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Soil contact and prescribed burning accelerate the decomposition of downed woody debris in boreal forests

Ekaterina Shorohova [a,*], Maria Shorohova [a], Henrik Lindberg [b], Ilkka Vanha-Majamaa [a]

[a] Natural Resources Institute Finland (Luke), Latokartanonkaari 9, Helsinki FI-00790, Finland
[b] Häme University of Applied Sciences, Visamäentie 35 A Box 230, Hämeenlinna FI-13101, Finland

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ABSTRACT

Deadwood enrichment and prescribed burning are closer-to-nature management practices intended to restore biodiversity and ecosystem services in Fennoscandian forests. However, their long-term effects on a key process—deadwood decomposition—remain unquantified. We investigated the decomposition of spruce and birch downed coarse woody debris (logs) 21 years after prescribed burning, tree retention, and deadwood enrichment in upland and paludified biotopes within managed mature *Myrtillus*-type Norway spruce forests. Cutting trees for deadwood enrichment accelerated decomposition by increasing soil contact. Prescribed burning increased volume loss, particularly in spruce logs, but this effect was weaker in paludified Sphagnum-dominated biotopes. When mass and volume losses of bark and secondary xylem were integrated, the main drivers of decomposition in descending importance were soil contact, Sphagnum cover, tree species, and burning. The total decomposition rate constant was higher for spruce (0.087 yr^{-1}) than for birch (0.066 yr^{-1}). The mean residence time of downed coarse woody debris was 49 years, ranging from 38 years for burned spruce logs to 104 years for spruce logs covered by Sphagnum. Our results demonstrate that restoration practices influence long-term decomposition dynamics. Deadwood enrichment and prescribed burning can hasten carbon and nutrient turnover from coarse woody debris in boreal forests.

1. Introduction

Deadwood is a critical component of forest ecosystems, sustaining biodiversity and driving key processes such as carbon and nutrient cycling (Stokland et al., 2012; Seibold et al., 2015; Löfroth et al., 2023). In the managed forests of northern Europe, the amount, diversity, and quality of deadwood have been severely reduced by intensive forest management, including timber harvesting, salvage logging, and long-term fire suppression (Siitonen, 2001). This reduction has led to a depletion of saproxylic habitats and a loss of fire-associated species, as the cessation of wildfires and prescribed burning has homogenized forest structures (Similä and Junninen, 2012; Halme et al., 2013). Consequently, active restoration interventions such as deadwood enrichment and prescribed burning are essential to rehabilitate biodiversity and increase ecosystem resilience in Fennoscandia (Sandström et al., 2019; Koivula and Vanha-Majamaa, 2020).

The ecological functions of deadwood depend on its quality and residence time, which are governed by decomposition rates (Löfroth et al., 2023; Wijas et al., 2024). Decomposition of deadwood is driven by a complex interplay of environmental factors (e.g., temperature, moisture), substrate attributes (e.g., tree species, size, bark characteristics), as well as structure and composition of wood-inhabiting communities (fungi, insects, bacteria, epixylic vegetation) (Rayner and Boddy, 1988; Russell et al., 2015). In forests, these factors are mediated by broader ecosystem characteristics, including site conditions, stand structure, and natural disturbance regimes and/or forest management (Shorohova and Kapitsa, 2014). While deadwood enrichment and prescribed burning are increasingly applied as closer-to-nature forest management and restoration practices in Fennoscandia, their long-term effects on decomposition pathways and deadwood dynamics remain poorly quantified (Sandström et al., 2019; Koivula and Vanha-Majamaa, 2020). The outcomes likely depend on a synergy of altered microclimate, substrate quantity and quality, and shifts in decomposer communities.

Deadwood enrichment, particularly when combined with canopy opening, can alter decomposition patterns by modifying the physical environment and wood-inhabiting communities. Increased light penetration raises insolation and reduces evapotranspiration, altering temperature and moisture regimes at both tree stand and woody debris piece

* Corresponding author.
E-mail address: ekaterina.shorokhova@luke.fi (E. Shorohova).

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scales (Kolstela et al., 2024; Schreiber et al., 2025; Starck et al., 2026). This can lead to substrate desiccation in upland sites or, conversely, to waterlogging and excess moisture and incorporating woody debris into the organic soil humus layer, i.e. burial under Sphagnum cover in paludified biotopes, the latter effectively halting decay (Moroni et al., 2015; Stokland et al., 2016). Direct solar radiation can also photochemically degrade lignin, potentially accelerating early-stage decomposition (Austin et al., 2016). Furthermore, cutting trees and leaving logs in direct ground contact can improve moisture retention and microbial colonization (Rajala et al., 2012; Shorohova and Kapitsa, 2014; Piaszczyk et al., 2022). The direct effect of solar radiation exposure and increased temperatures can increase microbial activity (Rubenstein et al., 2017). However, increased temperature variability and drought can selectively filter wood-inhabiting fungal communities, favouring stress-tolerant taxa like many brown-rot fungi (Pouska et al., 2017; Krah et al., 2018; Fukasawa, 2018; Perreault et al., 2023). In Norway spruce-dominated forests, sudden sun-exposure of retained trees can trigger bark beetle outbreaks (Lobinger, 1994), and rapid colonization of deadwood by dominant decomposers like *Fomitopsis pinicola*, which can shape decay pathways for decades (Vogel et al., 2017; Fukasawa et al., 2019). Bark fragmentation further influences microclimate and community assembly in downed logs (Dossa et al., 2018; Hagge et al., 2019). Additionally, this may cause the species-specific differences in the decomposition rates, since the conifer bark is disappearing faster as compared to deciduous one (Shorohova et al., 2016).

Prescribed burning can influence coarse woody debris decomposition through multiple direct and indirect pathways. Fire consumes and fragments outer tissues, increases the amount of substrate due to subsequent tree mortality, alters physical and chemical properties of woody debris (Esteves and Pereira, 2009; Marttila et al., 2024). These changes filter decomposer communities, favoring heat-resistant fungi and acid-tolerant brown-rot taxa over white-rot fungi (Soloviev et al., 1992; Arantes and Goodell, 2014; Edman and Eriksson, 2016; Fox et al., 2022). Fragmentation opens pathways for saproxylic insects for foraging and fungal ingress (Seibold et al., 2021). In cases of high burn severity, the resulting charcoal is highly recalcitrant, and charred surfaces may reduce moisture absorption, potentially slowing subsequent decay (Preston and Schmidt, 2006). Conversely, low- to moderate-severity prescribed burns can lead to warming of the substrate with only a small amount of char deposited on the surface (Vasander and Lindholm, 1985; Schimmel and Granström, 1996). Fire can also raise the water table in paludified sites (Simard et al., 2007), promoting log burial. Thus, deadwood enrichment and prescribed burning can have synergistic effects on decomposition processes in woody debris by altering microclimate, substrate quality, and decomposer community composition.

