/N slopes were, in median, -0.503 (ci: -0.700 ; -0.306), with a positive slope of 0.011 (ci: 0.007 ; 0.015). The picture was similar when considering two different relationships depending upon soil types (Figure S5 in Supporting Information S1). In mineral soils (mean unit SOC < 30), the intercept of the relationship between mean unit SOC and the $\delta^{13}\text{C}$ -C/N slopes was negative, with a median equal to -0.441 (ci: -0.661 ; -0.239). This indicates that OM becomes enriched in ^{13}C as C/N decreases for units with low C content. The slope was on average -0.009 (ci: -0.027 ; 0.008) in mineral soils, indicating no variation of the $\delta^{13}\text{C}$ -C/N relationship with increasing SOC content in mineral soils. In organic soils, the intercept and slopes of the relationship between the mean unit SOC and the $\delta^{13}\text{C}$ -C/N slopes were both null, with a median equal to -0.061 (ci: -0.273 ; 0.154) and 0.004 (ci: -0.007 ; 0.014). This indicates that both null (no fractionation) and positive $\delta^{13}\text{C}$ -C/N slopes (depletion in ^{13}C as C/N decreases) occur in units with high C content.

4. Discussion

4.1. Nitrogen

Our results invalidated H_N , with no variation of the $\delta^{15}\text{N}$ -C/N relationship along the gradient of soil C/N, whereas a positive relationship was expected. This points toward a constant fractionation retaining ^{15}N when past Arctic decomposition occurred ($\alpha_N < 1$). Following Dijkstra et al. (2008), it means that microbes excreted as much ^{14}N enriched NH_4^+ during decomposition in organic and mineral soils. In mineral soil and at low C content, that is, when carbon is expected to be limiting for microbial growth, fractionation is expected because microbes excrete excess N to maintain their stoichiometric (C/N) ratio. This excretion leads to the loss of ^{15}N depleted NH_4^+ and the

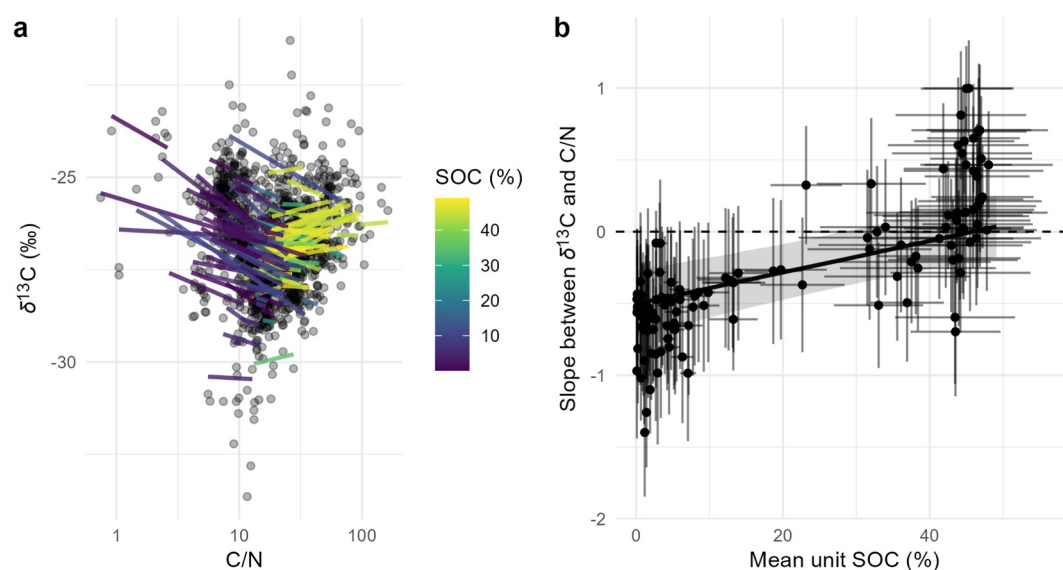


Figure 5. Relationships between (a) $\delta^{13}\text{C}$ and C/N for each soil unit and (b) $\delta^{13}\text{C}$ -C/N slopes and mean unit soil organic carbon (SOC). Colored lines represent the posterior median relationship estimated independently for each soil unit. Each point of panel b represents the median estimated slope and mean unit SOC, and the associated vertical and horizontal lines represent the mean absolute deviations around the median. The thick black line represents the median regression predictions, and the shaded area represents the associated 95% credible interval. Notice the logged x-axis in panel (a).

enrichment of microbial biomass in ^{15}N . This is in line with recent results showing that 20%–60% of nitrogen absorbed by microbes is mineralized (not used for biomass nor enzyme production) in the mineral horizons of Arctic soils (Wild et al., 2013, 2018). A similar nitrogen fractionation in organic soils is not expected, because micro-organisms are expected to use a higher proportion of N for growth in the presence of abundant C sources.

Within our conceptual framework, the observed $\delta^{15}\text{N}$ -C/N relationships are consistent with continued microbial NH_4^+ excretion during the accumulation of highly organic Arctic soils. This contrasts with observations from present-day active-layer organic horizons, where microbial communities are often considered to be more strongly nitrogen limited. Less than 30% of the N assimilated by microorganisms during decomposition was excreted in the organic horizons of current active layers across the Arctic (Wild et al., 2013, 2018). Glycine fertilization experiments showed that current Arctic microbes cycle N in microbial biomass, immobilizing it for years (Ravn et al., 2017; Sorensen et al., 2008b). However, these fertilization studies suggest that Arctic microbes may be colimited by C and N, as C fertilization does not increase mineral N production (Sorensen et al., 2008a). Although metadata describing vegetation composition and hydrological conditions were not consistently available across studies, the high SOC content of these soil units suggests that they predominantly originated from organic soils that accumulated under persistently waterlogged conditions favoring peat formation. Peat becomes more concentrated in recalcitrant molecules with depth and decomposition time (Hill et al., 2014), as discussed below. Moreover, anaerobic conditions leading to peat formation greatly limit the energy that microbes can obtain from OM degradation (Boye et al., 2017). These conditions can lead to a possible C limitation for microbes relying on more decomposed OM (Hill et al., 2014) and excess N excretion, as suggested by our results. Moreover, microbes may also be P limited in peat (Hill et al., 2014; Parvin et al., 2018), the limitation increasing with decomposition, when P becomes trapped in SOM (Margalef et al., 2017; Parvin et al., 2018) and the parent rock is not in contact with the soil surface as observed during boreal paludification (Simard et al., 2007). More studies are needed to determine if P limitation needs to be considered in the stoichiometric theories underlying microbial N fractionation in organic soils.

