

Ectomycorrhizal fungi as a reservoir of salmon-derived nitrogen in riparian forests

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Abstract

Pacific salmon deliver marine-derived nitrogen (MDN) to terrestrial ecosystems, subsidizing riparian soils, plants, and animals. Yet the role of soil fungi in incorporating and retaining this nutrient subsidy remains poorly understood. We investigated MDN incorporation into fungi, trees, and soils along three salmon streams in southwest Alaska, including Hansen Creek, the site of a 21-year salmon carcass manipulation. Sampling occurred two years after the manipulation ended, allowing us to examine persistent effects of long-term salmon inputs. We measured carbon and nitrogen concentrations and stable isotope ratios ($\delta^{15}\text{N}$, $\delta^{13}\text{C}$) across ecosystem pools and evaluated responses among ectomycorrhizal fungal (EMF) functional groups. MDN was detected in fungal sporocarps and tree foliage, with an estimated 28% of sporocarp N derived from salmon. Long-term carcass manipulation was also associated with elevated N concentrations in EMF sporocarps, indicating that salmon-derived N contributed measurably to fungal N nutrition. Responses were strongest among long- and medium-distance EMF exploration types. Together, these findings demonstrate that EMF incorporate and retain salmon-derived N and may represent an important biological reservoir and pathway for MDN in salmon-bearing riparian forests.

Introduction

The migration of anadromous fish such as Pacific salmon (*Oncorhynchus* spp.) from marine to freshwater environments transports a large nutrient pulse, which subsidizes freshwater and riparian ecosystems with marine-derived nitrogen (MDN; also commonly referred to as salmon-derived nitrogen) (Feddern et al. 2019, Gende et al. 2002, Larocque and Simard 2023, Quinn et al. 2018, Schindler et al. 2003). After salmon spawn and die, their carcasses are a significant food and nutrient source for numerous aquatic and terrestrial species, and therefore are associated with higher growth rates and population densities across taxa (Field and Reynolds 2013, Hilderbrand et al. 1999a, Minakawa et al. 2002, Schindler et al. 2013). Nutrients from salmon carcasses, most importantly nitrogen (N) and phosphorus (P), enter riparian forests from salmon streams in various ways, including transfer by predators and floods (Ben-David et al. 1998), excreta of predators and scavengers consuming carcasses (Hilderbrand et al. 1999b), and transfer of dissolved marine-derived nutrients from stream water through hyporheic flow and diffusion (O'Keefe and Edwards 2003). Nitrogen in salmon has a higher ratio of ^{15}N to ^{14}N compared to other N pools in freshwater and terrestrial ecosystems. Thus, salmon-derived N can be tracked quantitatively by measuring $^{15}\text{N}/^{14}\text{N}$ (expressed as $\delta^{15}\text{N}$) (Schindler et al. 2013). When salmon are abundant, MDN can contribute from 40–90% of the N in bears, fish and aquatic invertebrates (Hilderbrand et al. 1999b, Bilby et al. 1996, Chaloner et al. 2002, Claeson et al. 2006, Naiman et al. 2002). Further, MDN has been shown to increase primary and bacterial productivity by providing important limiting nutrients to aquatic plants and microbes (Moore et al. 2007).

Although the importance of MDN for animals, vegetation, and soils near and in salmon spawning streams is clear (Feddern et al. 2019, Quinn et al. 2018, Field and Reynolds 2013), the ecological significance of MDN for soil fungal processes and the capacity of fungi as an MDN sink in the soil

remains unexplored. In addition to the crucial role of saprotrophic and mycorrhizal fungi in organic matter decomposition, soil N and C cycling, and fungal-plant nutrient exchange, mycorrhizal fungi can also form interconnected networks with plants belowground (Rillig et al. 2025). In addition, some functional groups of ectomycorrhizal fungi (EMF), such as long-distance exploration types, have significant N retention capacity due to rhizomorphs and thick hyphal mats, which could allow them to retain MDN (Lilleskov et al. 2011). If mycorrhizal fungi are a sink for MDN, they can mediate the transfer of MDN to plants. If MDN provides an ecologically significant amount of N for fungal needs, it will further affect fungal-plant trading patterns. Furthermore, MDN could be transferred away from the stream to areas with lower N availability via fungal and plant root networks, as these networks typically are driven by source-sink dynamics (Walder and Van Der Heijden 2015). This nutrient flow would provide a subsidy to the surrounding forest beyond the salmon-bearing streams and rivers. Fungi could be sequestering MDN in hyphae, sporocarps, and their decomposition products, which would further affect the sequestration and cycling of MDN. Assessing the flow and significance of MDN in riparian systems requires estimating the ecological importance of MDN for fungal taxa and associated plants.

We examined the effects of a 21-year salmon carcass manipulation (legacy MDN) and current-season decomposing carcasses (recent MDN) on $\delta^{15}\text{N}$, $\delta^{13}\text{C}$, and nutrient concentrations in fungal sporocarps, foliage of the dominant tree species white spruce (*Picea glauca*) and paper birch (*Betula papyrifera*), and two soil horizons (O and A horizon), representing organic and mineral soils, in southwest Alaska. Importantly, sampling occurred two years after the manipulation ended, allowing us to test the persistence of legacy effects. We used stable isotopes to trace MDN and calculated %N and %C of fungi, plants, and soils to assess its potential ecological significance for these ecological components. Because MDN had previously been detected in bulk soil, soil ammonium, and white spruce foliage (Feddern et al. 2019, Quinn et al. 2018), we hypothesized that (H1) legacy and recent MDN would be detectable all across ecosystem components, particularly in N-tolerant or carcass-associated fungal taxa such as *Laccaria* and *Lactarius tabidus*. We further hypothesized that (H2) MDN would not alter N concentrations in these components, consistent with previous studies reporting no effect on white spruce, soil, or fungal C:N (Feddern et al. 2019, Quinn et al. 2018, Larocque 2022).