We investigated the decomposition of Norway spruce (*Picea abies* (L.) H. Karst.) and birch (*Betula pubescens* Ehrh. and *Betula pendula* Roth.) downed coarse woody debris 21 years after combined restoration treatments (live tree retention, deadwood enrichment, and prescribed burning) in managed southern boreal Norway spruce forest stands. The restoration treatments were intended for rehabilitation of threatened habitats and species composition (Vanha-Majamaa et al., 2007). Accounting for within-stand variation, we compared upland and paludified biotopes. We measured secondary xylem (wood tissue, hereafter 'xylem') and bark density, moisture, mass, and volume loss at multiple scales (small samples, stem sections, whole logs) and quantified bark cover loss, fungal rot type, and invertebrate consumption. Subsequently, we calculated the exponential decomposition rate constants and residence time for the stem sections and whole logs. We hypothesized species- and tissue-specific decomposition patterns, with mass- and volume-loss rates being positively influenced by deadwood enrichment and burning and negatively influenced by Sphagnum cover in paludified biotopes.

2. Materials and methods

2.1. Study area and experimental design

The study area is characterized by the mean annual temperature of + 3.1 °C, the mean length of the growing period of 160 days, and the mean annual precipitation of 670 mm. The granitic bedrock is covered by thick till deposits (Anon., 1995). The area has a history of slash-and-burn cultivation, which ceased in the late 19th century, and forest grazing was also historically common. Forest management relied primarily on selective cuttings until they were replaced by clear-cutting and artificial regeneration in the 1950s.

The study was conducted as part of the Evo restoration experiment in southern boreal Finland (Evo-Vesijako area; 61°N, 25°E) (Ahti et al., 1968). In 2001, twenty-four mesic, Norway spruce-dominated forest stands with an admixture of birch (*Betula pendula* Roth., *B. pubescens* Ehrh.), aspen (*Populus tremula* L.), and pine (*Pinus sylvestris* L.) were selected (Vanha-Majamaa et al., 2007). The age of the stands varied from 60 to 100 years, mean growing stock was 168 m^3 ha^{-1}. Each stand contained both an upland and a paludified biotope. Upland biotopes corresponded to the *Myrtillus* forest site type, with some areas resembling the *Oxalis-Myrtillus* type (Cajander, 1926). The paludified biotopes were more variable, comprising patches of paludified *Myrtillus* type and *Vaccinium myrtillus* spruce mire (Laine and Vasander, 2005).

The restoration treatments included partial cutting with dispersed retention trees with a volume of 50 m^3 ha^{-1}, when 5, 30 and 60 m^3 ha^{-1} of felled trees were left as downed logs. Half of the forest stands were burned. Each treatment had three replicates. Cuttings were performed in 2001 and burning in 2002 (Vanha-Majamaa et al., 2007). Untreated stands served as references but were not included in this study. Pre-treatment stand structures did not differ between upland and paludified biotopes (Lilja et al., 2005).

Two decades post-treatment, natural succession resulted in diverse, high-volume deadwood profiles, generally greater in upland than in paludified biotopes, with the highest deadwood volumes occurring in upland biotopes after prescribed burning without deadwood enrichment (Shorohova et al., 2024).

2.2. Log selection and field measurements

We focused on spruce and birch logs to ensure sufficient sample sizes across burned versus unburned stands and across deadwood-enrichment levels in both upland and paludified biotopes. To isolate treatment effects on downed woody debris decomposition, we selected only logs with a visible cut surface (i.e., created logs).

In 2022, we sampled 149 spruce and 19 birch logs (diameter at 1.3 m: 10–34 cm). Based on visual homogeneity in integrity, shape, bark and vegetation cover, height above ground, and decomposition state, each log was divided into one to three stem sections, termed 'decomposition units', yielding 318 spruce and 51 birch units. As controls, in 2023 we sampled mature living spruce (n = 21) and birch (n = 13) trees in the forest stands with and without prescribed burning and in both upland and paludified biotope (Table 1).

The following variables were recorded for each stem section: tree species; diameter at the base and top of the stem section and at the 1.3. m from tree base; decay class; length; height above ground (at the location of the sampling point); cover of bark (%); cover of epixylic vegetation, %; buried under Sphagnum cover or not; charred or not.

The lateral surface area ($S_{surface}$, m^2) of each stem section was calculated using the standard formula for the lateral surface area of a truncated cone.

2.3. Sample analysis

The samples from xylem with bark excluded were collected from the central point of each stem section using a handsaw, axe, knife, or soil

Table 1
Experimental design and the number of stem sections sampled.

Standing retention 50 m^3/ha and deadwood enrichment 5, 30 and 60 m^3/ha, 2001				No treatments			
Prescribed burning, 2002							
Downed coarse woody debris sampling, 2022				Control (living trees) sampling, 2023			
Burned		Unburned		Burned		Unburned	
Upland	Paludified	Upland	Paludified	Upland	Paludified	Upland	Paludified
82	77	109	101	8	8	7	8

borer. The proportional area occupied by non-decomposed xylem, voids (areas of complete decomposition), decay types (white rot or brown rot, various stages) was estimated macroscopically following established criteria (Araya, 1993). Brown rot was identified by reddish-brown discoloration and a tendency to break into cubical fragments; white rot was identified by whitish or bleached coloration (yellowish- or greyish-white), sometimes with pockets, yielding fibrous fragments. To account for volume loss during decomposition, the original shape of fragmented or highly decomposed logs was reconstructed for measurement. Voids in cross-sections were included in volume calculations. From each section, three to four small samples of regular shape (approximately 30–40 cm^3) were extracted, their dimensions measured, and their fresh mass recorded. In total, 558 spruce and 85 birch xylem samples were collected.

Bark sampling followed a similar protocol. Two to three rectangular bark samples (10–30 cm^2 each) were taken from each stem section, measured, and weighed, yielding 122 spruce and 55 birch samples. Control samples of non-decayed xylem were obtained from living trees using a 1-cm diameter increment borer. Control bark samples were collected from living trees using a hammer, chisel, and knife.

All samples were oven-dried at 103 °C for 48 h to constant mass. Xylem density (ρ_w, kg m^{-3}) and bark density (ρ_b, kg m^{-3}) were calculated as oven-dry mass divided by fresh sample volume. Moisture content was calculated as the percentage difference between wet and oven-dry mass. Bark area-specific mass (mass per unit surface area, m_b, g cm^{-2}) was calculated as the dry mass of a bark sample divided by its surface area (Suppl. S1).

2.4. Upscaling to stem section and log scales

The volume of individual stem sections was estimated using the formula for a truncated cone. For entire downed logs, volume was calculated using species-specific equations (Laasasenaho, 1982). For each stem section and whole log, a weighted average density and remaining mass were calculated, incorporating all measured volume losses including voids. The total area of remaining bark (Sf) on a section was calculated by multiplying its lateral surface area (*S*) by the proportion of bark cover (f). The total bark mass (M_{sb}) was then calculated as $Sf \times mb$.

2.5. Mass loss and decomposition rate calculations

Mass loss percentages for xylem, bark, and total mass (wood + bark) were calculated relative to the mean initial control mass. Control values were established from living trees: xylem density: 0.442 g cm^{-3} (spruce) and 0.522 g cm^{-3} (birch); bark density: 0.369 g cm^{-3} (spruce) and 0.660 g cm^{-3} (birch); bark area-specific mass: 0.212 g cm^{-2} (spruce) and 0.526 g cm^{-2} (birch); bark thickness: 0.578 cm (spruce) and 0.808 cm (birch).