Our results support the well-established pattern of ^{15}N enrichment with decomposition in Arctic soils (Figure 5a; Craine et al., 2015). Yet, we found far less available ^{15}N soil data than ^{13}C . We did not find evidence that N limitation overcame C limitation during the formation of organic soils leading to greater microbial N retention. If widespread carbon limitation also characterizes present-day Arctic microbial communities, then increasing inputs of labile OM associated with shrub expansion could stimulate microbial respiration (Myers-Smith et al., 2011).

More $\delta^{15}\text{N}$ soil profiles spanning a wider range of Arctic environments, together with controlled laboratory experiments, are needed to determine whether the conceptual framework of Dijkstra et al. (2008) adequately captures nitrogen cycling during Arctic OM accumulation or requires refinement to account for the specificity of Arctic decomposition processes. Such studies would also help clarify how these long-term accumulation pathways influence the vulnerability of permafrost OM to decomposition following thaw.

4.2. Carbon

Our results corroborated H_C , supporting the idea of different C fractionation in mineral (low SOC level, negative slope with C/N, Figure 5) and organic (high SOC level, positive slope with C/N) Arctic soils. Different fractionation suggests that the decomposition process in mineral and organic soils leads to different soil OM chemical compositions and thus to different sensitivity to the environmental conditions occurring after thaw.

At low SOC, we observed an enrichment in ^{13}C during decomposition ($\alpha_C < 1$). This is coherent with the enrichment expected following the limited microbial CO_2 reassimilation (Šantrůčková et al., 2018). Indeed, the fixation of ^{13}C depleted atmospheric CO_2 is not sufficient to explain the observed patterns as no mineral units were sampled in the active layer (see Table 2 for different possible explanatory mechanisms). In addition, the fractionation of carbon during decomposition has been discarded as a potential mechanism by recent experimental tests (Breecker et al., 2015). Such enrichment in ^{13}C during decomposition in low SOC soils echoes recent patterns observed in the Arctic. A positive correlation between $\delta^{13}\text{C}$ and the degree of decomposition measured by the ratio of alkyl-C to O/N alkyl-C and the ratio of O alkyl-C to methoxyl C of lignin has been reported in the study of different soil physical fractionations in the Arctic (Gentsch, Mikutta, Shibistova, et al., 2015; Prater et al., 2020). This suggests that microbially derived OM stored in finer or denser soil fractions were enriched in ^{13}C relative to particulate OM. Similarly, Hugelius et al. (2012) showed that OM became enriched in ^{13}C while humic compounds were concentrated in older and deeper OM of mineral horizons. Hutchings et al. (2019) found permafrost OM with a greater microbial signature to be enriched in ^{13}C relative to OM made of a higher proportion of plant materials. Consequently, the enrichment in ^{13}C with decomposition implies that soil OM becomes increasingly dominated by microbial-derived carbon, potentially associated with mineral surfaces (Prater et al., 2020). This progressive microbial transformation is expected to influence the composition of permafrost OM and may therefore help explain differences in its subsequent vulnerability to decomposition following thaw.

At high SOC ($>30\%$), we observed a potential depletion in ^{13}C during decomposition in some units ($\alpha_C > 1$), but the effect was, on average, small and variable. Assuming that such high SOC accumulation came from low redox conditions, we expected preservation of ^{13}C depleted compounds to drive the isotopic signature of OM in high SOC soils (Benner et al., 1987). The uncertain fractionation at high SOC and the increase of the $\delta^{13}\text{C}$ -C/N slope with SOC suggest that preservation of ^{13}C depleted compounds takes place in high SOC soils, but that other mechanisms must be accounted for to explain the variation of $\delta^{13}\text{C}$ in organic Arctic soils. Support for the preservation of ^{13}C depleted compounds in high SOC soils was measured in the Arctic. Prater et al. (2020) showed $\delta^{13}\text{C}$ to be negatively correlated with the proportion of carbohydrates and positively correlated with the proportion of lignin, lipids, and protein in particulate OM. Hutchings et al. (2019) found the most ^{13}C depleted OM in horizons with well-preserved lignin, ^{13}C enriched OM taking place in horizons with a high lignin degradation index. Interestingly, the proportion of humic compounds was lower in deeper, older and ^{13}C depleted organic horizons in the study of Hugelius et al. (2012). This supports the idea that OM accumulates in Arctic organic soils by preservation of recalcitrant compounds rather than by humification, with a low concentration of microbially derived compounds (Pastukhov et al., 2018; Prater et al., 2020). If confirmed, this implies that carbon released following thaw may derive from substrates whose composition has been shaped more by long-term preservation than by microbial processing, a distinction that could influence subsequent decomposition dynamics.

4.3. Past and Future Decomposition

Overall, the contrasting carbon fractionation patterns observed in mineral and organic permafrost soils suggest that OM follows distinct accumulation pathways in these two soil types. Consequently, the composition of the OM exposed after thaw, and potentially its subsequent decomposition, may differ between mineral and organic permafrost soils. It has been shown that OM age was not a proxy of the decomposition stage in a variety of Arctic

soils (e.g., Hutchings et al., 2019; Schirrmeister et al., 2011; Strauss et al., 2015). The contrasting C fractionation patterns are consistent with the hypothesis that OM stored in mineral permafrost horizons accumulated through extensive microbial processing before being trapped by permafrost. In contrast, the absence of comparable fractionation in organic soils suggests that OM accumulation was dominated by the preservation of plant-derived material rather than extensive microbial recycling. If these contrasting accumulation pathways are confirmed, they suggest that mineral and organic permafrost soils may expose OM with different characteristics following thaw. Whether these differences translate into contrasting decomposition responses remains to be tested experimentally. Nevertheless, recalcitrant molecules such as bacterial products are thought to be more sensitive to an increase in temperature than less cycled plant materials, suggesting an important increase in OM mineralization while the temperature of mineral soils increases (von Lützow & Kögel-Knabner, 2009). On the other hand, mineralization of OM in organic soils may be especially increased by a reduction in soil water content, which will depend upon the uncertain future balance between evaporation and precipitation (Vihma et al., 2016) and the alteration of drainage following thermoerosion (Fortier et al., 2007; Perreault et al., 2016).