Materials and Methods

Description of site and salmon carcass manipulation – We conducted this study at Hansen Creek (59°19'18.2"N 158°42'04.2"W), Happy Creek (59°19'22.0"N 158°43'02.1"W), and Yako Creek (59°16'34.0"N 158°42'22.5"W), three sockeye salmon streams that flow into Lake Aleknagik within the Wood River System north of Bristol Bay in southwest Alaska. Salmon spawn throughout the 2-km length of Hansen Creek and primarily in the lower 3.2 km and 1.6 km of Happy and Yako Creeks, respectively. Hansen Creek was the site of a 21-year salmon carcass manipulation established by Quinn et al. (2018), in which researchers moved salmon carcasses from one side of the stream to the other each day during the annual run from 1997 to 2018 (see SI for details). Quinn et al. (2018) evaluated effects of this manipulation on white spruce foliar N, $\delta^{15}\text{N}$, and growth rates in 2016, and Feddern et al. (2019) quantified effects on soil N cycling in 2017. We sampled in 2020, two years after the manipulation ended,

to assess legacy effects on stable isotope ratios and N concentrations in fungi, plants, and soils. We also examined the effect of decomposing carcasses from the current (2020) salmon run on all ecological components.

Sample collection and processing – We established three pairs of opposing-bank transects at Hansen Creek and three unpaired transects each at Happy and Yako Creeks, for a total of 12 transects. Sampling points were located 1, 3, 6, 10, 20, 40, 60, and 100 m from the active channel and spanned lower, middle, and upper stream reaches with typical riparian vegetation and high annual carcass abundance. At each point, we collected soil at 10–15 and 25–30 cm depth; these depths typically intersected the upper B horizon (Bhs) and deeper organic horizons (Oe and Oa), respectively (United States Department of Agriculture 2022). At all points except 3 m, we surveyed an 80-m² area centered on the soil core for fungal sporocarps. We counted all sporocarps and collected one representative sporocarp from each clump, yielding 267 samples for further analysis (SI Methods). Sporocarps were sorted, photographed, dried, and sequenced, and 253 yielded species- or genus-level identifications. We collected foliage from plant species within a 2-m radius of each soil core (except at 3 m), including moss and herb, shrub, and tree layers. For white spruce and paper birch, we sampled 3–5 g wet mass of current-year foliage from the nearest tree of each species, using unshaded branch tips 1–2 m above ground where possible. Foliage samples were frozen at – 20°C before analysis. Plant tissue, fungal sporocarps, and soil were dried at 60°C for 48 h and ground to < 212 µm with a ball mill.

We measured ¹⁵N:¹⁴N and ¹³C:¹²C ratios at the Washington State University Stable Isotope Core Laboratory. Two isotopically distinct glutamic acid standards were used for normalization, and NIST 1547 peach leaf was used for quality control. Stable isotope ratios are reported as δ¹⁵N and δ¹³C in per mil (‰) relative to atmospheric N₂ and Vienna Pee Dee Belemnite, respectively, using $\delta = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000$, where R is the heavy-to-light isotope ratio. The analysis also yielded C and N concentrations (Schoeninger et al. 1983). Gravimetric soil water content (g H₂O/g dry soil) was determined by drying 50–100 g of field-moist soil at 105°C for 48 h (Gardner 1986). Funding constraints limited total P analyses to 14 white spruce, 12 paper birch, four fungal sporocarps (two *Lactarius* and two *Paxillus*), and three organic soil samples (SI Methods; Figure S1, Table S3). We extracted and sequenced fungal DNA using the Oxford Nanopore Technologies workflow described by Russell (2023) (SI Methods). Raw reads were base-called and demultiplexed, consensus sequences were generated, and curated sequences were compared with GenBank, BOLD, UNITE, and in-house databases. Raw FASTQ data are available through the Macrolepiota of North America MycoMap project (MycoMap 2023). We assigned EMF exploration types using FungalTraits, FUNGuild, DEEMY, and literature sources (Bahr 2013, Hobbie and Agerer 2010, Nguyen et al. 2016, Pölme et al. 2020). Groups included long-distance (*Paxillus*, *Xerocomus*), medium-distance fringe (*Cortinarius*, *Tricholoma*, *Hebeloma*), medium-distance smooth (*Lactarius*, *Laccaria*, *Naucoria*, *Entoloma*, *Amanita*), and short-distance (*Russula*, *Inocybe*) types (Table S2).

Statistical analysis – We fit linear mixed-effects models for δ¹⁵N, δ¹³C, and %N of fungal sporocarps, white spruce, paper birch, organic soil, and mineral soil across 1–100 m at all streams, for a total of 15

model sets (Tables 1–2, Table S6). Full candidate models included distance and two carcass indicators: the 21-year carcass manipulation and the presence of a recently decomposing carcass. Carcass manipulation was coded as present at the 1- and 6-m Hansen Creek sampling locations (where carcasses were thrown each year during the manipulation) and absent elsewhere. A recent carcass was coded as present when a salmon carcass from the 2020 salmon run occurred < 2 m from a sampling location, following Drake et al. (2005), and absent otherwise. Fungal models additionally included trophic status and a random intercept for genus; all models included a random intercept for transect nested within stream. Response-specific predictors are listed in the SI. We selected best-fitting models using Akaike's Information Criterion corrected for small sample size (AICc) with the lmer function in R and also evaluated a predefined set of candidate models; both approaches gave similar results. We used variance inflation factors (VIFs) to assess collinearity, with $VIF > 3$ treated as evidence of high correlation among predictors (Everitt and Skrondal 2010).

To estimate the %MDN contribution to fungal N, we adjusted the standard two-source isotope mixing model for isotopic enrichment due to biogeochemical transformations that occur prior to fungal uptake, and for isotopic fractionation due to fungal–plant N transfer (Fig. 1). Two-source mixing models are typically used to estimate the %MDN contribution to vegetation and soil, where $\%MDN = ((SAM - TEM)/(MEM - TEM)) * 100$ (Kline et al. 1990, Bilby et al. 1996). In this model, %MDN is the percent of MDN in a sample, SAM is the $\delta^{15}N$ of the sample, TEM is the terrestrial end member ($\delta^{15}N$ value with 0% MDN), and MEM is the marine end member ($\delta^{15}N$ value with 100% MDN). However, these models do not account for biogeochemical transformations prior to fungal and plant uptake, and fungal-plant nutrient exchange. In order to account for these changes, we first found that biogeochemical transformations of salmon-derived N from the salmon carcass to the soil ammonium pool (from which fungi and plants likely draw their N) was 6.6‰ using Feddern et al. 2019 (Table S5), which corresponds to $\Delta_{decomposition}$. We then used the approach of Hobbie and Hobbie (2006) to estimate that fungi transfer 20% of their N to plant hosts (Table S4; SI Methods). With a 9‰ discrimination factor, this transfer corresponds to 1.8‰ enrichment of N retained by fungi, which corresponds to Δ_{trade} . We incorporated these corrections into the mixing model used to estimate the % fungal N derived from salmon (Fig. 1).