In cases where the measured remaining density or mass exceeded the control value, mass loss was set to zero. Annual decomposition rate constants (k) were calculated at the stem-section and whole-log scales using a single exponential decay model (Olson, 1963), based on mass remaining 21 years after tree death:

- k_w: decomposition rate constant for wood excluding bark (xylem).
- k_b: decomposition rate constant for bark, integrating mineralization, thinning (peeling, insect consumption), and fragmentation (sloughing). This was calculated from density loss, assuming constant bark thickness, and adjusted for the proportional bark cover (f).
- k_t: Total decomposition rate constant for downed coarse woody debris, calculated as the mass-weighted sum of k_w and k_b.

The residence time (t_{95}), defined as the time for 95% mass loss, was calculated as 3/k (Suppl. S1).

2.6. Statistical analysis

The effects of substrate and ecosystem attributes on mass loss (xylem, bark, and total) at the small-sample, stem-section and whole-log levels were analysed using generalized linear models (GLM) or generalized linear mixed models (GLMM), as appropriate (Suppl. S2). At the small-sample scale, bark density was analysed rather than bark density loss, as the control density was in many cases lower than the density recorded 21 years post-treatment. The analyses considered two categories of predictors and their interactions:

1. Substrate characteristics: Tree species, diameter, height above ground, decay type (white vs. brown rot, or their mixture), percent cover of bark, percent cover of epixylic vegetation, Sphagnum cover (buried/not buried), and charring (presence/absence).
2. Ecosystem characteristics**:** Biotope (upland vs. paludified), prescribed burning (burned vs. unburned), created deadwood volume level (5, 30, and 60 m^3 ha^{-1}).

Diameter, height above ground and the percent cover variables (bark, epixylic vegetation) were tested as both continuous and categorical predictors to identify the best functional form. The stand number was included as a random factor in mixed models to account for spatial nesting.

The optimal models were selected based on the likelihood-ratio test and Akaike's Information Criterion (AIC). Model-averaged estimates of the annual decomposition rate constants (k_w, k_b, k_t) and downed coarse woody debris residence times (t_{95}) were then calculated, weighted by the model support, for the main factors identified as significant drivers of mass loss (Table 2).

Associations between key continuous variables were assessed using Pearson's correlation and Spearman's rank correlation (Suppl. S3). Given the importance of moisture as a decay driver, we analysed how xylem and bark sample moisture varied with tree species, density, decay type, insect fragmentation, height above ground, and Sphagnum cover (Suppl. S4).

All statistical analyses were performed in R (version 4.0.5, GUI 1.74 Catalina build).

3. Results

3.1. Overall patterns and key drivers

Over the 21-year period, mass loss percentages for xylem, bark, and

Table 2
Mean (minimum–maximum) decomposition rate constants (k, year^{-1}) and residence times (t_{95}, years) for downed coarse woody debris at the stem-section and whole-log scales.

Factor		Xylem k_w	Bark k_b	Total k_t	Total t_{95}	Xylem k_w	Bark k_b	Total k_t	Total t_{95}
Height above ground, cm	< 10	Stem section, N = 324				Whole log, N = 155			
		0.087	0.386	0.087	45	0.080	0.446	0.081	43
		(0–0.172)	(0.011–0.548)	(0.004–0.182)	(16–716)	(0.012–0.122)	(0–0.548)	(0.016–0.124)	(24–184)
	> 10	Stem section, N = 37				Whole log, N = 7			
		0.059	0.262	0.059	84	0.052	0.412	0.054	75
		(0.006–0.124)	(0.025–0.548)	(0.006–0.116)	(26–532)	(0.014 – 0.091)	(0.053 – 0.548)	(0.019 – 0.095)	(32 – 160)
Sphagnum cover	Yes	Stem section, N = 27				Whole log, N = 5			
		0.069	0.372	0.066	91	0.061	0.342	0.052	81
		(0–0.155)	(0.019–0.548)	(0.004–0.122)	(25–716)	(0.012–0.120)	(0–0.548)	(0.016–0.094)	(32–184)
	No	Stem section, N = 338				Whole log, N = 158			
		0.085	0.372	0.085	46	0.079	0.445	0.081	43
		(0.006–0.172)	(0.009–0.548)	(0.006–0.182)	(17–532)	(0.014–0.122)	(0–0.548)	(0.019–0.124)	(24–160)
Burning	Yes	Stem section, N = 158				Whole log, N = 72			
		0.090	0.448	0.091	40	0.087	0.512	0.088	38
		(0.007–0.172)	(0.016–0.548)	(0.012–0.175)	(17–254)	(0.024–0.122)	(0–0.548)	(0.025–0.122)	(25–118)
	No	Stem section, N = 206				Whole log, N = 91			
		0.080	0.313	0.079	56	0.072	0.386	0.073	49
		(0–0.168)	(0.010–0.548)	(0.004–0.182)	(17–716)	(0.012–0.118)	(0–0.548)	(0.016–0.124)	(24–184)
Spruce, height above ground, cm	< 10	Stem section, N = 284				Whole log, N = 138			
		0.086	0.426	0.089	43	0.081	0.480	0.085	41
		(0–0.172)	(0.058 – 0.548)	(0.004 – 0.175)	(17–716)	(0.012 – 0.122)	(0.047 – 0.48)	(0.016 – 0.124)	(24 – 184)
	> 10	Stem section, N = 30				Whole log, N = 7			
		0.061	0.306	0.064	68	0.052	0.412	0.054	75
		(0.011 – 0.112)	(0.049 – 0.548)	(0.015 – 0.116)	(26–205)	(0.014 – 0.091)	(0.053 – 0.548)	(0.019 – 0.095)	(32 – 160)
Spruce, Sphagnum cover	Yes	Stem section, N = 20				Whole log, N = 3			
		0.061	0.445	0.065	104	0.049	0.387	0.053	93
		(0 – 0.116)	(0.091 – 0.548)	(0.004 – 0.122)	(25–716)	(0.012 – 0.089)	(0.065 – 0.548)	(0.016 – 0.094)	(32 – 184)
	No	Stem section, N = 294				Whole log, N = 142			
		0.086	0.413	0.089	41	0.081	0.479	0.084	41
		(0.007 – 0.172)	(0.049 – 0.548)	(0.012 – 0.175)	(17 – 254)	(0.014 – 0.122)	(0.047 – 0.548)	(0.019 – 0.124)	(22 – 160)
Spruce, burning	Yes	Stem section, N = 146				Whole log, N = 67			
		0.090	0.476	0.093	38	0.087	0.534	0.090	36
		(0.007 – 0.172)	(0.085 – 0.548)	(0.012 – 0.175)	(17 – 254)	(0.024 – 0.122)	(0.065 – 0.548)	(0.028 – 0.122)	(25 – 108)
	No	Stem section, N = 168				Whole log, N = 78			
		0.079	0.362	0.082	51	0.074	0.428	0.077	48
		(0–0.148)	(0.050–0.548)	(0.004–0.157)	(19–716)	(0.012–0.118)	(0.047–0.548)	(0.016–0.124)	(24–184)
Spruce mean		Stem section, N = 314				Whole log, N = 145			
		0.084	0.415	0.087	45	0.080	0.477	0.083	42
		(0–0.172)	(0.050–0.548)	(0.004–0.175)	(17–716)	(0.012–0.122)	(0.048–0.548)	(0.016–0.124)	(24–183)
Birch, burning	Yes	Stem section, N = 12				Whole log, N = 5			
		0.097	0.121	0.068	64	0.084	0.219	0.058	61
		(0.024–0.149)	(0.016–0.548)	(0.013–0.149)	(20–223)	(0.036–0.120)	(0–0.548)	(0.025–0.082)	(36–118)
	No	Stem section, N = 38				Whole log, N = 13			
		0.083	0.082	0.064	77	0.060	0.136	0.053	61
		(0.006–0.168)	(0.010–0.548)	(0.006–0.182)	(17–532)	(0.033–0.109)	(0–0.548)	(0.030–0.091)	(33–100)
Birch, mean		Stem section, N = 50				Whole log, N = 18			
		0.088	0.092	0.066	74	0.067	0.159	0.055	61
		(0.006–0.168)	(0.010–0.548)	(0.006–0.182)	(17–532)	(0.033–0.120)	(0–0.548)	(0.025–0.091)	(33–118)
Total mean		Stem section, N = 364				Whole log, N = 163			
		0.084	0.372	0.084	49	0.077	0.441	0.080	44
		(0–0.172)	(0.010–0.548)	(0.004–0.182)	(17–716)	(0.012–0.122)	(0–0.548)	(0.016–0.124)	(24–184)