Even if our study revealed generalities about past Arctic soil formation, the response to climate change will depend upon multiple factors that natural stable isotope profiles cannot reveal. For example, there is increasing evidence that mineral protection occurs in the Arctic and may limit OM mineralization (Gentsch, Mikutta, Shibistova, et al., 2015, 2018). Moreover, microbial communities in permafrost may have a reduced enzymatic capacity to degrade newly thawed OM, thereby limiting initial decomposition following thaw (Monteux et al., 2020). Recently accessible molecular characterization techniques and biomarkers provide useful information about both the processes at play during OM accumulation and the potential response of OM to a change in condition (Mueller et al., 2015; Polyakov & Abakumov, 2020; Prater et al., 2020). All these aspects and tools need to be integrated with isotopic approaches to increase our understanding of Arctic OM sensitivity to climate change.

5. Conclusion

In this study, we proposed a theoretical framework describing C and N fractionation during the formation of Arctic soils. Hypotheses derived from this framework have been tested against a pan-Arctic data set of active layer and permafrost cores or profiles. Our results suggested similar N fractionation in mineral and organic soils. Based on the proposed theoretical framework, it suggests that microbial C limitation has been ubiquitous during the past formation of Arctic soils. This has important implications for the future decomposition of permafrost OM. Greater vegetation growth and active layer thaw are expected to provide labile C at greater depth, which may stimulate the decomposition of old materials previously stored in permafrost (Keuper et al., 2020; Pegoraro et al., 2019). Organic matter in mineral permafrost soils appears to have accumulated through extensive microbial processing, leading to the progressive incorporation of ^{13}C -enriched microbial-derived compounds. In contrast, organic permafrost soils appear to have accumulated primarily through the preferential preservation of relatively ^{13}C -depleted plant compounds under waterlogged, anoxic conditions. Within our conceptual framework, these contrasting patterns suggest that carbon limitation was expressed through different OM accumulation pathways depending on soil type: extensive microbial transformation in mineral soils versus selective preservation of plant-derived material in organic soils. By influencing the composition and degree of microbial transformation of OM prior to thaw, these pathways may contribute to contrasting decomposition responses under climate warming. Because Arctic climate change is expected to modify the seasonality of precipitation (Vihma et al., 2016) and alter soil hydrology following permafrost thaw, with responses varying from increased waterlogging to enhanced drainage depending on local conditions (Fortier et al., 2007; Perreault et al., 2016), the environmental conditions under which organic-rich permafrost accumulated may differ markedly from those prevailing after thaw. These shifts in hydrological conditions may therefore influence the decomposition trajectories of previously frozen OM and ultimately the fate of Arctic carbon stocks under climate change.

Conflict of Interest

The authors declare no conflicts of interest relevant to this study.

Availability Statement

The R, stan codes and data used to realize theoretical computations, fit models and draw figures are available in the *ArcticIsotopes* github repository archived in the Zenodo repository (Deschamps et al., 2025a). The data sets are in separate text files, combined and uniformized in a code available in the repository. In addition, the complete data set is archived separately in the Zenodo repository (Deschamps et al., 2025b). Both the software used in this study are open-source and publicly available: R (<https://cran.r-project.org/>) and stan (<https://mc-stan.org/>).