Results

Environmental drivers of $\delta^{15}N$ and %N in soil, fungi, and vegetation – The carcass manipulation increased fungal $\delta^{15}N$, while recent decomposing carcasses had a marginal positive effect ($P = 0.062$; Fig. 2, Table 1). Saprotrophic fungi had significantly lower $\delta^{15}N$ than mycorrhizal fungi (Table 1). Foliar $\delta^{15}N$ of both white spruce and paper birch also increased with the carcass manipulation, whereas organic and mineral soil $\delta^{15}N$ did not show legacy effects of MDN. Organic soil $\delta^{15}N$ did, however, increase near recently decomposing carcasses. Fungal sporocarp %N was higher on the salmon-enhanced bank in the unadjusted comparison (Wilcoxon rank-sum $P = 0.032$; Fig. 2) and showed a significant positive association with carcass manipulation in the mixed model ($P = 0.047$; Table 2). Saprotrophic fungi had

significantly higher %N than mycorrhizal fungi (Table 2). The updated isotope mixing model estimated that 28% of fungal sporocarp N was derived from salmon.

Table 1. Top linear mixed-effects models for fungal, white spruce, paper birch, organic soil, and mineral soil $\delta^{15}\text{N}$ across 1–100 m along three salmon streams in southwest Alaska. Models report conditional R^2 , coefficient estimates $\pm$ SE, P values, and VIFs. All models included a random intercept for transect nested within stream; the fungal model also included a random intercept for genus. GWC is gravimetric water content (g H_2O /g dry soil). For trophic status, the intercept represents the mycorrhizal mean and coefficients give differences relative to mycorrhizal fungi; the negative saprotroph coefficient indicates lower $\delta^{15}\text{N}$ in saprotrophs. NA, not applicable.

Response variable	Conditional R^2	Covariates	Value $\pm$ SE	P-value	VIF
Fungi $\delta^{15}\text{N}$ (n = 265)	0.83	Intercept	9.89 $\pm$ 1.57	< 0.001	NA
		Carcass manipulation	2.98 $\pm$ 0.83	< 0.001	1.75
		Decomposing carcass	1.12 $\pm$ 0.60	0.062	1.59
		$\text{Log}_e(\text{distance})$	-0.93 $\pm$ 0.17	< 0.001	2.18
		Organic soil GWC	0.38 $\pm$ 0.15	0.014	1.71
		Organic soil $\delta^{15}\text{N}$	0.49 $\pm$ 0.11	< 0.001	2.14
		Trophic status: saprotroph	-4.47 $\pm$ 0.97	< 0.001	1.04
		Trophic status: unknown	-3.30 $\pm$ 2.28	0.160	1.03
White spruce $\delta^{15}\text{N}$ (n = 74)	0.88	Mineral soil C:N	-0.10 $\pm$ 0.04	0.013	1.51
		Intercept	-0.60 $\pm$ 1.03	0.561	NA
		Carcass manipulation	3.00 $\pm$ 0.67	< 0.001	1.65
		$\text{Log}_e(\text{distance})$	-0.84 $\pm$ 0.14	< 0.001	2.02
		Organic soil GWC	0.28 $\pm$ 0.13	0.034	1.43
		Organic soil $\delta^{15}\text{N}$	0.47 $\pm$ 0.11	< 0.001	3.38
		Mineral soil $\delta^{15}\text{N}$	0.20 $\pm$ 0.12	0.104	2.05
Paper birch $\delta^{15}\text{N}$ (n = 69)	0.84	Mean fungal $\delta^{15}\text{N}$	0.07 $\pm$ 0.05	0.154	1.84
		Intercept	-2.21 $\pm$ 1.13	0.057	NA
		Carcass manipulation	2.55 $\pm$ 0.89	0.006	1.57
		$\text{Log}_e(\text{distance})$	-0.57 $\pm$ 0.17	0.001	2.00
		Mean mycorrhizal fungal $\delta^{15}\text{N}$	0.18 $\pm$ 0.05	0.002	1.60
		Organic soil GWC	0.56 $\pm$ 0.14	< 0.001	1.57
Organic soil $\delta^{15}\text{N}$ (n = 97)	0.66	Organic soil $\delta^{15}\text{N}$	0.47 $\pm$ 0.10	< 0.001	2.10
		Intercept	7.68 $\pm$ 0.78	< 0.001	NA
		Carcass manipulation	1.39 $\pm$ 0.82	0.093	1.28
		Decomposing carcass	-1.27 $\pm$ 0.60	0.036	1.32
		Organic soil GWC	-0.33 $\pm$ 0.13	0.015	1.21
Mineral soil $\delta^{15}\text{N}$ (n = 96)	0.61	$\text{Log}_e(\text{distance})$	-0.83 $\pm$ 0.14	< 0.001	1.35
		Intercept	6.39 $\pm$ 0.60	< 0.001	NA
		$\text{Log}_e(\text{distance})$	-0.31 $\pm$ 0.10	0.003	NA

Table 2. Top models for fungal, white spruce, paper birch, organic soil, and mineral soil %N across 1–100 m from both banks of Hansen Creek, Alaska. Models report conditional R^2 , coefficient estimates $\pm$ SE, P values, and VIFs. All models included a random intercept for transect nested within stream; the fungal model also included a random intercept for genus. GWC is gravimetric water content (g H_2O /g dry soil). For trophic status, the intercept represents the mycorrhizal mean and coefficients give differences relative to mycorrhizal fungi; the positive saprotroph coefficient indicates higher %N in saprotrophs. NA, not applicable.