total mass varied widely (0–90%) across all scales, from individual samples to whole logs. Decomposition dynamics differed substantially between xylem and bark tissues. The main drivers of decomposition, with scale- and tissue-dependent importance, were soil contact (quantified as height above ground, range: 0–33 cm), Sphagnum cover, prescribed burning, and tree species (Suppl. S2).

At the small-sample scale, xylem and bark densities were not correlated. Bark density and area-specific mass were weakly correlated (Suppl. S3). Moisture content in both xylem and bark increased with decreasing density, with a steeper relationship observed in xylem (Fig. 1, Suppl. S4). Moisture content was influenced by both ecosystem- and substrate-scale factors. Xylem moisture was significantly higher in paludified biotopes, slightly higher on logs with epixylic vegetation, and lower on logs suspended above ground (Fig. 1, Suppl. S4). Bark moisture was lower in birch than in spruce logs. Bark covering wood with white or mixed rot was slightly moister than bark over wood with only brown rot (Suppl. S4).

The mass loss of small xylem samples varied greatly, and no appropriate statistical model could be fitted to these data. Bark sample density was higher for birch than for spruce (Suppl. 5).

After 21 years, void space from complete decomposition accounted for an average of 17% of the initial reconstructed volume. This percentage of totally decomposed xylem was higher in burned sites, in spruce versus birch, and in upland versus paludified biotopes (Fig. 2, Suppl. S6). Decay type composition also differed: spruce wood exhibited a mix of brown and white rot, with the proportion of white rot being lower in burned and upland sites. Birch wood decomposed almost exclusively via white rot. The share of brown rot was higher in upland biotopes and in burned sites compared to their paludified and unburned counterparts (Suppl. S6).

Xylem mass and volume loss were inhibited by Sphagnum cover (7% of stem sections were buried) and accelerated by prescribed burning and soil contact (Figs. 3, 4; Suppl. S2). Sphagnum cover slowed xylem decay by an average of 21%. Xylem decomposition was not significantly influenced by other tested factors, including tree species, log size, charring, bark cover, epixylic vegetation, deadwood enrichment level,

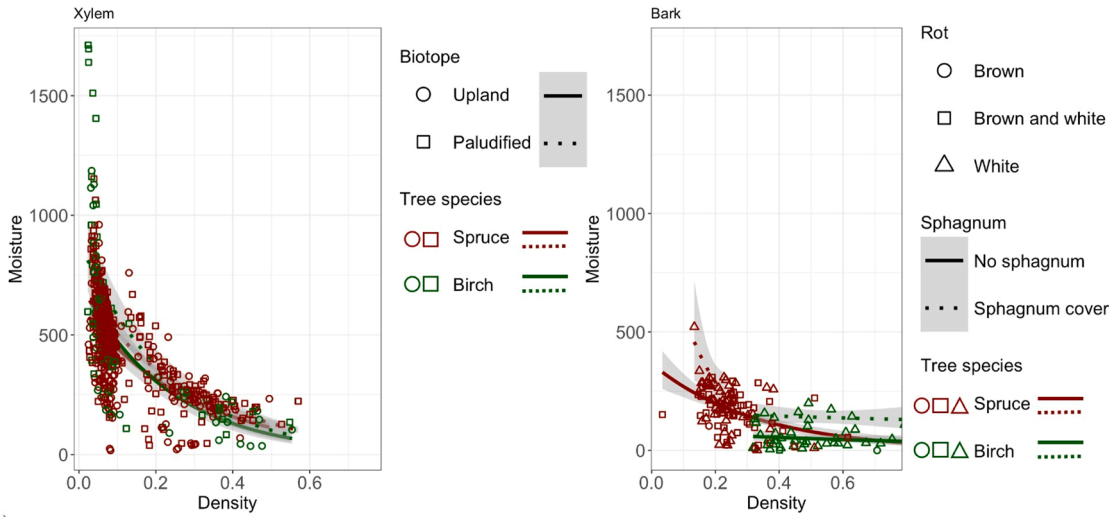

Fig. 1. Moisture content of secondary xylem (wood) and bark samples as a function of their density, biotope (upland vs. paludified), tree species (spruce vs. birch), and decay type 21 years post-restoration. Regression lines and standard error (SE) bands are derived from the best-fitted statistical models (Suppl. 3).

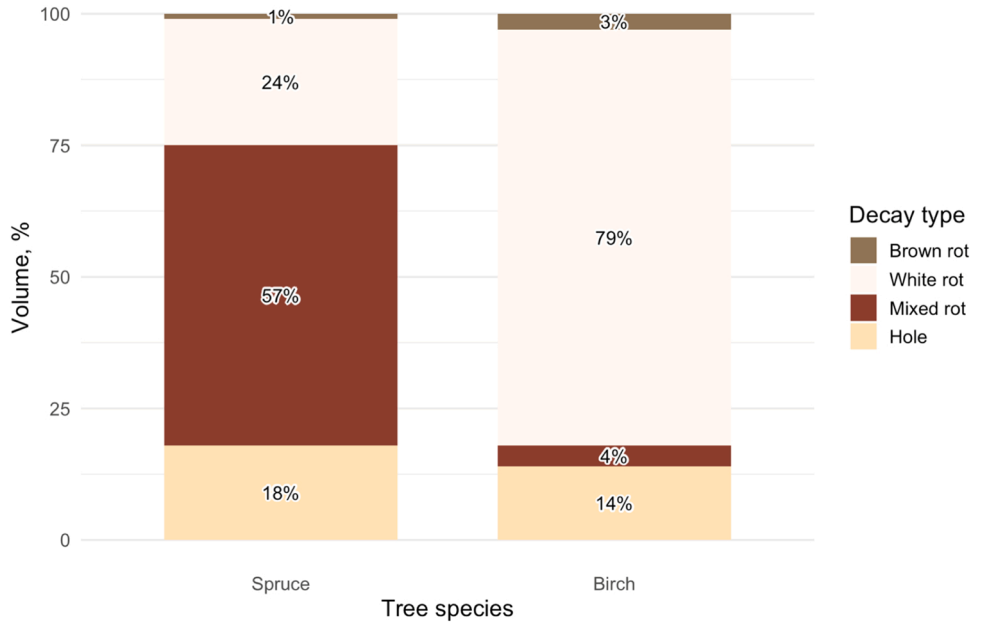

Fig. 2. Decomposition patterns in spruce and birch xylem. Mean proportional shares of white rot, brown rot, their mixture, and completely decomposed fragments (voids/holes) within the total volume, estimated for the entire dataset 21 years after the implementation of restoration treatments.

or biotope type.