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References

- Abbott, B. W., & Jones, J. B. (2015). Permafrost collapse alters soil carbon stocks, respiration, CH₄, and N₂O in upland tundra. *Global Change Biology*, 21(12), 4570–4587. <https://doi.org/10.1111/gcb.13069>
- Acton, P., Fox, J., Campbell, E., Rowe, H., & Wilkinson, M. (2013). Carbon isotopes for estimating soil decomposition and physical mixing in well-drained forest soils. *Journal of Geophysical Research: Biogeosciences*, 118(4), 1532–1545. <https://doi.org/10.1002/2013JG002400>
- Alwell, C., Giesler, R., Klaminder, J., Leifeld, J., & Rollog, M. (2011). Stable carbon isotopes as indicators for environmental change in peatlands. *Biogeosciences*, 8(7), 1769–1778. <https://doi.org/10.5194/bg-8-1769-2011>
- Amundson, R., & Baisden, W. T. (2000). Stable isotope tracers and mathematical models in soil organic matter studies. *Methods in Ecosystem Science*, 1, 117–137. https://doi.org/10.1007/978-1-4612-1224-9_9
- Amundson, R., Stern, L., Baisden, T., & Wang, Y. (1998). The isotopic composition of soil and soil-respired CO₂. *Geoderma*, 82(1–3), 83–114. [https://doi.org/10.1016/S0016-7061\(97\)00098-0](https://doi.org/10.1016/S0016-7061(97)00098-0)
- Andersson, R. A., Meyers, P., Hornibrook, E., Kuhry, P., & Möhr, C.-M. (2012). Elemental and isotopic carbon and nitrogen records of organic matter accumulation in a Holocene permafrost peat sequence in the east European Russian arctic. *Journal of Quaternary Science*, 27(6), 545–552. <https://doi.org/10.1002/jqs.2541>
- Baisden, W. T., Amundson, R., Cook, A. C., & Brenner, D. L. (2002). Turnover and storage of C and N in five density fractions from California annual grassland surface soils. *Global Biogeochemical Cycles*, 16(4), 16–64. <https://doi.org/10.1029/2001gb001822>
- Benner, R., Fogel, M. L., Sprague, E. K., & Hodson, R. E. (1987). Depletion of C in lignin and its implications for stable carbon isotope studies. *Nature*, 329(6141), 708–710. <https://doi.org/10.1038/329708a0>
- Billings, W. D. (1987). Constraints to plant growth, reproduction, and establishment in Arctic environments. *Arctic and Alpine Research*, 19(4), 357–365. <https://doi.org/10.1080/00040851.1987.12002616>
- Blaser, M., & Conrad, R. (2016). Stable carbon isotope fractionation as tracer of carbon cycling in anoxic soil ecosystems. *Current Opinion in Biotechnology*, 41, 122–129. <https://doi.org/10.1016/j.copbio.2016.07.001>
- Bockheim, J. G. (2007). Importance of cryoturbation in redistributing organic carbon in permafrost-affected soils. *Soil Science Society of America Journal*, 71(4), 1335–1342. <https://doi.org/10.2136/sssaj2006.0414N>
- Bowling, D. R., Pataki, D. E., & Randerson, J. T. (2008). Carbon isotopes in terrestrial ecosystem pools and CO₂ fluxes. *New Phytologist*, 178(1), 24–40. <https://doi.org/10.1111/j.1469-8137.2007.02342.x>
- Boye, K., Noël, V., Tfaily, M. M., Bone, S. E., Williams, K. H., Bargar, J. R., & Fendorf, S. (2017). Thermodynamically controlled preservation of organic carbon in floodplains. *Nature Geoscience*, 10(6), 415–419. <https://doi.org/10.1038/ngeo2940>
- Breecker, D. O., Bergel, S., Nadel, M., Tremblay, M. M., Osuna-Orozco, R., Larson, T. E., & Sharp, Z. D. (2015). Minor stable carbon isotope fractionation between respired carbon dioxide and bulk soil organic matter during laboratory incubation of topsoil. *Biogeochemistry*, 123(1–2), 83–98. <https://doi.org/10.1007/s10533-014-0054-3>
- Camino-Serrano, M., Tifafi, M., Balesdent, J., Hatté, C., Peñuelas, J., Cornu, S., & Guenet, B. (2019). Including stable carbon isotopes to evaluate the dynamics of soil carbon in the land-surface model ORCHIDEE. *Journal of Advances in Modeling Earth Systems*, 11(11), 3650–3669. <https://doi.org/10.1029/2018MS001392>
- Canadell, J. G., Monteiro, P. M. S., Costa, M. H., Cotrim da Cunha, L., Cox, P. M., Eliseev, A. V., et al. (2021). Global carbon and other biogeochemical cycles and feedbacks. In V. Masson-Delmotte, P. Zhai, A. Pirani, S. L. Connors, C. Péan, S. Berger, et al. (Eds.), *Climate change 2021: The physical science basis. Contribution of Working Group I to the sixth assessment report of the intergovernmental Panel on climate change* (pp. 673–816). Cambridge University Press. <https://doi.org/10.1017/9781009157896.007>
- Chapin, D. M. (1996). Nitrogen mineralization, nitrification, and denitrification in a high arctic lowland ecosystem, Devon Island, N.W.T., Canada. *Arctic and Alpine Research*, 28(1), 85–92. <https://doi.org/10.1080/00040851.1996.12003151>
- Conrad, R. (2005). Quantification of methanogenic pathways using stable carbon isotopic signatures: A review and a proposal. *Organic Geochemistry*, 36(5), 739–752. <https://doi.org/10.1016/j.orggeochem.2004.09.006>
- Craine, J. M., Brookshire, E. N. J., Cramer, M. D., Hasselquist, N. J., Koba, K., Marin-Spiotta, E., & Wang, L. (2015). Ecological interpretations of nitrogen isotope ratios of terrestrial plants and soils. *Plant and Soil*, 396(1–2), 1–26. <https://doi.org/10.1007/s11104-015-2542-1>
- Davidson, E. A., & Janssens, I. A. (2006). Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. *Nature*, 440(7081), 165–173. <https://doi.org/10.1038/nature04514>
- Deschamps, L., Paillassa, J., Maire, V., & Lévesque, E. (2025a). Data and codes for the 'C and N isotopic fractionation along permafrost profiles across the Arctic: A data-reanalysis' paper (Version 1.0.0) [Datasets and codes]. <https://doi.org/10.5281/zenodo.15350471>
- Deschamps, L., Paillassa, J., Maire, V., & Lévesque, E. (2025b). Complete data for the 'C and N isotopic fractionation along permafrost profiles across the Arctic: A data-reanalysis' paper (Version 1.0.0) [Dataset]. <https://doi.org/10.5281/zenodo.15388260>
- Dijkstra, P., Laviolette, C. M., Coyle, J. S., Doucet, R. R., Schwartz, E., Hart, S. C., & Hungate, B. A. (2008). ¹⁵N enrichment as an integrator of the effects of C and N on microbial metabolism and ecosystem function. *Ecology Letters*, 11(4), 389–397. <https://doi.org/10.1111/j.1461-0248.2008.01154.x>
- Ehleringer, J. R., Buchmann, N., & Flanagan, L. B. (2000). Carbon isotope ratios in belowground carbon cycle processes. *Ecological Applications*, 10(2), 412–422. [https://doi.org/10.1890/1051-0761\(2000\)010\[0412:CIRIBC\]2.0.CO;2](https://doi.org/10.1890/1051-0761(2000)010[0412:CIRIBC]2.0.CO;2)
- Farquhar, G. D., Ehleringer, J. R., & Hubick, K. T. (1989). Carbon isotope discrimination and photosynthesis. *Annual Review of Plant Physiology and Plant Molecular Biology*, 40(1), 503–537. <https://doi.org/10.1146/annurev.pp.40.060189.002443>
- Fortier, D., Allard, M., & Pivrot, F. (2006). A late-holocene record of loess deposition in ice-wedge polygons reflecting wind activity and ground moisture conditions, Bylot Island, eastern Canadian Arctic. *The Holocene*, 16(5), 635–646. <https://doi.org/10.1191/0959683606hl960rp>
- Fortier, D., Allard, M., & Shur, Y. (2007). Observation of rapid drainage system development by thermal erosion of ice wedges on bylot Island, Canadian arctic Archipelago. *Permafrost and Periglacial Processes*, 18, 229–243. <https://doi.org/10.1002/ppp>