Response variable	Conditional R ²	Covariates	Value ± SE	P-value	VIF
Fungi %N (n = 216)	0.79	Intercept	4.71 ± 0.34	< 0.001	NA
		Carcass manipulation	0.45 ± 0.28	0.047	1.02
		Trophic status: saprotroph	1.84 ± 0.41	< 0.001	1.02
		Trophic status: unknown	1.18 ± 1.22	0.348	1.03
White spruce %N (n = 73)	0.53	Intercept	1.17 ± 0.11	0.011	NA
Paper birch %N (n = 67)	0.53	Intercept	2.82 ± 0.24	< 0.001	NA
		Log _e (distance)	-0.06 ± 0.02	0.025	1.00
		Mean mycorrhizal fungal %N	-0.09 ± 0.05	0.043	1.00
Organic soil %N (n = 97)	0.63	Intercept	1.19 ± 0.13	< 0.001	NA
		Organic soil GWC	0.17 ± 0.03	< 0.001	1.00
		Log _e (distance)	-0.08 ± 0.03	0.004	1.00
Mineral soil %N (n = 96)	0.55	Intercept	0.96 ± 0.13	< 0.001	NA
		Carcass manipulation	0.34 ± 0.20	0.099	1.10
		Decomposing carcass	-0.28 ± 0.15	0.070	1.34
		Log _e (distance)	-0.11 ± 0.04	0.003	1.37

Fungal sporocarps by genus, trophic status, and functional group – We observed 828 fungal sporocarps and collected 267. Of the 267 sequenced fungal sporocarps, we identified 84% to species and 11% to genus. We identified a total of 32 genera and 74 species of fungi, including 17 previously unidentified species (Table 3, Table S1). Of the identified sporocarps, 83% were ectomycorrhizal and 17% were saprotrophic (Table 3). Saprotrophic fungi were not found < 10 m from either bank, except for one *Stropharia pseudocyanea*, whereas mycorrhizal fungi were abundant across all distances from the stream bank (Figure S2). The most common genera included *Lactarius* (66), *Cortinarius* (33), *Paxillus* (32), and *Russula* (30) (Table 3). Five species constituted ~ 50% of all collected sporocarps: *Lactarius tabidus* (59), *Paxillus involutus* (26), *Hebeloma leucosarx* (13), *Russula betularum* (11), and *Laccaria sp-AK01* (9) – *Cortinarius* and *Russula* had the highest species diversity (14 and 9 species, respectively; Table 3).

Table 3

Trophic status, exploration type (for mycorrhizal fungi), count, mean $\delta^{15}\text{N}$ and standard deviation (SD), and mean $\delta^{13}\text{C}$ and SD for fungal taxa collected along three salmon streams in southwest Alaska. Taxa are ordered by increasing mean $\delta^{15}\text{N}$. Higher-level taxonomic entries are included where genus-level identification was unavailable. DNA sequencing was unsuccessful for eight samples.

Genus	Trophic status	Exploration type	Count	$\delta^{15}\text{N}$ (‰ vs. air)	$\delta^{15}\text{N}$ SD (‰ vs. air)	$\delta^{13}\text{C}$ (‰ vs. VPDB)	$\delta^{13}\text{C}$ SD (‰ vs. VPDB)
<i>Tubaria</i>	saprotroph		1	-0.7	0.0	-22.1	0.0
<i>Cystoderma</i>	saprotroph		1	-0.1	0.0	-25.8	0.0
<i>Psathyrella</i>	saprotroph		8	0.6	3.5	-25.9	1.1
<i>Clitocybe</i>	saprotroph		1	1.0	0.0	-24.8	0.0
<i>Hypholoma</i>	saprotroph		6	2.3	1.5	-24.5	0.9
<i>Ampulloclitocybe</i>	saprotroph		9	2.4	1.4	-25.7	0.8
<i>Gymnopilus</i>	saprotroph		1	2.7	0.0	-26.1	0.0
<i>Psilocybe</i>	saprotroph		1	3.0	0.0	-25.2	0.0
Family Lycoperdaceae	saprotroph		1	3.2	0.0	-25.9	0.0
<i>Pholiota</i>	saprotroph		2	3.3	3.9	-22.6	1.1
<i>Pluteus</i>	saprotroph		1	3.6	0.0	-23.7	0.0
<i>Rhodocollybia</i>	saprotroph		1	3.9	0.0	-24.9	0.9
<i>Protostropharia</i>	saprotroph		1	4.3	0.0	-26.8	0.0
<i>Stropharia</i>	saprotroph		4	4.7	6.0	-24.2	2.2
<i>Apioperdon</i>	saprotroph		1	4.8	0.0	-22.2	0.0
<i>Russula</i>	mycorrhizal	short	29	4.9	3.1	-26.5	1.3
<i>Pseudoclitocybe</i>	saprotroph		1	5.1	0.0	-27.0	0.0
<i>Laccaria</i>	mycorrhizal	short/medium smooth	13	5.3	4.1	-25.5	0.7
<i>Zhuliangomyces</i>	saprotroph		1	5.3	0.0	-26.5	0.0
<i>Entoloma cetratum/turbidum</i>	saprotroph		3	5.4	4.5	-25.2	0.7
<i>Cystodermella</i>	saprotroph		1	6.1	0.0	-25.5	0.0