Bark mass and volume loss were dependent on tree species, prescribed burning, and height above ground. Spruce logs lost their bark on average 4.5 times faster as compared to birch logs. Proximity to the ground accelerated spruce bark decomposition but had no effect on birch bark. Burning slowed the decomposition of birch bark. No other factors significantly influenced bark mass loss. At the whole-log scale, burning did not significantly affect total bark mass loss (Suppl. S2).

When integrating the mass and volume proportions of both tissues, the relative importance of decomposition drivers for decomposition units (stem sections) was: soil contact, Sphagnum cover, tree species, prescribed burning. For whole logs the effect of prescribed burning was not significant (Suppl. 2).

3.2. *Decomposition rates and residence times*

The annual decomposition rate constants (k) for stem sections and whole logs ranged from 0 to 0.174 yr^{-1} . The mean annual rate based on total mass loss (0.084 yr^{-1}) did not differ from that based on xylem mass loss alone (Table 2). However, the contribution of bark to the total decomposition rate was significant for birch but not for spruce.

Total mass loss of spruce logs was accelerated by soil contact and burning and inhibited by Sphagnum cover at both stem-section and whole-log scales (Fig. 4, Table 2, Suppl. S2). Spruce logs decomposed 1.6 times faster than birch logs (mean k: 0.087 yr^{-1} vs. 0.066 yr^{-1}).

The mean residence time (t_{95}) for CWD at the stem-section scale was 49 years (range: 17–716 years). It varied from 38 years for burned spruce logs to 104 years for Sphagnum-covered spruce logs. Log position had a pronounced effect: mean residence times were 45 years for lying logs and 84 years for leaning logs, despite a maximum suspension height

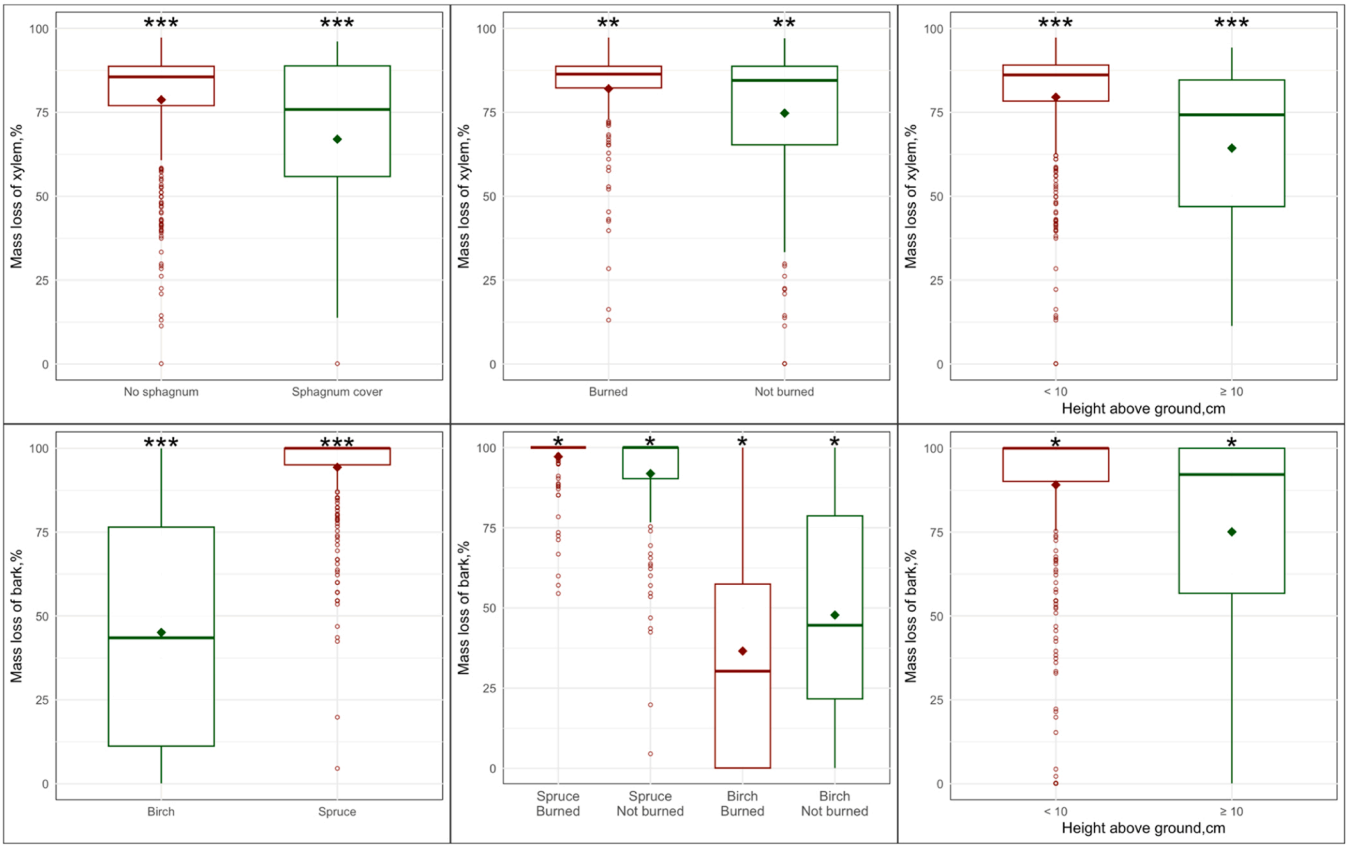

Fig. 3. Mass loss of secondary xylem (wood) and bark for individual stem sections in relation to tree species identity, height above ground, Sphagnum moss cover, and prescribed burning 21 years post-restoration. Boxplots are based on the results of generalized linear mixed models (GLMM) or generalized linear models (GLM) (Suppl. 5). The plots display median values (central line), means (diamond symbol), first and third quartiles (box), and maximum/minimum values (whiskers), with individual data points overlaid.

of only 33 cm (Table 2, Fig. 4 and 5).

Whole logs exhibited lower mean decomposition rates for xylem and for total mass (xylem + bark) compared to stem sections (decomposition units), with an average difference of 8%. In contrast, bark decomposition rates were generally higher for whole logs, except when logs were buried under Sphagnum (Table 2, Suppl. S2). The largest scale-related discrepancies were observed for birch: bark decomposition rates were 50% higher, and total decomposition rates were 24% higher at the whole-log versus stem-section scale (Table 2, Suppl. S2).