- Gabry, J., & Češnovar, R. (2022). Cmdstanr: R interface to "CmdStan". Retrieved from <https://mc-stan.org/cmdstanr/>
- Gentsch, N., Mikutta, R., Alves, R. J. E., Barta, J., Čapek, P., Gittel, A., et al. (2015). Storage and transformation of organic matter fractions in cryoturbated permafrost soils across the Siberian Arctic. *Biogeosciences*, 12(14), 4525–4542. <https://doi.org/10.5194/bg-12-4525-2015>
- Gentsch, N., Mikutta, R., Shibistova, O., Wild, B., Schneckner, J., Richter, A., et al. (2015). Properties and bioavailability of particulate and mineral-associated organic matter in Arctic permafrost soils, Lower Kolyma Region, Russia. *European Journal of Soil Science*, 66(4), 722–734. <https://doi.org/10.1111/ejss.12269>
- Gentsch, N., Wild, B., Mikutta, R., Čapek, P., Diáková, K., Schrumpp, M., et al. (2018). Temperature response of permafrost soil carbon is attenuated by mineral protection. *Global Change Biology*, 24(8), 3401–3415. <https://doi.org/10.1111/gcb.14316>
- Graven, H., Allison, C. E., Etheridge, D. M., Hammer, S., Keeling, R. F., Levin, I., et al. (2017). Compiled records of carbon isotopes in atmospheric CO₂ for historical simulations in CMIP6. *Geoscientific Model Development*, 10(12), 4405–4417. <https://doi.org/10.5194/gmd-10-4405-2017>
- Grosse, G., Harden, J., Turetsky, M., McGuire, A. D., Camill, P., Tarnocai, C., et al. (2011). Vulnerability of high-latitude soil organic carbon in North America to disturbance. *Journal of Geophysical Research*, 116(3), G00K06. <https://doi.org/10.1029/2010JG001507>
- Hicks Pries, C. E., Schuur, E. A. G., & Crummer, K. G. (2012). Holocene carbon stocks and carbon accumulation rates altered in soils undergoing permafrost thaw. *Ecosystems*, 15(1), 162–173. <https://doi.org/10.1007/s10021-011-9500-4>
- Hill, B. H., Elonen, C. M., Jicha, T. M., Kolka, R. K., Lehto, L. R. L. P., Sebestyen, S. D., & Seifert-Monson, L. R. (2014). Ecoenzymatic stoichiometry and microbial processing of organic matter in northern bogs and fens reveals a common P-limitation between peatland types. *Biogeochemistry*, 120(1–3), 203–224. <https://doi.org/10.1007/s10533-014-9991-0>
- Hobbie, E. A., & Ouimet, A. P. (2009). Controls of nitrogen isotope patterns in soil profiles. *Biogeochemistry*, 95(2), 355–371. <https://doi.org/10.1007/s10533-009-9328-6>
- Hobbie, J. E., Hobbie, E. A., Drossman, H., Conte, M., Weber, J. C., Shamhart, J., & Weinrobe, M. (2009). Mycorrhizal fungi supply nitrogen to host plants in Arctic tundra and boreal forests: ¹⁵N is the key signal. *Canadian Journal of Microbiology*, 55(1), 84–94. <https://doi.org/10.1139/W08-127>
- Hugelius, G., Routh, J., Kuhry, P., & Crill, P. (2012). Mapping the degree of decomposition and thaw remobilization potential of soil organic matter in discontinuous permafrost terrain. *Journal of Geophysical Research*, 117(2). <https://doi.org/10.1029/2011JG001873>
- Hugelius, G., Strauss, J., Zubrzycki, S., Harden, J. W., Schuur, E. A. G., Ping, C. L., et al. (2014). Estimated stocks of circumpolar permafrost carbon with quantified uncertainty ranges and identified data gaps. *Biogeosciences*, 11(23), 6573–6593. <https://doi.org/10.5194/bg-11-6573-2014>
- Hutchings, J. A., Bianchi, T. S., Kaufman, D. S., Kholodov, A. L., Vaughn, D. R., & Schuur, E. A. G. (2019). Millennial-scale carbon accumulation and molecular transformation in a permafrost core from Interior Alaska. *Geochimica et Cosmochimica Acta*, 253, 231–248. <https://doi.org/10.1016/j.gca.2019.03.028>
- Keuper, F., Wild, B., Kumm, M., Beer, C., Blume-Werry, G., Fontaine, S., et al. (2020). Carbon loss from northern circumpolar permafrost soils amplified by rhizosphere priming. *Nature Geoscience*, 13(8), 560–565. <https://doi.org/10.1038/s41561-020-0607-0>
- Koven, C. D., Lawrence, D. M., & Riley, W. J. (2015). Permafrost carbon–climate feedback is sensitive to deep soil carbon decomposability but not deep soil nitrogen dynamics. *Proceedings of the National Academy of Sciences*, 112(12), 3752–3757. <https://doi.org/10.1073/pnas.1415123112>