Genus	Trophic status	Exploration type	Count	$\delta^{15}\text{N}$ (‰ vs. air)	$\delta^{15}\text{N}$ SD (‰ vs. air)	$\delta^{13}\text{C}$ (‰ vs. VPDB)	$\delta^{13}\text{C}$ SD (‰ vs. VPDB)
<i>Lactarius</i>	mycorrhizal	medium smooth	67	6.8	3.2	-26.3	0.9
<i>Lyophyllaceae</i>	unknown		1	6.8	0.0	-25.5	0.0
<i>Amanita</i>	mycorrhizal	short/medium smooth	1	7.1	0.0	-25.7	0.0
<i>Entoloma sericatum</i>	mycorrhizal	medium smooth	5	7.4	2.0	-25.3	1.3
<i>Melanoleuca</i>	saprotroph		1	7.9	0.0	-25.7	0.0
Genera not identified			8	8.5	6.3	-26.1	0.9
Order Boletales	mycorrhizal	long	5	9.0	0.9	-26.2	0.9
<i>Inocybe</i>	mycorrhizal	short	2	9.4	4.2	-26.9	1.3
<i>Naucoria</i>	mycorrhizal	short/medium smooth	3	9.4	8.5	-26.9	1.4
<i>Cortinarius</i>	mycorrhizal	medium fringe	34	9.5	2.7	-26.1	1.0
<i>Hebeloma</i>	mycorrhizal	medium fringe	16	9.8	3.7	-26.4	0.9
<i>Paxillus</i>	mycorrhizal	long	32	10.7	4.3	-26.0	0.8
<i>Limacella</i>	unknown		1	11.8	0.0	-27.3	0.0
<i>Xerocomus</i>	mycorrhizal	long	2	11.9	8.5	-25.2	0.4
<i>Tricholoma</i>	mycorrhizal	medium fringe	2	12.7	0.8	-25.6	1.0

Long-term carcass manipulation significantly increased $\delta^{15}\text{N}$ in long- and medium-distance smooth types, while recently decomposing carcasses significantly increased $\delta^{15}\text{N}$ in medium-distance fringe types (Table S2). Saprotrophic fungi had significantly lower $\delta^{15}\text{N}$ (3.4 ± 2.3 , $n = 45$) than mycorrhizal fungi (saprotroph $\delta^{15}\text{N} = 3.4 \pm 2.3$, $n = 45$, mycorrhizal $\delta^{15}\text{N} = 8.9 \pm 3.1$, $n = 222$; Table 1, Table 3, Fig. 3). *Xerocomus* had the highest mean $\delta^{15}\text{N}$ of 17.9‰, followed by *Tricholoma* at 12.7‰ and *Paxillus* at 10.7‰ (Table 3, Figure S2). Genera with the lowest mean $\delta^{15}\text{N}$ were *Tubaria* at -0.7‰ and *Cystoderma* at -0.1‰ (Table 3, Figure S2). Mean $\delta^{15}\text{N}$ for all genera are listed in Table 3. *Entoloma* species were divided into saprotrophic (*Entoloma certratum*, *Entoloma turbidum*) and mycorrhizal (*Entoloma sericatum*) species (Table 3, Table S1).

Discussion

MDN is present in fungi, soil, and plants – We predicted that MDN would be present in fungi, plants, and soil (H1). The carcass manipulation increased $\delta^{15}\text{N}$ in fungal sporocarps, as well as the foliage of white spruce and paper birch, demonstrating a persistent legacy of MDN two years after the end of the manipulation (Fig. 1, Table 1). MDN from the carcass manipulation was previously detected in white spruce in 2016 (Quinn et al. 2018), and our study shows that salmon-transported MDN was also present in ectomycorrhizal fungal sporocarps, indicating that EMF immobilized MDN from salmon carcasses. We also found that EMF incorporated MDN from recent decomposing salmon carcasses in the current season (within ~ 1 – 2 months), which suggests that EMF can take up MDN quickly from freshly decomposing salmon carcasses and also immobilize MDN from long-term salmon carcass deposition events, likely from soil N pools enriched with MDN (Feddern et al. 2019). Our results are supported by the only other study examining the effects of MDN on fungi, which showed increased fungal sporocarp $\delta^{15}\text{N}$ along a salmon density gradient across 16 streams (Larocque 2022). It is not surprising that EMF incorporate MDN. The primary source of N and P in most boreal forests is organic litter, which decomposes and releases nutrients relatively slowly (Chapin et al. 2011). Salmon tissues are nutrient-rich and are quickly broken down by decomposers, with skeletonization occurring within 6–10 weeks (Drake et al. 2005, Drake et al. 2006). Salmon carcass decomposition is a spatially localized and temporally limited N pulse, in which inorganic N (ammonium and nitrate) typically increases within a few meters around carcasses for up to 5 months (Drake et al. 2005). EMF are efficient nutrient scavengers and would readily take advantage of the available N in their vicinity. EMF likely immobilize MDN from both the inorganic and organic soil N pools and utilize these nutrients to support maintenance, growth, sporocarp production, and N transfer to plant hosts in exchange for C. Although we did not formally evaluate MDN transfer away from the stream bank through fungal or plant root networks, our results indicate that the $\delta^{15}\text{N}$ signal can be detected as far as 20 m from the stream bank, suggestive of transport away from the stream. There was no significant legacy effect in bulk organic or mineral soil, likely due to the fact that bulk soil and biological tissues integrate N over very different pools and timescales. Bulk soil contains a large amount of organic N, much of which is relatively unavailable to plants and fungi. A relatively small amount of MDN entering that large pool can therefore become diluted enough that the difference between the carcass-enhanced and depleted banks is difficult to detect. Meanwhile, fungi and plants acquire N disproportionately from the small, biologically available fraction of soil N, particularly ammonium and other labile compounds, so they can retain a much stronger MDN signal than the bulk soil from which those compounds ultimately originate.

MDN increases fungal, but not soil or plant, N concentrations – We predicted that MDN would not affect N concentrations in soil, plants, or fungi (H2) due to previous studies showing that MDN did not significantly alter C:N ratios of fungal sporocarps, white spruce, or bulk soil (Feddern et al. 2019, Quinn et al. 2018, Larocque 2022). Although MDN did not increase N concentrations in soils or plant foliage (Fig. 2, Table 2), %N of EMF sporocarps was significantly higher on the salmon-enhanced bank than on the salmon-depleted bank (Fig. 2, Table 2). This indicates, contrary to our second hypothesis, that long-

term MDN inputs increased the N concentration of fungal tissue, with up to 28% of sporocarp N attributed to salmon-derived N, a substantial fraction of fungal N. Together, these findings provide evidence that EMF actively incorporate MDN and that salmon-derived N represents a biologically meaningful component of fungal N nutrition, rather than simply leaving an isotopic signature in fungal tissue. The persistence of an MDN signal in fungal sporocarps two years after the carcass manipulation ended further indicates that long-term salmon inputs can have lasting effects on the fungal N pool. The %N of EMF did not vary with short-term MDN from nearby decomposing carcasses, suggesting that detectable changes in fungal tissue N concentration may require sustained or repeated nutrient inputs rather than a single recent pulse. Although the carcass manipulation artificially increased carcass input to one bank of Hansen Creek, meaning that the fungal response may not represent the contemporary response to MDN input throughout this system, it may more closely approximate fungal responses under historically greater salmon returns, prior to commercial fishing operations that harvest 60–75% of the sockeye salmon run in this system each season and thereby considerably reduce the abundance of sockeye salmon returning to Hansen Creek (Alaska Department of Fish and Wildlife 2022).