4. Discussion

Our results show that cutting trees for deadwood enrichment promoted faster decay primarily by ensuring soil contact, underscoring the importance of wood–soil interactions for decomposition. Prescribed burning also accelerated volume loss, especially in spruce logs, although the effect was dampened in paludified biotopes where Sphagnum mosses dominate. Integrating mass and volume losses across bark and secondary xylem, we found that decomposition was driven mainly by soil contact, followed by Sphagnum cover, tree species, and burning, in descending order of importance.

The mean annual decomposition rate constants (k) for downed woody debris in our study (5.2–9.0% mass loss yr^{-1}) fall within the upper range reported for boreal forests (Seibold et al., 2021). The observed decomposition dynamics two decades post-restoration reflect a multi-scale interplay between environmental and substrate characteristics. Given the mean residence time of 49 years for stem sections, our sampling at 21 years likely captured a period of high decomposition activity, consistent with models showing accelerating relative mass loss rates up to ~50–60% mass loss (Freschet et al., 2012).

The variation in decomposition rates and residence times in our study was remarkably high, nearly matching the 244-fold global range where deadwood persists from 3 to 750 years (Harmon et al., 2020). This underscores the highly heterogeneous, mosaic nature of decay processes within and among logs felled simultaneously, driven by internal gradients in tissue density, volume, and mass (Edelmann et al., 2023; Khanina et al., 2023).

4.1. Key drivers of decomposition

4.1.1. Log position and microclimate

Height above ground (i.e., degree of soil contact) was the strongest predictor of mass and volume loss. This aligns with the understanding that microclimate, particularly moisture, often explains more variance in decomposition rates than substrate identity (Shorohova and Kapitsa, 2014; Přívětivý and Šamonil, 2021). Wood-decay fungi, the primary decomposers in boreal forests, require moist conditions for initial colonization, and moisture remains a critical, often rate-limiting driver, especially in early decay stages (Boddy, 2001; Kahl et al., 2017). As decay progresses, water becomes a metabolic product, linking its availability directly to decomposer activity (Soloviev, 1992). Our results support this moisture-dependency: sample moisture increased with decreasing density, reflecting decay progress. Furthermore, as compared to wood moisture, bark moisture is more environmentally regulated by microclimate, soil contact, and epixylic vegetation (Shorohova et al., 2016). We found that the presence of white rot in the underlying secondary xylem positively influenced bark moisture, likely facilitating its microbial decay. The persistent internal decay mosaic within each log suggests that moisture gradients and limitation were operative throughout the decomposition process.

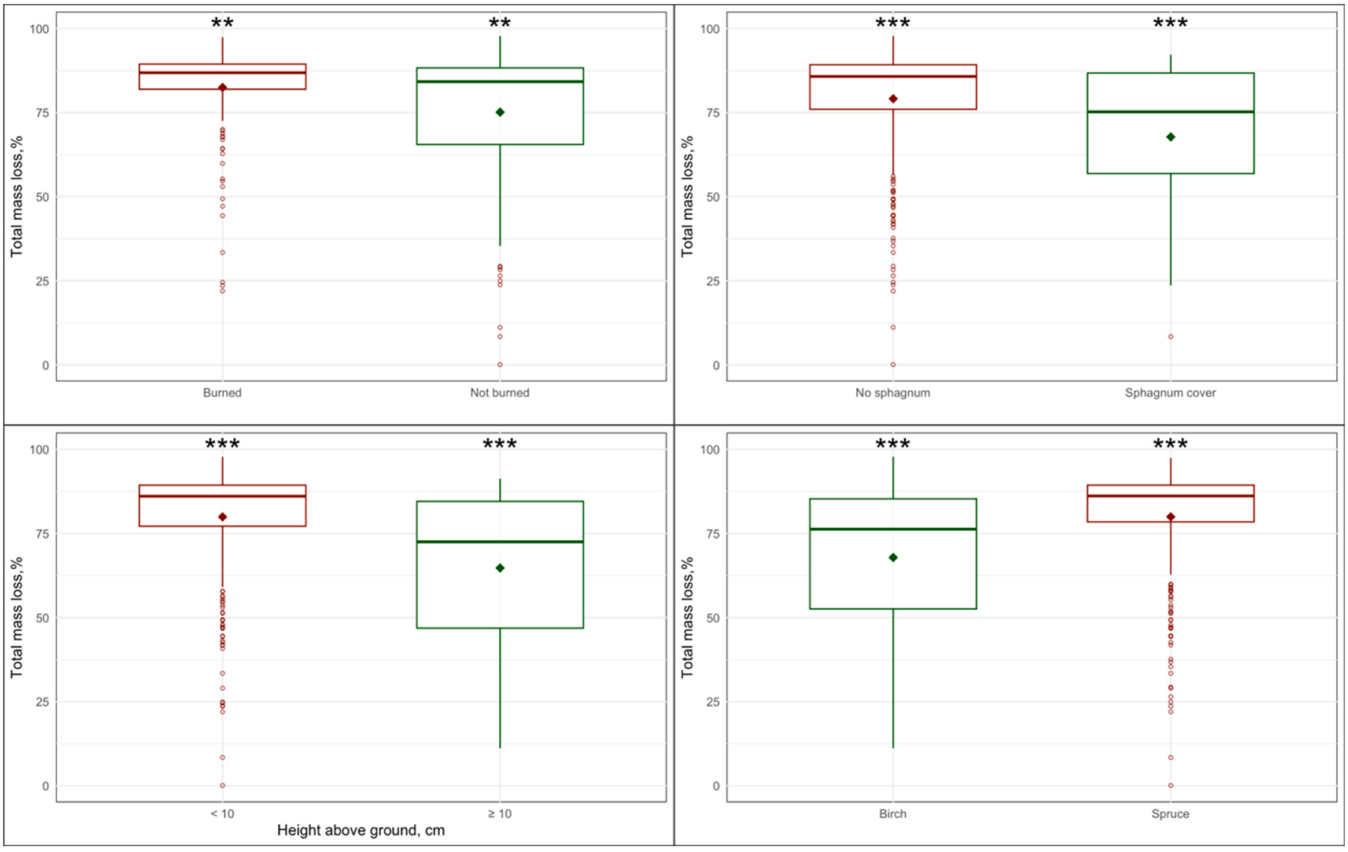

Fig. 4. Total mass loss (secondary xylem (wood) + bark) for individual stem sections in relation to tree species identity, height above ground, Sphagnum moss cover, and prescribed burning 21 years post-restoration. Boxplots are based on the results of generalized linear mixed models (GLMM) or generalized linear models (GLM) (Suppl. 5).