- Koven, C. D., Ringeval, B., Friedlingstein, P., Ciais, P., Cadule, P., Khvorostyanov, D., et al. (2011). Permafrost carbon-climate feedbacks accelerate global warming. *Proceedings of the National Academy of Sciences*, 108(36), 14769–14774. <https://doi.org/10.1073/pnas.1103910108>
- Krüger, J. P., Leifeld, J., & Alewell, C. (2014). Degradation changes stable carbon isotope depth profiles in peatlands. *Biogeosciences*, 11(12), 3369–3380. <https://doi.org/10.5194/bg-11-3369-2014>
- Lamarque, L. J., Félix-Faure, J., Deschamps, L., Lévesque, E., Cusson, P. O., Fortier, D., et al. (2023). Hydrological regime and plant functional traits jointly mediate the influence of Salix spp. on soil organic carbon stocks in a high Arctic tundra. *Ecosystems*, 26(6), 1238–1259. <https://doi.org/10.1007/s10021-023-00829-1>
- Lerch, T. Z., Nunan, N., Dignac, M.-F., Chenu, C., & Mariotti, A. (2011). Variations in microbial isotopic fractionation during soil organic matter decomposition. *Biogeochemistry*, 106(1), 5–21. <https://doi.org/10.1007/s10533-010-9432-7>
- Loisel, J., Garneau, M., & Hélie, J.-F. (2009). Modern Sphagnum δ¹³C signatures follow a surface moisture gradient in two boreal peat bogs, James Bay lowlands, Québec. *Journal of Quaternary Science*, 24(3), 209–214. <https://doi.org/10.1002/jqs>
- MacCoun, R., & Perlmutter, S. (2015). Blind analysis: Hide results to seek the truth. *Nature*, 526(7572), 187–189. <https://doi.org/10.1038/526187a>
- Margalef, O., Sardans, J., Fernández-Martínez, M., Molowny-Horas, R., Janssens, I. A., Ciais, P., et al. (2017). Global patterns of phosphatase activity in natural soils. *Scientific Reports*, 7(1), 1–13. <https://doi.org/10.1038/s41598-017-01418-8>
- Melillo, J. M., Aber, J. D., Linkins, A. E., Ricca, A., Fry, B., & Nadelhoffer, K. J. (1989). Carbon and nitrogen dynamics along the decay continuum: Plant litter to soil organic matter. *Plant and Soil*, 115(2), 189–198. <https://doi.org/10.1007/BF0202587>
- Miner, K. R., Turetsky, M. R., Malina, E., Bartsch, A., Tamminen, J., McGuire, A. D., et al. (2022). Permafrost carbon emissions in a changing Arctic. *Nature Reviews Earth & Environment*, 3(1), 55–67. <https://doi.org/10.1038/s43017-021-00230-3>
- Monteux, S., Keuper, F., Fontaine, S., Gavazov, K., Hallin, S., Juhanson, J., et al. (2020). Carbon and nitrogen cycling in Yedoma permafrost controlled by microbial functional limitations. *Nature Geoscience*, 13(12), 794–798. <https://doi.org/10.1038/s41561-020-00662-4>
- Moore, T., & Basiliko, N. (2006). Decomposition in boreal peatlands. In R. K. Wieder & D. H. Vitt (Eds.), *Boreal peatland ecosystems* (pp. 125–143). Springer Berlin Heidelberg. https://doi.org/10.1007/978-3-540-31913-9_7
- Moore, T. R., Paré, D., & Boutin, R. (2008). Production of dissolved organic carbon in Canadian forest soils. *Ecosystems*, 11(5), 740–751. <https://doi.org/10.1007/s10021-008-9156-x>
- Mooshammer, M., Wanek, W., Hämmerle, I., Fuchslueger, L., Hofhansl, F., Knoltsch, A., et al. (2014). Adjustment of microbial nitrogen use efficiency to carbon:nitrogen imbalances regulate soil nitrogen cycling. *Nature Communications*, 5, 1–7. <https://doi.org/10.1038/ncomms4694>
- Mueller, C. W., Rethemeyer, J., Kao-Kniffin, J., Löppmann, S., Hinkel, K. M., & Bockheim, J. G. (2015). Large amounts of labile organic carbon in permafrost soils of northern Alaska. *Global Change Biology*, 21(7), 2804–2817. <https://doi.org/10.1111/gcb.12876>
- Myers-Smith, I. H., Forbes, B. C., Wilking, M., Hallinger, M., Lantz, T., Blok, D., et al. (2011). Shrub expansion in tundra ecosystems: Dynamics, impacts and research priorities. *Environmental Research Letters*, 6(4), 045509. <https://doi.org/10.1088/1748-9326/6/4/045509>
- Nadelhoffer, K., Shaver, G., Fry, B., Giblin, A., Johnson, L., & McKane, R. (1996). ¹⁵N natural abundances and N use by tundra plants. *Oecologia*, 107(3), 386–394. <https://doi.org/10.1007/BF00328456>
- Nadelhoffer, K. J., & Fry, B. (1988). Controls on natural nitrogen-15 and carbon-13 abundances in forest soil organic matter. *Soil Science of America Journal*, 52(6), 1633–1640. <https://doi.org/10.2136/sssaj1988.03615995005200060024x>