Given the openness of the N cycle, substantial N can be lost through volatilization, leaching, and denitrification under high inputs (Feddern et al. 2019). Fungi may intercept part of this MDN before it is lost from soil. Most EMF in our study were medium- or long-distance exploration types, many of which form rhizomorphs and extensive hyphal mats associated with N retention and high standing mycelial biomass (Bahr 2013, Ekblad et al. 2013). Bahr (2013) estimated that newly produced EMF mycelium could assimilate $6 \text{ kg N ha}^{-1} \text{ month}^{-1}$, illustrating the potentially substantial capacity of belowground EMF biomass to immobilize available N. Because we measured sporocarps rather than belowground mycelium, we cannot directly estimate the total MDN stock in EMF at Hansen Creek. Published estimates place EM mycelial N stocks at $121\text{--}187 \text{ kg N ha}^{-1}$ in spruce and spruce–oak forests (Wallander et al. 2004), equivalent to an illustrative $\sim 34\text{--}52 \text{ kg MDN ha}^{-1}$ if the 28% MDN fraction observed in sporocarps were representative of mycelial N; site-specific mycelial biomass and isotope measurements are needed to constrain this budget.

In the only other study to examine the effects of MDN on fungi, fungal C:N did not change across a salmon density gradient in 16 salmon streams (Larocque 2022), in contrast to our results. However, high biogeochemical variability among streams may make it challenging to capture the response of fungal C:N to increasing salmon density, whereas a finer-scale, within-stream comparison using a controlled carcass manipulation may be better able to detect such a response. Furthermore, other N-addition studies have shown increases in fungal %N with N addition (Hobbie et al. 2019). The ecological significance of MDN in riparian systems has been debated for several decades, and results have been mixed (Walsh et al. 2020). However, our study demonstrated that long-term salmon inputs increased N content per unit sporocarp biomass and altered fungal tissue stoichiometry. We accounted for multiple soil biogeochemical and other variables when evaluating the effect of the carcass manipulation on fungal %N. In previous studies, stem density, basal area density, and overstory species composition did not differ significantly with carcass manipulation at Hansen Creek from 1–6 m (Quinn et al. 2018). Therefore, we conclude that the increase in fungal %N was primarily associated with the carcass

manipulation. Together with the substantial proportion of sporocarp N attributed to MDN and the persistence of the isotopic signal two years after the manipulation ended, this result indicates that salmon-derived N can make a biologically meaningful contribution to fungal N nutrition and that EMF may represent an important reservoir of MDN in riparian forests.

Fungal MDN use varied by functional type – We further examined the effects of MDN by functional exploration type and found that long-term carcass manipulation significantly increased $\delta^{15}\text{N}$ in long- and medium-distance smooth types, while recently decomposing carcasses significantly increased $\delta^{15}\text{N}$ in medium-distance fringe types (Table S2). Long- and medium-distance EMF have long-distance transport structures called rhizomorphs and extensive extraradical hyphae that allow them to maintain a large network structure, forage over large distances, and exploit nutrient patches (Lilleskov et al. 2011 Moeller et al. 2014). Many species can break down organic N and increase available nutrient pools (Lilleskov et al. 2024, Northrup et al. 1995). These fungi incur a high C cost for plant hosts and are competitively dominant in low-nutrient (N or P) environments, where resources are rare or patchy (Moeller et al. 2014). Short-distance EMF forage over much smaller areas, have more fluid and adaptive hyphae, and a lower C cost for plant hosts relative to long and medium distance types (Moeller et al. 2014). These fungi tend to dominate in nutrient-rich environments (Lilleskov et al. 2011).

It is possible that only long- and medium-distance foragers absorbed MDN because of their capacity to maintain extensive networks, mine nutrient hotspots, forage over large distances, and access organic N (Lilleskov et al. 2024), all of which would be beneficial for plants to gain access to nutrients from carcasses more efficiently. These EMF have fungal rhizomorphs that allow for distributing and mining nutrients in spatially heterogeneous and patchy nutrient environments, and thus could be competitively superior in areas of high soil nutrient levels since these fungi could obtain patchily-distributed nutrients for plant hosts efficiently (Larocque 2022). Fungal-plant trading increases when nutrient patches are unevenly distributed, as fungal hyphae have higher search efficiency and lower metabolic maintenance costs than plant roots, leading to higher plant C allocation to fungal partners (Bending and Read 1995, Peay et al. 2011). Long-distance and some medium-distance exploration types also generally have higher proteolytic capacity to decompose complex organic compounds and access organic N (Lilleskov et al. 2024, Vaario et al. 2019), thus giving this functional group an advantage at the site of carcass manipulation. In addition, these fungal types have high N retention due to their capacity to form rhizomorphs that can store and retain N and prevent leaching (Bahr 2013). These traits allow these exploration types to have high-standing mycelial biomass in boreal forests and indicate that these fungal functional groups could retain, utilize, and trade MDN with plant hosts for a substantial amount of time, from months to years, after initial absorption within this system. In contrast, it is likely that short-distance foragers turn over too quickly for long-term N retention (Ekblad et al. 2013).