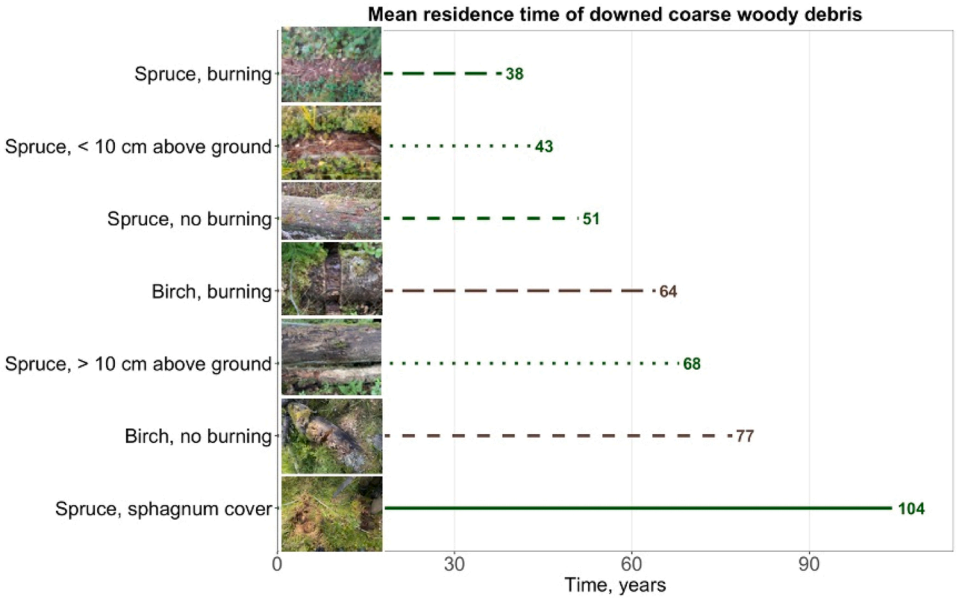

Fig. 5. Mean residence time (t_{95}) for downed coarse woody debris at the stem-section scale, as determined by the most significant decomposition drivers. Photographs by E. Shorohova and M. Shorohova.

Proximity to the ground may also alleviate potential nitrogen limitation of decomposition (Hu et al., 2018; Romashkin et al., 2021) by facilitating nitrogen translocation from soil and litter via fungal networks (Watkinson et al., 2006) and through colonization by bryophytes. This occurs via fungal translocation of nitrogen from soil and litter (Watkinson et al., 2006) and through colonization by bryophytes, including the N-fixing mosses (DeLuca et al., 2002; Smith et al., 2015). The N-fixing mosses, such as *Pleurozium schreberi*, *Hylocomium splendens*, and *Ptilium crista-castrensis* are common in our experimental spruce forests (manuscript on the understorey vegetation succession in the Evo

experiment, in prep.). This nitrogen enrichment effect may be particularly significant in burned sites, where soil nitrogen content can increase (Köster et al., 2024).

The effect of soil contact was more pronounced at the stem-section scale than at the whole-log scale (Table 2). This is likely because height above ground varied considerably along individual logs due to terrain or contact with other debris. A methodological limitation is that our analysis was based on height at the time of sampling; logs may have been suspended for unknown periods with potentially slower decay rates, meaning our study may underestimate the full magnitude of this driver.

Sphagnum cover was the second key driver, slowing decomposition of xylem while having no detectable effect on bark mass loss. This suppressive effect aligns with evidence that Sphagnum mosses exert the strongest inhibitory influence among bryophytes on underlying xylem decay (Stokland and Alfredsen, 2024). The absence of an effect on bark is likely due to tissue-specific factors: in spruce, the minimal remaining bark cover provided little substrate for microbial decay, while for birch, the 21-year study period was shorter than the bark's residence time, potentially obscuring drivers of its long-term decomposition. The relatively moderate overall reduction in xylem decay (21%) and its weaker expression at the whole-log scale, where complete burial was rare, can be explained by the dynamics of the overgrowth process. Debarked spruce trunks, which bryophytes typically colonize more slowly (Dossa, 2018), were likely already partially decomposed by the time Sphagnum burial occurred. Consequently, the recorded effect primarily represents the Sphagnum influence during later decay stages.

4.1.2. Tree species identity and tissue-specific dynamics

Tree species identity was the third-most important factor, regulating decomposition through anatomical and physico-chemical traits (Weedon et al., 2009; Lombardi et al., 2012). Contrary to the typical pattern of faster angiosperm decay (Weedon et al., 2009), we found no significant interspecific difference in xylem mass loss. Spruce xylem decomposed at rates comparable to birch, likely due to the rapid colonization of cut logs by aggressive brown-rot fungi like *Fomitopsis pinicola* (Berglund et al., 2011) — a pattern also observed by Edelmann et al. (2023), and enhanced fragmentation from fire or insects.

Interspecific differences were instead driven by contrasting bark decomposition dynamics. Spruce bark was lost 4.5 times faster than birch bark. Bark decomposition in coarse woody debris is governed by its initial cover and the time and mode of tree mortality (Ulyshen, 2016), with subsequent fragmentation and invertebrate consumption shaping the decay environment. Microbial decay is further controlled by bark's chemical and anatomical structure (Shorohova et al., 2016; Mamai et al., 2018; Kazartsev et al., 2018).

Although we lack direct data on bark cover dynamics, we assume that shortly after the restoration treatments, spruce bark was largely fragmented, consumed by bark beetles (Eriksson et al., 2006), and/or combusted. This is reflected in the low average bark cover on spruce logs at sampling (7%; 5% burned, 7% unburned). In contrast, the typically flammable birch bark (Sobol et al., 2023) was rarely fully combusted; instead, it often persisted as a slightly charred layer over highly decomposed xylem, with a mean cover of 75% on burned sites. Thus, the pronounced species-specific difference in bark decomposition is attributed to: (1) initially lower and more fragmented bark cover on spruce, (2) faster density loss in remaining spruce bark, and (3) the inhibitory effect of charring on birch bark decay. The initially low and fragmented bark cover on spruce logs also explains the absence of a detectable bark-cover effect on underlying xylem decomposition.

4.1.3. Prescribed burning

Prescribed burning emerged as a significant, long-term ecosystem-scale driver, exerting a net positive effect on xylem and total mass loss. The sole negative impact was observed on birch bark decomposition.

Enhanced xylem decomposition after burning can be explained by two complementary pathways. First, non-microbial processes played a key role: fire directly consumed wood, increased void space through volume depletion, and fragmented logs. This physical breakdown created extensive pathways for subsequent colonization by invertebrates and fungi. Second, microbial pathways were also important. The heat shock from fire can elevate fungal decay rates (Carlsson et al., 2017). Furthermore, fire acts as a strong environmental filter, shifting fungal community composition towards more active decomposers, a pattern confirmed in our study area (Berglund et al., 2011; Ramberg et al., 2023). This shift was reflected in the observed decay type patterns in spruce. In burned sites, the overall share of pure white rot was lower, while the proportion of wood with mixed white- and brown-rot fungi within the same stem section was higher. Pure brown rot was rare (4% of logs), likely because the rapid loss of bark on spruce logs and their subsequent coverage by bryophytes created conditions less favourable for common brown-rot fungi like *Fomitopsis pinicola*, which prefer bark-covered wood and drier conditions (Renvall, 1995; Pouska et al., 2016; Kawasaki et al., 2026). The most common decay type was a mixture of both rots, consistent with successional changes in fungal communities (Ottosson et al., 2014; Kawasaki et al., 2026).