- Nuzzo, R. (2015). How scientists fool themselves – And how they can stop. *Nature*, 526(7572), 182–185. <https://doi.org/10.1038/526182a>
- O'Brien, B. J., & Stout, J. D. (1978). Movement and turnover of soil organic matter as indicated by carbon isotope measurements. *Soil Biology and Biochemistry*, 10(4), 309–317. [https://doi.org/10.1016/0038-0717\(78\)90028-7](https://doi.org/10.1016/0038-0717(78)90028-7)
- Olefeldt, D., Turetsky, M. R., Crill, P. M., & McGuire, A. D. (2013). Environmental and physical controls on northern terrestrial methane emissions across permafrost zones. *Global Change Biology*, 19(2), 589–603. <https://doi.org/10.1111/gcb.12071>
- OpenAI. (2024). ChatGPT [large language model]. Retrieved from <https://chatgpt.com/>
- Parnas, H. (1975). Model for decomposition of organic material by microorganisms. *Soil Biology and Biochemistry*, 7(2), 161–169. [https://doi.org/10.1016/0038-0717\(75\)90014-0](https://doi.org/10.1016/0038-0717(75)90014-0)
- Parvin, S., Blagodatskaya, E., Becker, J. N., Kuzyakov, Y., Uddin, S., & Dorodnikov, M. (2018). Depth rather than microrelief controls microbial biomass and kinetics of C-N-P- and S-cycle enzymes in peatland. *Geoderma*, 324(March), 67–76. <https://doi.org/10.1016/j.geoderma.2018.03.006>
- Pastukhov, A., Knoblauch, C., Yakovleva, E. v., & Kaverin, D. A. (2018). Markers of soil organic matter transformation in Permafrost peat mounds of Northeastern Europe. *Eurasian Soil Science*, 51(1), 42–53. <https://doi.org/10.1134/S1064229318010131>
- Paul, E. A. (2016). The nature and dynamics of soil organic matter: Plant inputs, microbial transformations, and organic matter stabilization. *Soil Biology and Biochemistry*, 98, 109–126. <https://doi.org/10.1016/j.soilbio.2016.04.001>
- Pegoraro, E., Mauritz, M., Bracho, R., Ebert, C., Dijkstra, P., Hungate, B. A., et al. (2019). Glucose addition increases the magnitude and decreases the age of soil respired carbon in a long-term permafrost incubation study. *Soil Biology and Biochemistry*, 129, 201–211. <https://doi.org/10.1016/j.soilbio.2018.10.009>
- Perreault, N., Lévesque, E., Fortier, D., & Lamarque, L. J. (2016). Thermo-erosion gullies boost the transition from wet to mesic tundra vegetation. *Biogeosciences*, 13(4), 1237–1253. <https://doi.org/10.5194/bg-13-1237-2016>
- Ping, C. L., Jastrow, J. D., Jorgenson, M. T., Michaelson, G. J., & Shur, Y. L. (2015). Permafrost soils and carbon cycling. *SOIL*, 1(1), 147–171. <https://doi.org/10.5194/soil-1-147-2015>
- Polyakov, V., & Abakumov, E. v. (2020). Humic acids isolated from selected soils from the Russian arctic and antarctic: Characterization by two-dimensional ¹H-¹³C HETCOR and ¹³C CP/Mas NMR spectroscopy. *Geosciences*, 10(1), 15. <https://doi.org/10.3390/geosciences10010015>
- Prater, I., Zubrzycki, S., Buegger, F., Zoor-Füllgraff, L. C., Angst, G., Dannenmann, M., & Mueller, C. W. (2020). From fibrous plant residues to mineral-associated organic carbon - The fate of organic matter in Arctic permafrost soils. *Biogeosciences*, 17(13), 3367–3383. <https://doi.org/10.5194/bg-17-3367-2020>
- Price, G. D., McKenzie, J. E., Pilcher, J. R., & Hoper, S. T. (1997). Carbon-isotope variation in Sphagnum from hummock-hollow complexes: Implications for Holocene climate reconstruction. *The Holocene*, 7(2), 229–233. <https://doi.org/10.1177/095968369700700211>
- Ravn, N. M. R., Elberling, B., & Michelsen, A. (2017). The fate of ¹³C/¹⁵N labelled glycine in permafrost and surface soil at simulated thaw in mesocosms from high arctic and subarctic ecosystems. *Plant and Soil*, 419(1–2), 201–218. <https://doi.org/10.1007/s11104-017-3322-x>
- Ravn, N. R., Elberling, B., & Michelsen, A. (2020). Arctic soil carbon turnover controlled by experimental snow addition, summer warming and shrub removal. *Soil Biology and Biochemistry*, 142, 107698. <https://doi.org/10.1016/j.soilbio.2019.107698>
- R Core Team. (2022). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. Retrieved from <https://www.r-project.org/>
- Repo, M. E., Susiluoto, S., Lind, S. E., Jokinen, S., Elsakov, V., Biasi, C., et al. (2009). Large N₂O emissions from cryoturbated peat soil in tundra. *Nature Geoscience*, 2(3), 189–192. <https://doi.org/10.1038/ngeo434>
- Rohatgi, A. (2021). WebPlotDigitizer (4.5). Retrieved from <https://automeris.io/WebPlotDigitizer>
- Rubino, M., Etheridge, D. M., Trudinger, C. M., Allison, C. E., Battle, M. O., Langenfelds, R. L., et al. (2013). A revised 1000 year atmospheric $\delta^{13}\text{C}$ -CO₂ record from Law Dome and South Pole, Antarctica. *Journal of Geophysical Research: Atmospheres*, 118(15), 8482–8499. <https://doi.org/10.1002/jgrd.50668>
- Šantrůčková, H., Kotas, P., Bárta, J., Ulrich, T., Čapek, P., Palmtag, J., et al. (2018). Significance of dark CO₂ fixation in arctic soils. *Soil Biology and Biochemistry*, 119, 11–21. <https://doi.org/10.1016/j.soilbio.2017.12.021>
- Schirrmeyer, L., Bobrov, A., Raschke, E., Herzschuh, U., Strauss, J., Pestryakova, L. A., & Wetterich, S. (2018). Late Holocene ice-wedge polygon dynamics in northeastern Siberian coastal lowlands. *Arctic Antarctic and Alpine Research*, 50(1), e1462595. <https://doi.org/10.1080/15230430.2018.1462595>
- Schirrmeyer, L., Bobrov, A., Raschke, E., & Wetterich, S. (2018b). Sediment data from polygon core in the Siberian Arctic. *Alfred Wegener Institute - Research Unit Potsdam, PANGAEA*. <https://doi.org/10.1594/PANGAEA.887931>
- Schirrmeyer, L., Grosse, G., Wetterich, S., Overduin, P. P., Strauss, J., Schuur, E. A. G., & Hubberten, H.-W. (2011). Fossil organic matter characteristics in permafrost deposits of the northeast Siberian Arctic. *Journal of Geophysical Research*, 116(3), G00M02. <https://doi.org/10.1029/2011JG001647>
- Schneider Von Deimling, T., Grosse, G., Strauss, J., Schirrmeyer, L., Morgenstern, A., Schaphoff, S., et al. (2015). Observation-based modelling of permafrost carbon fluxes with accounting for deep carbon deposits and thermokarst activity. In *Biogeosciences*, (Vol. 12, Issue (11), pp. 3469–3488). Copernicus GmbH. <https://doi.org/10.5194/bg-12-3469-2015>
- Schuur, E. A. G., Vogel, J. G., Crummer, K. G., Lee, H., Sickman, J. O., & Osterkamp, T. E. (2009). The effect of permafrost thaw on old carbon release and net carbon exchange from tundra. *Nature*, 459(7246), 556–559. <https://doi.org/10.1038/nature08031>
- Simard, M., Lecomte, N., Bergeron, Y., Bernier, P. Y., & Paré, D. (2007). Forest productivity decline caused by successional paludification of boreal soils. *Ecological Applications*, 17(6), 1619–1637. <https://doi.org/10.1890/06-1795.1>
- Sinsabaugh, R. L., Manzoni, S., Moorhead, D. L., & Richter, A. (2013). Carbon use efficiency of microbial communities: Stoichiometry, methodology and modelling. In *Ecology Letters*, (Vol. 16, Issue (7), pp. 930–939). <https://doi.org/10.1111/ele.12113>
- Sjögersten, S., Caul, S., Daniell, T. J., Jurd, A. P. S., O'Sullivan, O. S., Stapleton, C. S., & Titman, J. J. (2016). Organic matter chemistry controls greenhouse gas emissions from permafrost peatlands. *Soil Biology and Biochemistry*, 98, 42–53. <https://doi.org/10.1016/j.soilbio.2016.03.016>
- Skrzypek, G., Kaluzny, A., Wojtuń, B., & Jedrysek, M. O. (2007). The carbon stable isotopic composition of mosses: A record of temperature variation. *Organic Geochemistry*, 38(10), 1770–1781. <https://doi.org/10.1016/j.orggeochem.2007.05.002>
- Skrzypek, G., Paul, D., & Wojtuń, B. (2008). Stable isotope composition of plants and peat from Arctic mire and geothermal area in Iceland. *Polish Polar Research*, 29(4), 365–376.
- Soetaert, K., & Herman, P. M. J. (2009). *A practical guide to ecological modelling using R as a simulation platform*. Springer. <https://doi.org/10.1111/j.1442-9993.2010.02180.x>
- Soetaert, K., Petzoldt, T., & Setzer, R. W. (2010). Solving differential equations in R: Package deSolve. In *Journal of Statistical Software*, (Vol. 33(Iss. 9)). <https://doi.org/10.18637/jss.v033.i09>
- Sorensen, P. L., Michelsen, A., & Jonasson, S. (2008a). Nitrogen uptake during one year in subarctic plant functional groups and in microbes after long-term warming and fertilization. *Ecosystems*, 11(8), 1223–1233. <https://doi.org/10.1007/s10021-008-9204-6>