Incorporating fungal–plant trading when estimating MDN contributions – Two-source mixing models (Kline et al. 1990, Bilby et al. 1996) are typically used to estimate the %MDN contribution to vegetation and soil. However, this model assumes that the $\delta^{15}\text{N}$ of MDN is not altered between carcass decomposition and absorption by plants or fungi, and that reference sites have similar biogeochemical

properties to sites with salmon. Both assumptions are false at Hansen Creek, and likely other riparian systems as well (Feddern et al. 2019). Many factors affect the $\delta^{15}\text{N}$ of soil, fungi, and plants (Table 1), and the $\delta^{15}\text{N}$ of these components can decrease dramatically with distance from the stream edge (Fig. 2), indicating that selecting a site outside the reach of salmon would not only violate the assumption that sites are biogeochemically similar, but would also lead to over-estimation of the %MDN contribution.

Salmon N undergoes transformations that increase the $\delta^{15}\text{N}$ of salmon-derived N in the soil ammonium pool, the likely pool used by plants, suggesting an overestimation of the % MDN contribution to plants in studies that use the two-source mixing model (Feddern et al. 2019). However, there is an additional N transformation step that occurs before MDN reaches plants. White spruce and paper birch form strong partnerships with EMF in boreal forests, with high levels of N exchange between EMF and plant hosts, resulting in strong symbiosis-mediated fractionation (Hobbie and Hobbie 2006). When soil MDN is taken up by fungi, ^{15}N -depleted MDN is transferred to plant hosts, while fungi become enriched in ^{15}N relative to $\delta^{15}\text{N}$ of available soil N. Not accounting for this could lead to an underestimation of the %MDN contribution to plants, as the ultimate $\delta^{15}\text{N}$ value that is used for the sample (in this case, plants) is lower due to ^{15}N fractionation during fungal N transfer. We provide an expanded isotope mixing model that accounts for fractionation due to fungal-plant nutrient exchange and additional biogeochemical transformations of salmon-derived N prior to fungal and plant uptake, providing a more mechanistically appropriate estimate of MDN contributions to fungi and plants (Fig. 1).

Conclusion – We detected a persistent MDN signal in EMF sporocarps and tree foliage two years after a 21-year salmon carcass manipulation, and estimated that 28% of sporocarp N near the salmon-enhanced bank was derived from salmon. Responses were strongest among long- and medium-distance EMF exploration types, consistent with their capacity to exploit patchy nutrient resources. The carcass manipulation increased fungal %N, indicating that sustained MDN inputs can influence fungal N status. Together, these findings indicate that salmon-derived N constitutes a biologically meaningful component of fungal N nutrition, and identify EMF as a potentially important biological reservoir and transfer pathway for MDN, while also highlighting the need to quantify belowground mycelial stocks directly. Because salmon populations are declining in many regions (Mills et al. 2013), changes in MDN supply could alter fungal-mediated N cycling, although the magnitude of this effect remains unknown. Models of MDN flow should account for both pre-uptake biogeochemical transformations and fungal–plant isotopic fractionation. A complete understanding of salmon-derived nutrient cycling therefore requires fungi to be considered alongside soils and plants.

Declarations

Competing Interests

Dr. Erik Lilleskov, an author of this study, is on the Editorial Board of Mycorrhiza.

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The authors declare they have no financial interests.

Author Contribution

Conceptualization, A.Y.P., E.A.H., G.H., A.L., E.L., K.V., K.K.M., D.V., and A.M.B.; Methodology, A.Y.P., E.A.H., G.H., A.L., E.L., K.V., K.K.M., D.V., and A.M.B.; Statistical Analysis, A.Y.P., E.A.H., G.H., E.L., and A.M.B.; Investigation, A.Y.P., E.A.H., G.H., A.L., E.L., K.K.M., K.V., D.V., and A.M.B.; Writing & Editing, A.Y.P., E.A.H., G.H., A.L., E.L., K.K.M., K.V., D.V., and A.M.B.

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Data Availability

All raw data and code have been archived at Harvard Dataverse (<https://doi.org/10.7910/DVN/MBDP2I>). All analyses are fully reproducible.

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Figures

$$\%MDN_{fungi} = \frac{sample \delta^{15}N - terrestrial \delta^{15}N}{(\delta^{15}N_{salmon} + \Delta_{decomposition} + \Delta_{trade}) - terrestrial \delta^{15}N}$$

$$\Delta_{trade} = T_r \varepsilon_{trade}$$

Fig. 1 Expanded two-source isotope mixing model used to estimate the percentage of fungal N derived from MDN. The salmon end-member $\delta^{15}N$ is adjusted for isotopic enrichment from salmon carcasses before fungal uptake ($\Delta_{decomposition}$) and for fractionation associated with fungal–plant N transfer (Δ_{trade}), which is calculated from the transfer ratio (T_r) and the discrimination factor (ε_{trade})

Figure 1

See image above for figure legend.