Bark loss did not uniformly increase after fire, revealing a species-specific response. Thin spruce bark was likely combusted or rapidly sloughed off due to beetle activity. In contrast, the intensity of prescribed burning, which is typically lower than in wildfires (Vasander and Lindholm, 1985; Schimmel and Granström, 1996), was insufficient to fully combust the denser birch bark. Instead, it often remained as a persistent slightly charred layer, which subsequently inhibited microbial decay. This aligns with findings the study on stumps' decomposition after clear-cutting in boreal forests: prescribed burning facilitated bark fragmentation and slowed down the decomposition of un-fragmented parts of bark on the stumps (Shorohova et al., 2012).

4.2. Scale dependence and non-significant factors

Several factors hypothesized to be important did not emerge as direct predictors of mass loss at the scales analysed. The volume of created deadwood was not a significant predictor for xylem or bark mass loss after 21 years, aligning with findings from stumps a decade after after partial versus complete harvesting in southern boreal forests (Shorohova et al., 2008). Initial canopy openness effects on microclimate related to reduced moisture (Błońska et al., 2024) were likely overwhelmed by subsequent tree regeneration creating a favourable decomposition environment (Shorohova et al., in prep.). Initial effects of canopy openness on the bark beetle activity foraging on and fragmenting spruce bark were possibly enhanced by burning and/or levelled out by subsequent bark loss. No differences in wood-inhabiting communities related to deadwood volume were found either five (Berglund et al., 2011) or 16 (Ramberg et al., 2023) years after the treatments. However, our sampling was skewed towards sites with higher deadwood volumes, which may obscure potential volume effects.

Nevertheless, independently of the amount of deadwood created, four mechanisms can explain how deadwood enrichment indirectly accelerates decomposition. First, compared to trees that die standing, uproot, or break, cut trees more frequently reach full ground contact, significantly altering the internal microenvironment and decomposer communities within logs. Second, cutting per se accelerates decay processes in logs, as demonstrated by Edelmann et al. (2025). Third, the associated canopy opening and increased deadwood abundance can stimulate bark beetle activity. This promotes bark loss on spruce logs and facilitates the subsequent invasion of decay fungi into the wood, hastening its decomposition (Hagge et al., 2019). Fourth, there is potential for synergistic, positive effects between the volume of created deadwood and prescribed burning, likely mediated through enhanced physical fragmentation of both bark and xylem.

Biotope (upland vs. paludified) was not a direct explanatory variable for mass loss of downed logs. Its influence was mediated through higher

wood moisture in paludified areas and, crucially, through the substrate-scale effect of Sphagnum burial, which was a better predictor. In our study, charring—typically a thin fragmented surface layer—did not influence xylem mass loss or bark density at the sample scale. Rather, the ecosystem-level effect of prescribed burning was a stronger predictor of downed woody debris decomposition than localized charring. Debris size did not significantly influence decomposition rates, as its effects were likely dominated by the stronger drivers of soil contact, burning, and Sphagnum cover. This aligns with other multi-factorial studies in boreal forests (Shorohova et al., 2008; Shorohova and Kapitsa, 2014). Total cover of epixylic vegetation appeared to indirectly accelerate decay by increasing wood moisture, though it was not a primary predictive factor. A more nuanced analysis separating functional groups, such as nitrogen-fixing feather mosses, might reveal stronger and more specific effects on decomposition processes.

4.3. Implications for research and management

Much progress has been made in measuring the drivers of deadwood pool sizes, inputs, and outputs across the planet (Russell et al., 2015; Wijas et al., 2024). However, outstanding knowledge gaps highlight opportunities for future research. The role of interacting biotic and abiotic drivers of deadwood outputs is not yet understood. The representation of deadwood dynamics in global models is rudimentary (Wijas et al., 2024). Future Earth system model development would require additional efforts to couple the deadwood output mechanisms and drivers. Our results can refine ecosystem models by providing decomposition constants that disentangle the effects of soil contact, burning, and Sphagnum cover. A key finding for model parameterization is the differing role of bark: its decomposition significantly influences total decomposition rates for birch but not for spruce, consistent with other boreal studies (Romashkin et al., 2021).

The explicit incorporation of deadwood enrichment or retention into adaptive forest management and restoration practices is targeted to increase climate resilience, benefit biodiversity and tree regeneration (Sandström et al., 2019; Swanson et al., 2023; Wijas et al., 2024). Our study contributes to answering one of crucial questions: What role does deadwood have in slowing carbon from entering the atmosphere as greenhouse gases? In managed boreal forests, carbon is sequestered in created downed logs for approximately 49 years on average. Prescribed burning shortens this to 40 years, while shifting towards deciduous species (birch residence time: ~74 years) or leaving logs in paludified patches (spruce under Sphagnum: up to 104 years) can extend it.

The high prevalence of brown and mixed rot indicates a substantial transfer of lignin-rich residues to the long-term soil carbon pool. As showed in previous studies, the increased amount of organic carbon in soil is recorded not only directly below deadwood but also few meters away from it (Stokland and Alfredsen, 2024 and references therein). However, key knowledge gaps remain regarding the interaction of biotic and abiotic drivers and the influence of charred wood on soil processes, highlighting crucial avenues for integrating deadwood dynamics into Earth system models (Wijas et al., 2024). A methodological note is that in our study, the decay types, their extent and spatial distribution were evaluated visually. More precise estimations should prioritize longitudinal monitoring and employ methods like dilute alkali solubility (Schilling et al., 2015) to quantify decay types beyond visual assessment.

Our results provide implications for the deadwood enrichment strategies. Created deadwood decomposes rapidly due to ground contact and fragmentation, especially after prescribed burning. Moreover, from a biodiversity perspective, created deadwood alone cannot substitute for natural deadwood (Koivula and Vanha-Majamaa, 2020; Komonen et al., 2024). To ensure a persistent deadwood continuum, strategies should combine creation with the retention of existing deadwood and the use of prescribed burning alongside tree retention to maintain natural mortality over decades (Shorohova et al., 2024).

5. Conclusions

In boreal forests, restoration practices that include deadwood enrichment and prescribed burning exert long-lasting, multi-decadal effects on decomposition processes in downed logs. Within upland biotopes, the combination of deadwood enrichment, tree retention, and prescribed burning accelerates carbon and nutrient turnover in coarse woody debris. In contrast, in paludified biotopes, the accelerating effects of restoration treatments on decomposition are substantially mitigated by the covering of logs by Sphagnum mosses. This divergence in post-treatment decomposition dynamics underscores the importance of considering biotope-specific conditions in restoration planning. Overall, decomposing logs are expected to substantially influence soil organic carbon composition and stock, with the mode and rate of decay determining the long-term fate of woody carbon in the ecosystems.

CRediT authorship contribution statement

Ekaterina Shorohova: Writing – review & editing, Writing – original draft, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization. **Henrik Lindberg:** Writing – review & editing, Methodology, Investigation. **Maria Shorohova:** Writing – review & editing, Visualization, Methodology, Investigation. **Ilkka Vanha-Majamaa:** Writing – review & editing, Project administration, Investigation, Funding acquisition, Conceptualization.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2026.124037.

Data availability

Data will be made available on request.

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