- Sorensen, P. L., Michelsen, A., & Jonasson, S. (2008b). Ecosystem partitioning of ^{15}N -glycine after long-term climate and nutrient manipulations, plant clipping and addition of labile carbon in a subarctic heath tundra. *Soil Biology and Biochemistry*, 40(9), 2344–2350. <https://doi.org/10.1016/j.soilbio.2008.05.013>
- Stan Development Team. (2022). Stan modeling Language users guide and reference manual (Vol. 2). Retrieved from <https://mc-stan.org>.30.
- Stapel, J. G., Schirrmeister, L., Overduin, P. P., Wetterich, S., Strauss, J., Horsfield, B., & Mangelsdorf, K. (2016a). *Geochemistry of sediment core BK-8*. PANGAEA. <https://doi.org/10.1594/PANGAEA.867979>
- Stapel, J. G., Schirrmeister, L., Overduin, P. P., Wetterich, S., Strauss, J., Horsfield, B., & Mangelsdorf, K. (2016b). Microbial lipid signatures and substrate potential of organic matter in permafrost deposits: Implications for future greenhouse gas production. *Journal of Geophysical Research: Biogeosciences*, 121, 2652–2666. <https://doi.org/10.1002/2016JG003483>.Received
- Strauss, J., Schirrmeister, L., Mangelsdorf, K., Eichhorn, L., Wetterich, S., & Herzschuh, U. (2015). Organic matter quality of deep permafrost carbon - A study from Arctic Siberia. *Biogeosciences*, 11(11), 15945–15989. <https://doi.org/10.5194/bg-11-15945-2014-supplement>
- Sulzman, E. W. (2008). Stable isotope chemistry and measurement: A primer. In *Stable isotopes in ecology and environmental science* (2nd ed., pp. 1–21). <https://doi.org/10.1002/9780470691854.ch1>
- Tahmasebi, F., Longstaffe, F. J., & Zazula, G. (2018). Nitrogen isotopes suggest a change in nitrogen dynamics between the late pleistocene and modern time in Yukon, Canada. *PLoS One*, 13(2), e0192713. <https://doi.org/10.1371/journal.pone.0192713>
- Trumbore, S. (2000). Age of soil organic matter and soil respiration: Radiocarbon constraints on belowground C dynamics. *Ecological Applications*, 10(2), 399–411. [https://doi.org/10.1890/1051-0761\(2000\)010\[0399:AOSOMA\]2.0.CO;2](https://doi.org/10.1890/1051-0761(2000)010[0399:AOSOMA]2.0.CO;2)
- Vaughn, L. J. S., & Torn, M. S. (2019). 14C evidence that millennial and fast-cycling soil carbon are equally sensitive to warming. *Nature Climate Change*, 9(6), 467–471. <https://doi.org/10.1038/s41558-019-0468-y>
- Vihma, T., Screen, J., Tjernström, M., Newton, B., Zhang, X., Popova, V., et al. (2016). The atmospheric role in the Arctic water cycle: A review on processes, past and future changes, and their impacts. In *Journal of Geophysical Research: Biogeosciences* (Vol. 121, Issue (3), pp. 586–620). Blackwell Publishing Ltd. <https://doi.org/10.1002/2015JG003132>
- von Lützow, M., & Kögel-Knabner, I. (2009). Temperature sensitivity of soil organic matter decomposition-what do we know? *Biology and Fertility of Soils*, 46(1), 1–15. <https://doi.org/10.1007/s00374-009-0413-8>
- Werth, M., & Kuzyakov, Y. (2010). ^{13}C fractionation at the root-microorganisms-soil interface: A review and outlook for partitioning studies. *Soil Biology and Biochemistry*, 42(9), 1372–1384. <https://doi.org/10.1016/j.soilbio.2010.04.009>
- Wetterich, S., Kizyakov, A., Fritz, M., Wolter, J., Mollenhauer, G., Meyer, H., et al. (2020). The cryostratigraphy of the Yedoma cliff of Sobo-Sise Island (Lena delta) reveals permafrost dynamics in the central Laptev Sea coastal region during the last 52kyr. *The Cryosphere*, 14(12), 4525–4551. <https://doi.org/10.5194/tc-14-4525-2020>
- Wetterich, S., & Schirrmeister, L. (2017a). *Sediment data from the pingo exposure AWI_12P-1908-A*. PANGAEA. <https://doi.org/10.1594/PANGAEA.884357>
- Wetterich, S., & Schirrmeister, L. (2017b). *Sediment data from the pingo exposure AWI_12P-2008-A*. PANGAEA. <https://doi.org/10.1594/PANGAEA.884358>
- Wetterich, S., & Schirrmeister, L. (2017c). *Sediment data from the pingo exposure AWI_12P-2208-A*. PANGAEA. <https://doi.org/10.1594/PANGAEA.884359>
- Wetterich, S., Schirrmeister, L., Nazarova, L., Palagushkina, O., Bobrov, A., Pogossyan, L., et al. (2018). Holocene thermokarst and pingo development in the Kolyma Lowland (NE Siberia). *Permafrost and Periglacial Processes*, 29(3), 182–198. <https://doi.org/10.1002/ppp.1979>
- Wild, B., Alves, R. J. E., Bárta, J., Čapek, P., Gentsch, N., Guggenberger, G., et al. (2018). Amino acid production exceeds plant nitrogen demand in Siberian tundra. *Environmental Research Letters*, 13(3), 034002. <https://doi.org/10.1088/1748-9326/aaa4fa>
- Wild, B., Schnecker, J., Bárta, J., Čapek, P., Guggenberger, G., Hofhansl, F., et al. (2013). Nitrogen dynamics in Turbic Cryosols from Siberia and Greenland. *Soil Biology and Biochemistry*, 67, 85–93. <https://doi.org/10.1016/j.soilbio.2013.08.004>
- Windirsch, T., Grosse, G., Ulrich, M., Schirrmeister, L., Fedorov, A. N., Konstantinov, P., et al. (2019). *Carbon characteristics of permafrost core PG-YUK15-Alas1 from Yukechi Alas, Central Yakutia*. PANGAEA. <https://doi.org/10.1594/PANGAEA.898743>
- Windirsch, T., Grosse, G., Ulrich, M., Schirrmeister, L., Fedorov, A. N., Konstantinov, P. Y., et al. (2020). Organic carbon characteristics in ice-rich permafrost in alas and Yedoma deposits, central Yakutia, Siberia. *Biogeosciences*, 17(14), 3797–3814. <https://doi.org/10.5194/bg-17-3797-2020>
- Xu, C., Guo, L., Ping, C.-L., & White, D. M. (2009). Chemical and isotopic characterization of size-fractionated organic matter from cryoturbated tundra soils, northern Alaska. *Journal of Geophysical Research*, 114(3). <https://doi.org/10.1029/2008JG000846>
- Zhu, D., Peng, S., Ciais, P., Zech, R., Krinner, G., Zimov, S., & Grosse, G. (2016). Simulating soil organic carbon in yedoma deposits during the Last Glacial Maximum in a land surface model. *Geophysical Research Letters*, 43(10), 5133–5142. <https://doi.org/10.1002/2016GL068874>