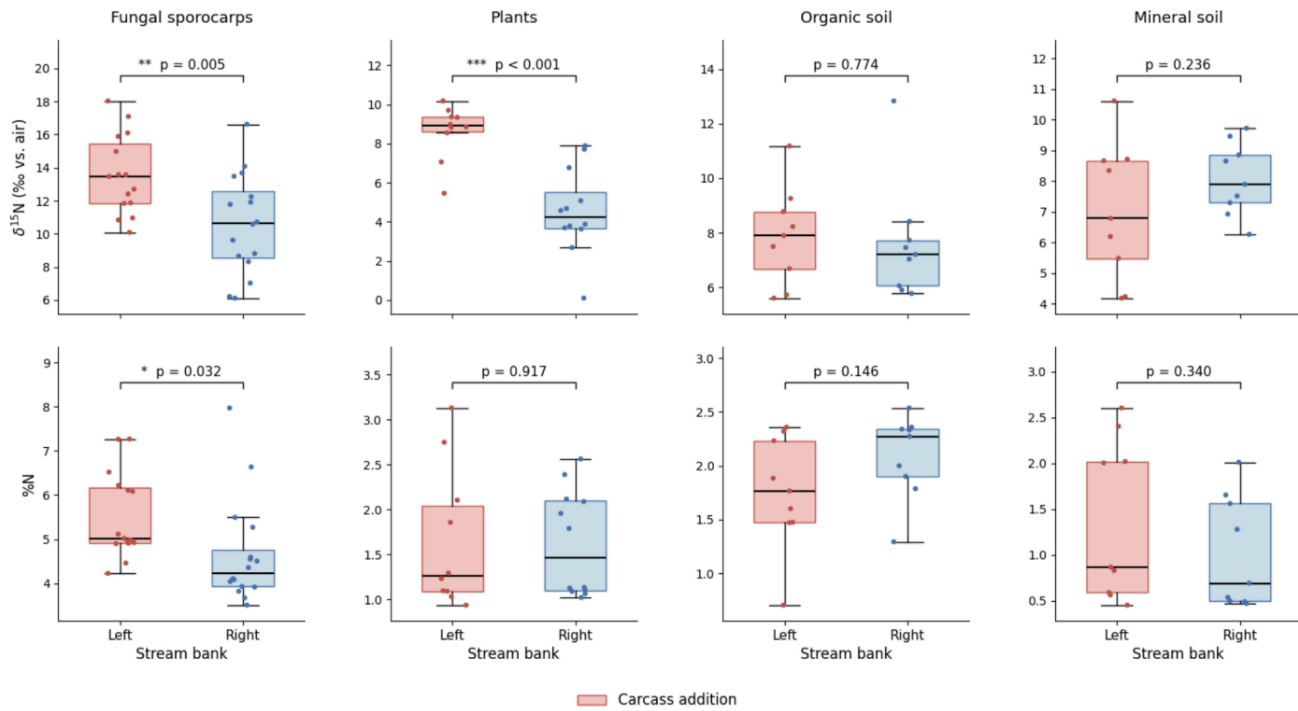


Figure 2

$\delta^{15}\text{N}$ and %N of fungal sporocarps, plant foliage (paper birch and white spruce), organic soil, and mineral soil sampled 1–6 m from the stream edge on the left (salmon-enhanced) and right (salmon-depleted) banks of Hansen Creek, Alaska. Brackets show Wilcoxon rank-sum tests and P values. Boxplots summarize the distributions, and points show individual observations

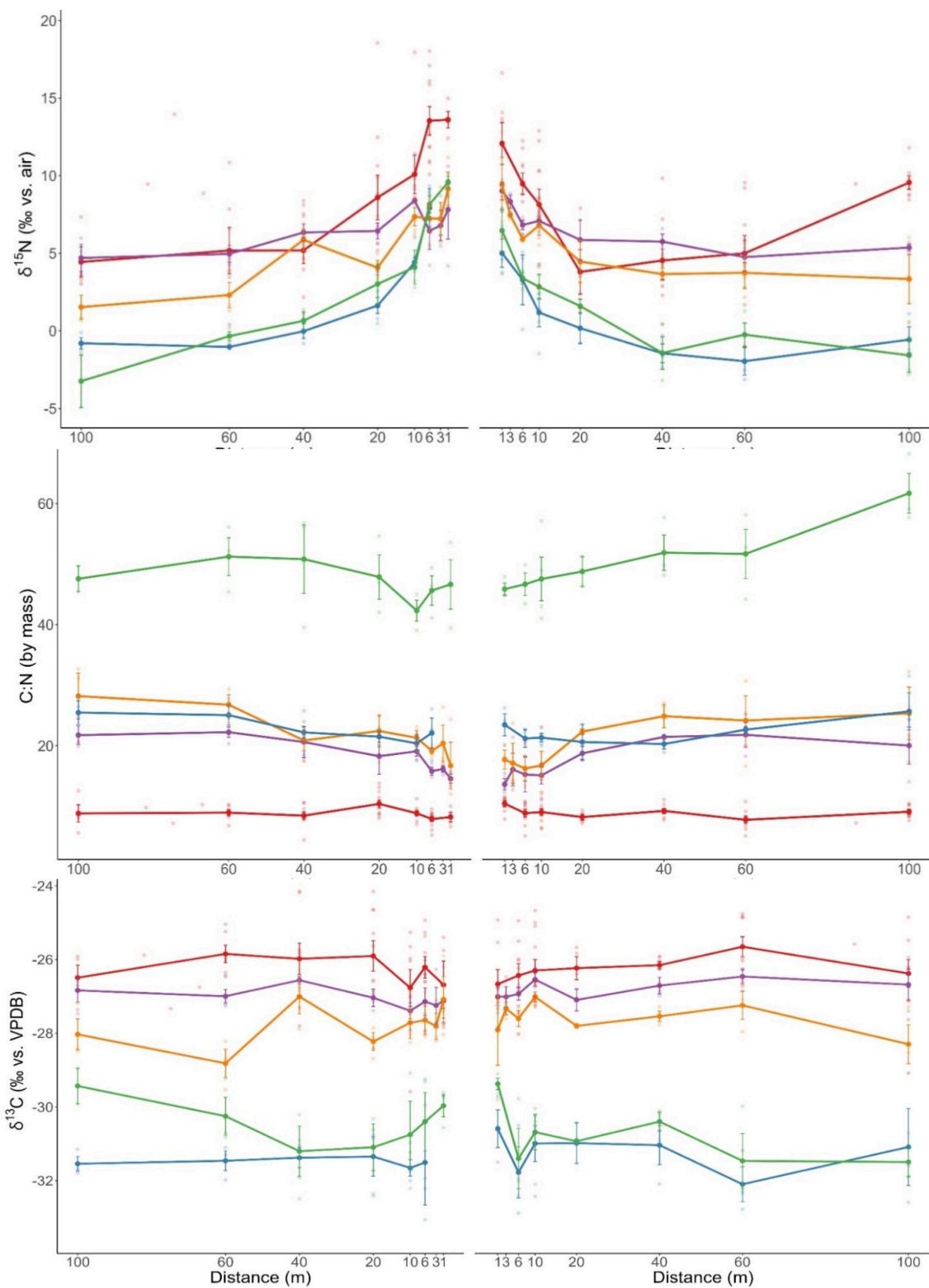


Figure 3

Mean values of $\delta^{15}\text{N}$, C:N, and $\delta^{13}\text{C}$ for fungi, white spruce, paper birch, organic soil and mineral soil 1–100 m away from the bank of Hansen Creek on both sides

Supplementary Files

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